

Original Research

Relationship between climatic factors and the flea index of two plague hosts in Xilingol League, Inner Mongolia Autonomous Region

Lu Zhang^{a,1}, Zihao Wang^{b,1}, Nan Chang^b, Meng Shang^c, Xiaohui Wei^a, Ke Li^a, Jinyu Li^c, Xinchang Lun^a, Haoqiang Ji^c, Qiyong Liu^{a,b,c,*,2}

^a National Key Laboratory of Intelligent Tracking and Forecasting for Infectious Diseases, National Institute for Communicable Disease Control and Prevention, Chinese Centre for Disease Control and Prevention, WHO Collaborating Centre for Vector Surveillance and Management, Beijing 102206, China

^b School of Public Health, Nanjing Medical University, Nanjing 211166, China

^c School of Public Health, Cheeloo College Medicine, Shandong University, Jinan 250012, China

ARTICLE INFO

Article history:

Received 29 March 2024

Revised 8 July 2024

Accepted 8 July 2024

Available online 10 July 2024

Keywords:

Climate change

Plague

Flea

Meriones unguiculatus

Spermophilus dauricus

ABSTRACT

Climatic factors are closely associated with the occurrence of vector-borne diseases, and they also influence the distribution of vectors. The occurrence of plague is closely related to the population dynamics of fleas and their host animals, as well as climatic conditions. This study focused on Xilingol League, utilizing climatic and flea index data from 2012 to 2021. Spearman correlation and "Boruta" importance analysis were conducted to screen for climatic variables. A generalized additive model (GAM) was employed to investigate the influence of climatic factors and rodent density on the flea index. GAM analysis revealed distinct trends in flea index among different rodent hosts. For *Meriones unguiculatus*, the flea index declined with increased density and with higher humidity, yet rose with greater lagged sunshine duration. For *Spermophilus dauricus*, an initial increase in flea index with density was observed, followed by a decrease, and a rise in the index was noted when ground temperatures were low. This study reveals the nonlinear interactions and lag effects among climatic factors, density, and flea index. Climatic factors and density variably influence the flea index of two *Yersinia pestis* hosts. This research advances the prediction and early warning efforts for plague control, providing a theoretical basis for rodent and flea eradication strategies.

© 2024 Chinese Medical Association Publishing House. Published by Elsevier BV. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Climatic factors are closely related to the occurrence of infectious diseases, particularly vector-borne diseases. While there is a fluctuating decline in the incidence of vector-borne infectious diseases in China from 2005 to 2020, the level remains significantly high, with an evident trend of expanding endemic areas, and the risk they pose to human beings still exists [1]. Furthermore, climatic factors can influence the population and distribution of hosts for vector-borne diseases and the vectors themselves [2], resulting in new epidemic risks.

* Corresponding author: National Key Laboratory of Intelligent Tracking and Forecasting for Infectious Diseases, National Institute for Communicable Disease Control and Prevention, Chinese Center for Disease Control and Prevention, Beijing 102206, China.

E-mail address: liuqiyong@icdc.cn (Q. Liu).

¹ These authors contributed equally to this work.

² Given his role as the Guest Editor, Qiyong Liu had no involvement in the peer-review of this article and had no access to information regarding its peer-review. Full responsibility for the editorial process for this article was delegated to the Associate Editor-in-Chief William J. Liu.

<https://doi.org/10.1016/j.bsheal.2024.07.004>

2590-0536/© 2024 Chinese Medical Association Publishing House. Published by Elsevier BV.

This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

The interplay between climatic factors and infectious diseases is realized through a complex series of pathways involving various components of the natural world, rendering the relationship challenging to trace [3]. Some studies indicate that the combined effects of climate with factors such as latitude, altitude, seasonality, and interannual variability influence infectious diseases in nonlinear manners [4].

In many parts of the world, the plague continues to pose significant threats, especially in Africa where there has been an upward trend in both cases and affected countries over the past few decades [3]. The transmission of the plague is intricately linked with the ecology of rodents [5], flea ecology [6], climatic conditions, and other environmental circumstances [7]. Research by K. Kreppel et al. [8] in Madagascar identifies a complex nonlinear relationship between temperature, precipitation, and the occurrence of the plague. A study by L. Xu et al. [9] of plague in China during the 19th and 20th centuries found that the association between the intensity of human plague and precipitation was nonlinear, being positive under dry conditions and negative under wet conditions.

Some studies have preliminarily shown that in the semi-arid grasslands of the Inner Mongolia Autonomous Region, higher rainfall pro-

HIGHLIGHTS

Scientific question

Climate factors are closely associated with the occurrence of vector-borne infectious diseases. The plague remains a significant threat, with its transmission linked to complex interactions among rodent ecology, flea ecology, and climatic conditions. To date, there has been no research on the impact of meteorological factors on the flea indices in rodent populations in Xilingol League.

Evidence before this study

The impacts of climatic factors on infectious diseases are mediated through a series of complex pathways. Previous studies have shown that climatic factors affect infectious diseases in a nonlinear manner.

New findings

Our research indicated that the flea index on *Meriones unguiculatus* decreased with increasing rodent density, was negatively correlated with the current monthly average humidity, and was positively correlated with the lagged monthly accumulated sunshine. For the *Spermophilus dauricus*, the flea index initially increased and then decreased with rising rodent density, and partially increased when the current monthly average ground temperature was low.

Significance of the study

This study explores the changes in rodent and flea index mediated by climatic factors using the Generalized Additive Model (GAM), and demonstrates that the GAM can effectively predict the flea index in rodents. This research may advance the early warning and forecasting efforts for plague outbreaks, provide references for plague monitoring, and offer a theoretical basis for rodent and flea control measures.

theoretical foundation for early forecasting, warning, and prevention of plague.

2. Materials and methods

2.1. Study area

The Xilingol League in the Inner Mongolia Autonomous Region is selected as the area of study. The region, situated between 42°32'–46°41' N latitude and 111°59'–120°00' E longitude, is characterized by strong winds, aridity, and cold temperatures typical of the northern temperate continental climate. This area is a high-risk plague region due to the overlap of three different types of plague natural foci. The distribution range of *M. unguiculatus* encompasses all 11 banners (counties) except for Duolun County. Meanwhile, *S. dauricus* inhabits all 12 banners (counties) within the entire league.

2.2. Data acquisition

Flea index on rodents and density data were collected from the Plague Control Management Information System of Chinese Center for Disease Control and Prevention (CDC), which includes surveillance data for 12 banners (counties) of Xilingol League from 2012 to 2021. After removing missing values, there were 291 cases of density data and flea index data for *M. unguiculatus*, while there were 284 cases of density data and flea index data for *S. dauricus*. Concurrent climatic data was obtained from the Centre for Resource Environment Science and Data of the Chinese Academy of Science (CRES, <https://www.resdc.cn/Default.aspx>) and included temperature, ground temperature, relative humidity, accumulated precipitation, sunshine hours, wind speed, and atmospheric pressure. Considering the developmental cycle of fleas, which spans 3–6 weeks [16], we analyzed the lag effect of climatic factors on the flea index from the previous month into the model for analysis.

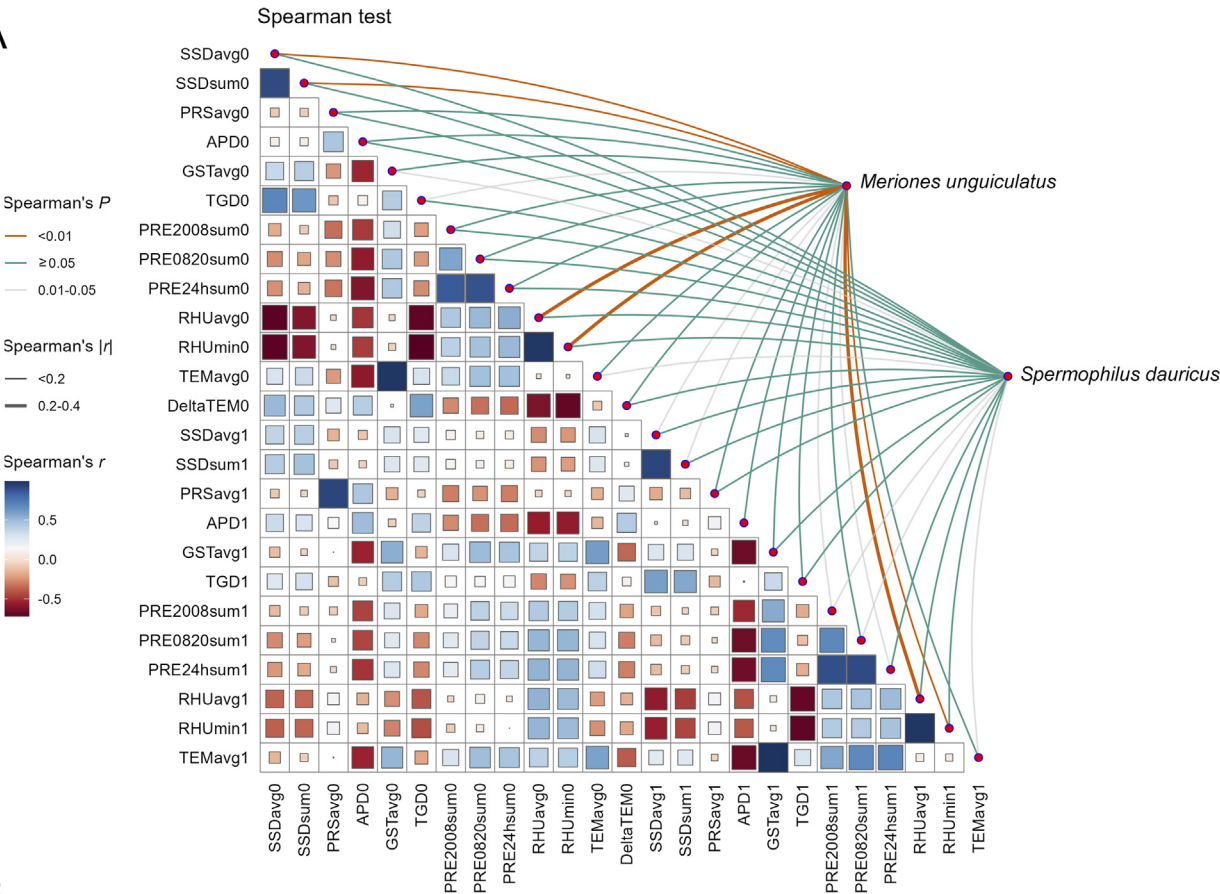
2.3. Descriptive analysis and feature selection for climatic variables

The SPSS 19.0 software was used to organize the flea index data, density data, and climatic data on a monthly basis from 2012 to 2021. Their mean, standard deviation, variance, minimum, quartiles, and maximum values were calculated to understand the distribution of these factors. We used Spearman's analysis in SPSS 19.0 and the package "Boruta" in R 4.2.3 to refine our selection of pertinent climate factors. The Spearman correlation test, a non-parametric statistical test, was specifically employed in the context of the GAM, given its capability to detect non-linear relationships. Spearman's method was first used to identify variables that displayed significant correlations with the response variable. Boruta, a feature selection tool, was then used to rigorously prune predictors that did not show any significant impact on the dependent variable. In particular, box plots were generated to showcase the importance of each climatic factor, as determined by Boruta. During the Boruta calculations, the data were shuffled and variables were ranked by importance. Only those variables that exceeded the shadowmax score threshold were retained for subsequent analyses. While the initial screening of relevant variables was undertaken with the Spearman correlation test, these variables were then subjected to the more stringent Boruta feature selection process. The combination of Spearman and Boruta provides a comprehensive and rigorous filtering of predictors, ensuring only the most relevant are considered in the subsequent stages of the research. As shown in Fig. 1. Additionally, to rule out multicollinearity among the climatic factors, the variance inflation factor (VIF) was used to test for multicollinearity.

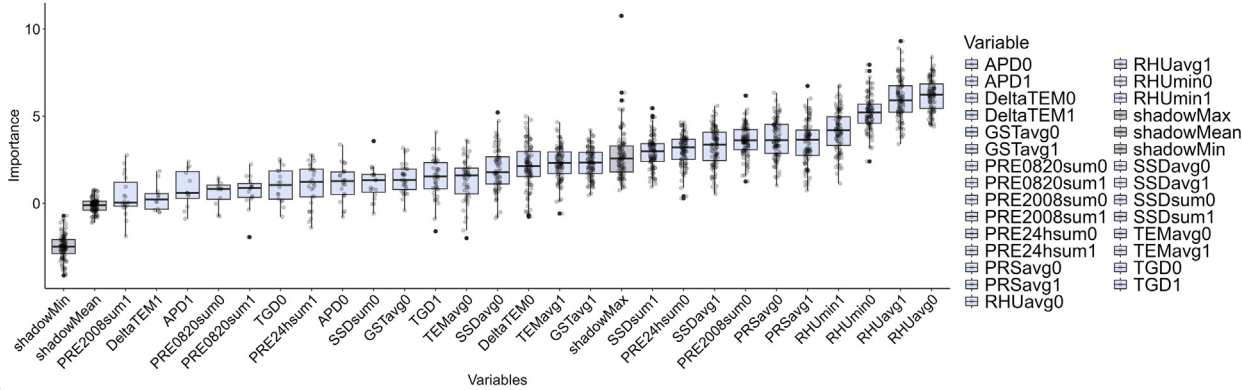
notes seed production and grass growth, consequently boosting the population of gerbils [10]. Fleas, ectothermic parasites, rely on their hosts for temporary habitats and on abiotic conditions for survival [11]. Beyond causing irritant and allergic dermatitis in humans, fleas are primary vectors for significant diseases such as the plague and typhus fever [12]. Factors like temperature, precipitation, and relative humidity directly affect flea growth and survival [13], while it has been shown that the rat body flea index is also affected by rat density and climatic factors [14].

Currently, there is limited research on the impact of climatic factors and density on the flea index in Xilingol League. This study selects the 12 banners (counties) of Xilingol League as the research area from 2012 to 2021, and it focuses on the dominant rodent species involved in plague transmission in the region, which include the *Meriones unguiculatus* (*M. unguiculatus*) (accounting for 46.28 % of the population), and the *Spermophilus dauricus* (*S. dauricus*) (27.67 %) [15]. Employing the generalized additive model (GAM), this investigation aims to explore the nonlinear relationships and lag effects between climatic factors, density, and the rodent flea index. The findings offer a comprehensive and in-depth understanding of the interplay between density and climatic factors in influencing variations in the flea index. This understanding enhances our grasp of the impact of climatic conditions on the occurrence of plague in the region. The results provide a

A



B



C

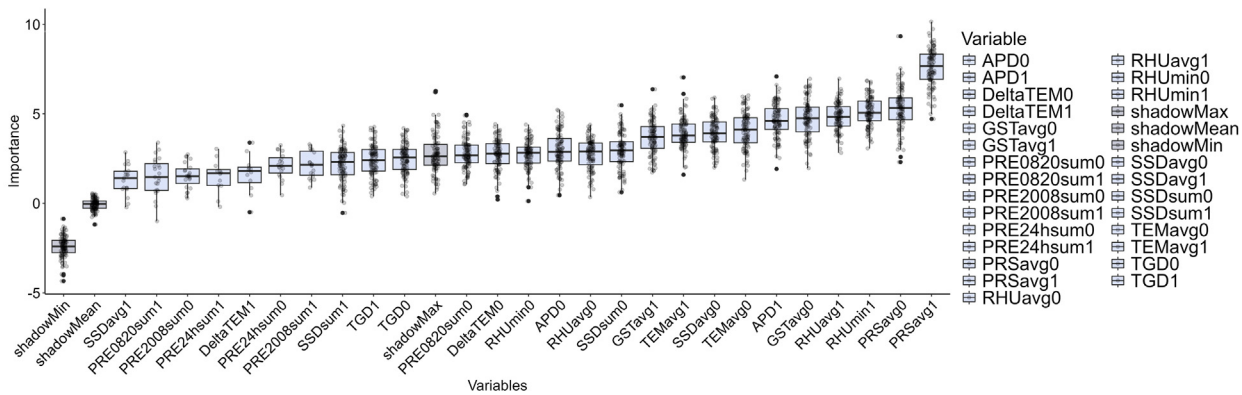


Table 1

Descriptive analysis of flea index, density, and climatic factors in Xilingol League (2012–2021).

Variables	M	S	S ²	Min	P ₂₅	P ₅₀	P ₇₅	Max
<i>Meriones unguiculatus</i> flea index	1.22	1.50	2.26	0.00	0.27	0.69	1.71	11.00
<i>Spermophilus dauricus</i> flea index	3.92	3.61	13.02	0.00	1.25	3.13	5.50	27.00
<i>Meriones unguiculatus</i> density	2.48	2.04	4.17	0.05	1.00	2.07	3.46	12.53
<i>Spermophilus dauricus</i> density	1.28	1.19	1.42	0.01	0.20	1.00	2.00	6.33
Monthly average temperature (TEMavg)	3.81	13.75	188.97	−25.80	−9.26	5.34	16.50	27.00
Monthly average Temperature difference (DeltaTEM)	12.79	1.69	2.85	7.24	11.62	12.69	13.96	18.59
Monthly average ground temperature (GSTavg)	7.45	14.30	204.56	−21.34	−5.52	7.87	21.10	33.23
Monthly average temperature gradient difference (TGD)	26.09	10.85	117.77	−7.88	20.24	28.36	34.21	48.26
Monthly average sunshine hours (SSDavg)	8.08	1.40	1.97	2.90	7.08	8.16	9.16	12.40
Monthly accumulated sunshine hours (SSDsum)	242.20	46.70	2,180.60	32.60	208.63	242.20	278.60	371.00
Monthly average relative humidity (RHUavg)	53.92	12.85	165.20	22.23	44.49	54.84	64.10	83.90
Monthly minimum relative humidity (RHUmin)	31.96	13.43	180.49	8.58	21.42	29.87	39.53	73.71
Monthly average atmospheric pressure (PRSAvg)	886.17	20.23	409.10	845.45	868.34	889.75	902.24	926.25
Monthly average air pressure difference (APD)	5.22	1.29	1.67	2.63	4.20	5.15	6.09	12.41
Monthly average nighttime accumulated rainfall (PRE2008)	11.00	14.79	218.60	0.00	1.30	4.75	15.00	99.60
Monthly average daytime accumulated rainfall (PRE0820)	14.53	21.78	474.42	0.00	1.20	4.90	19.30	203.00
Monthly accumulated precipitation (PRE2020)	25.71	33.31	1,109.25	0.00	3.10	11.75	36.88	271.20

Abbreviations: M, mean; S, standard deviation; S², variance; Min, minimum value; P₂₅, P₅₀, P₇₅ stand for the 25th, 50th, and 75th percentiles, respectively; Max, maximum value.

Table 2

Results of collinearity test for variables included in the GAM.

Hosts	Variables	Tolerance error	VIF
<i>Meriones unguiculatus</i>	Density	0.941	1.062
	Current monthly average humidity	0.791	1.264
	Lagged monthly accumulated sunshine hours	0.771	1.296
<i>Spermophilus dauricus</i>	Density	0.982	1.018
	Current monthly average ground temperature	0.982	1.018

Abbreviations: GAM, generalized additive model; VIF, variance inflation factor.

2.4. Modeling the relationship between climatic variables, density, and flea index

GAM is an extension of generalized linear model (GLM) and additive models. By fitting non-parametric functions, it estimates the overly complex, nonlinear relationships between a dependent variable and several independent variables. This makes it broadly applicable. GAM doesn't restrict the form of independent variables and fits them in a non-parametric manner. The individual explanatory components of the GAM do not have to be the independent variables themselves but can be various forms of smoothing functions of the independent variables. This makes it a flexible model capable of discerning non-monotonic, non-linear relationships. However, GAM also has limita-

tions as it offers only an approximate description of the real relationships between independent and dependent variables. The expression for GAM is:

$$g(\mu_i) = \beta_0 + f_1(x_{1i}) + f_2(x_{2i}) + f_3(x_{3i}) + \dots + \varepsilon \quad (1)$$

In the above equation, $g(\mu_i)$ represents the coupling function, which can be any kind of distribution in the exponential family of distributions, such as normal distribution, binomial distribution, Poisson distribution, negative binomial distribution, and so on. $f_1(x_{1i})$, $f_2(x_{2i})$, $f_3(x_{3i})$,..... represent various smoothing functions, such as smooth spline, local regression, natural cubic spline, etc. β_0 represents the intercept and ε is the error term. In this research, the influence of

Fig. 1. Preliminary screening of climatic variables in the effect of rat density on the flea index. A) Spearman correlation between climatic variables and rat body flea index-environmental variables. B) Analysis of the significance of climatic factors affecting the rat body flea index of the *Meriones unguiculatus* using the Boruta algorithm. C) Evaluation of the significance of climatic variables influencing the flea index in *Spermophilus dauricus* using the Boruta algorithm. Abbreviations: APD0, current monthly average air pressure difference; APD1, lagged monthly average air pressure difference; DeltaTEM0, current monthly average temperature difference; DeltaTEM1, lagged monthly average temperature difference; GSTavg0, current monthly average ground temperature; GSTavg1, lagged monthly average ground temperature; PRE0820sum0, current monthly average daytime accumulated rainfall; PRE0820sum1, lagged monthly average daytime accumulated rainfall; PRE2008sum0, current monthly average nighttime accumulated rainfall; PRE2008sum1, lagged monthly average nighttime accumulated rainfall; PRE24hsum0, current monthly accumulated precipitation; PRE24hsum1, lagged monthly accumulated precipitation; PRSAvg0, current monthly average atmospheric pressure; PRSAvg1, lagged monthly average atmospheric pressure; RHUavg0, current monthly average relative humidity; RHUavg1, lagged monthly average relative humidity; RHUmin0, current monthly minimum relative humidity; RHUmin1, lagged monthly minimum relative humidity; SSDavg0, current monthly average sunshine hours; SSDavg1, lagged monthly average sunshine hours; SSDsum0, current monthly accumulated sunshine hours; SSDsum1, lagged monthly accumulated sunshine hours; TEMavg0, current monthly average temperature; TEMavg1, lagged monthly average temperature; TGD0, current monthly average temperature gradient difference; TGD1, lagged monthly average temperature gradient difference.

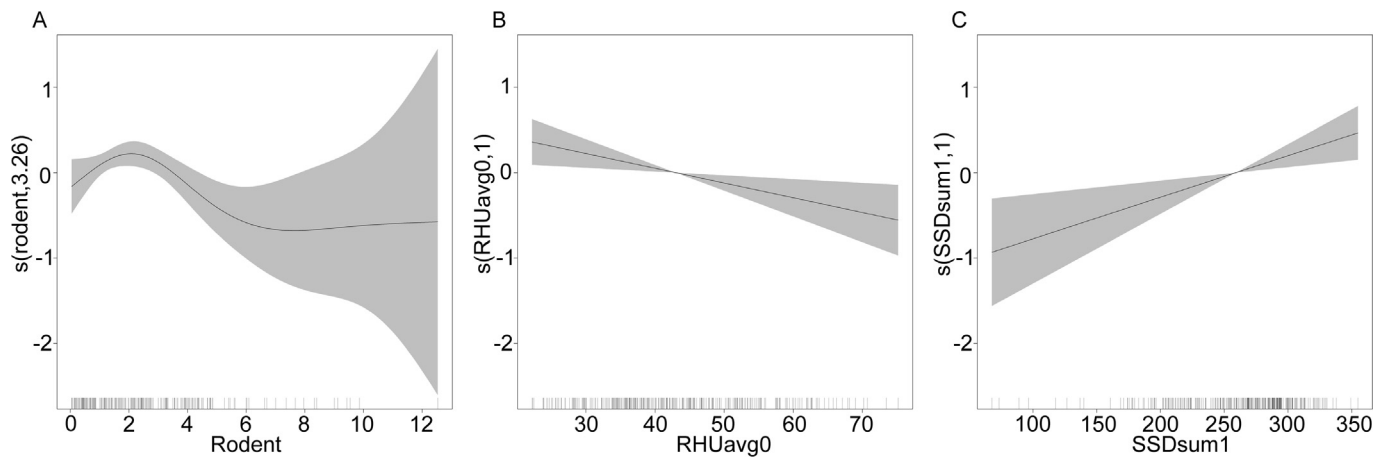


Fig. 2. Analysis results of generalized additive model (GAM) for the flea index in *Meriones unguiculatus*. The x-axis represents the observed values of the explanatory variables, while the y-axis represents the smooth fitted values of the explanatory variables with their corresponding degrees of freedom estimates in parentheses. A) Relationship between density and flea index. B) Relationship between current monthly average humidity and flea index. C) Relationship between lagged monthly accumulated sunshine hours and flea index. Abbreviations: RHUavg, monthly average relative humidity; SSDsum, monthly accumulated sunshine hours.

weather factors and density on the flea index of different rodent species is analyzed. As the number of fleas on rodents follows an almost Poisson distribution and to avoid overdispersion, the quasi-Poisson distribution is adopted as the link function for this study. The chosen dependent variable is the flea index on dominant rodent species for each month from 2012 to 2021 in the Xilingol League. The independent variables are climatic factors for the applicable month and region. The “mgcv” package in R 4.2.3 was used for modeling and analysis.

3. Results

3.1. Monthly distribution of the dominant rodent flea index and climatic factors in the study area

From 2012 to 2021, the average flea index of the *M. unguiculatus* in the Xilingol League is 1.22, with a variance of 2.26, and the density in the region is 2.48, with a variance of 4.17. The *S. dauricus* has an average flea index of 3.92, with a variance of 13.02, and a density of 1.28, with a variance of 1.42 (Table 1). Regarding the climatic data in Xilingol League for the same period, the monthly average temperature is 3.81 °C with a variance of 188.97, fluctuating between −25.80 °C and 27.00 °C. The variance is larger than the mean. The monthly average ground temperature is 7.45 °C with a variance of 204.56, fluctuat-

ing between −21.34 °C and 33.23 °C. Again, the variance exceeds the mean. The monthly cumulative rainfall average is 25.71 mm with a massive variance of 1,109.25, ranging between 0 mm and 271.20 mm. The variance is significantly larger than the average. The monthly average temperature and cumulative rainfall in the Xilingol League exhibit considerable fluctuations. Details of other climatic factors can be found in Table 1.

3.2. Effects of density and climatic factors on flea index in *M. unguiculatus*

Spearman correlation analysis reveals that the monthly flea index negatively correlates with current monthly average humidity, current monthly minimum humidity, lagged (by one month) monthly average humidity, lagged monthly minimum humidity, lagged monthly average daytime accumulated rainfall, and lagged monthly accumulated precipitation ($P < 0.05$). Positive correlations are observed with factors such as current monthly average sunshine hours, current monthly accumulated sunshine hours, lagged monthly accumulated sunshine hours, lagged monthly average ground temperature, and current monthly average temperature gradient difference ($P < 0.05$).

The final model incorporates variables such as the density of the *M. unguiculatus*, current monthly average humidity, and lagged monthly accumulated sunshine hours. These variables are derived from screened climate and density data. A manual backward elimination method is used to exclude variables to achieve the lowest generalized

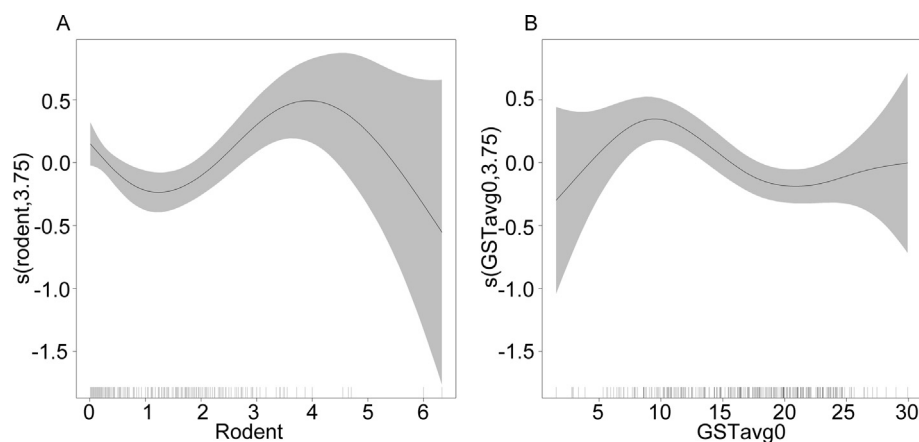


Fig. 3. Analysis results of generalized additive model (GAM) for the flea index in *Sperophilus dauricus*. A) Relationship between density and flea index. B) Relationship between current monthly average ground temperature and flea index. Abbreviation: GSTavg, monthly average ground temperature.

cross validation (GCV) score for our model. The final GCV score obtained is 1.256. Subsequent tests for multicollinearity show that all VIFs are less than 2.000, indicating that there is no multicollinearity among the variables (Table 2).

GAM analysis shows that the flea index on *M. unguiculatus* exhibits a general declining trend in relation to their density ($P < 0.05$), a negative correlation with current monthly average humidity ($P < 0.01$), and a positive correlation with lagged monthly accumulated sunshine hours ($P < 0.01$) (Fig. 2).

3.3. Effects of density and climatic factors on the flea index in *S. dauricus*

The Spearman correlation analysis demonstrates that the flea index for *S. dauricus* is negatively correlated with the current monthly average ground temperature and current monthly average temperature ($P < 0.05$). A positive correlation is observed with lagged monthly minimum relative humidity and lagged monthly average relative humidity ($P < 0.05$).

In the model, the density of the *S. dauricus* and the current monthly average ground temperature is incorporated. These variables are meticulously selected through a stepwise backward elimination method based on subsequent data screening and vole density, resulting in the lowest GCV value for the model, which stood at 2.767. Further collinearity tests are conducted, and the VIF value for each included variable is found to be less than 2.000 (Table 2). This suggests that there is no collinearity among the variables.

The results of the GAM model reveal that the flea index on the *S. dauricus* initially exhibits a partially ascending trend followed by a decline in response to density ($P < 0.01$). When the current monthly average ground temperature is relatively low, there is a partial increase in the flea index ($P < 0.01$) (Fig. 3).

4. Discussion

Our study reveals that in the natural plague foci of Xilingol League, there exists a nonlinear relationship between the flea index of two dominant host species and density as well as local climatic factors, with a lagged effect also present with climatic factors. The climatic elements affecting the flea index of each dominant rodent species vary and have different lag periods, possibly due to seasonal variations in the impact of climatic factors on different rodent species and their parasitic fleas, along with divergent adaptabilities and sensitivities to these factors. According to the study by L. Čepelka et al. [17] in Europe, climatic factors have different impacts on the populations of two rodents, *Apodemus flavicollis* (*A. flavicollis*) and *Apodemus sylvaticus* (*A. sylvaticus*). Specifically, higher temperatures in the vegetation season and lower temperatures during winter positively affect the *A. flavicollis* population, whereas lower temperatures in the vegetation season and higher temperatures in winter positively influence the *A. sylvaticus* population [17]. Even within the same rodents in different regions, responses to climate can vary: in the typical Erdos desert region [18], an increase in precipitation correlates positively with the abundance of the *M. unguiculatus*, whereas in the central-southern agricultural and pastoral area of the Inner Mongolia Autonomous Region [19], the correlation is negative. The response of different flea species to climate also varies: for instance, temperature and humidity have differential impact, with research by B. Krasnov et al. [20] indicating that fleas in North America show the strongest response to variations in precipitation, while those in South America, Europe, and Asia are more strongly influenced by temperature differences.

In this study, the flea index and density of *M. unguiculatus* generally exhibited a declining trend. L. Xu et al. [21] found a strong negative correlation between the density of *M. unguiculatus* and their flea index, which is consistent with our findings. However, the flea index

and density of *S. dauricus* showed a partially increasing trend followed by a decline. The study of L. Xu et al. [21] showed a positive correlation between the flea index and the density of *S. dauricus*, claiming that a higher density of the voles leads to a higher parasitic load. Conversely, P. Stapp [22] argued that a higher density of voles led to a decrease in the vole's flea index. Our study elucidated the non-linear relationship between the flea index and the density, indicating a rising trend before it declined.

This study found that the flea index of *M. unguiculatus* was negatively correlated with the current monthly average humidity. Humidity has a significant impact on fleas: excessive precipitation and subsequent increased humidity can lead to more fungi and mites in rat burrows, thereby reducing the number of fleas [23,24]. Similar outcomes were found by D. Eads et al. [25] in *Cynomys ludovicianus* (*C. ludovicianus*) in northeastern New Mexico, USA, where flea numbers doubled in dry years compared to relatively humid years. Dry conditions positively affect flea numbers, with flea index increasing during the dry season [26]. Research by Z. Li [27] found a negative correlation between the flea index of the main parasitic fleas on *M. unguiculatus*, such as the *Nosopsyllus* (*Gerbillophilus*) *laeviceps*, and relative humidity, which is consistent with the results of this study. Within this study, the flea index exhibits a positive correlation with the lagged monthly accumulated sunshine hours, indicating that as the number of sunshine hours increases, the flea index also increases. Many flea species utilize light for object localization, and adult fleas move directionally toward light sources [28,29]. It is possible that an appropriate increase in sunlight duration could help fleas move from one location to another, potentially expanding their range and increasing the chances of finding new hosts, thereby facilitating an increase in flea populations [30].

Fleas are highly sensitive to changes in temperature, particularly during their developmental stages [31]. The stability of the environmental conditions during flea development can enhance the stability of flea populations since fleas have limited tolerance to environmental fluctuations [32,33]. However, D. Eads et al. [34] found that *S. dauricus*, unlike other rodents such as the *M. unguiculatus*, hibernated in burrows during the winter. These voles create nests in deeper burrows, which offer a stable microclimate, enhancing the survival and reproduction rates of fleas. Accordingly, the quantity of fleas does not decrease when the temperature is lower. L. Shuai et al. [35] demonstrated that the parasitic load on *S. dauricus* showed a seasonal variation. For instance, the tick population on the vole peaks in summer, while fleas are most abundant in spring. Our results showed that as the temperature increased, the flea index of *S. dauricus* started to decrease. M. Denny et al. [36] studied wild rodents captured in Berlin and found the highest number of fleas on the rodents in spring and the highest number of ticks in summer. Therefore, the decrease in fleas on *S. dauricus* may be due to other parasite loads on them, including ticks and mites.

Predicting and warning about the flea index is significantly beneficial in plague management. This study applies mathematical methods to predict the dynamic changes in the flea index of dominant rodent species, providing a quantitative perspective for research, and serving as a practical statistical model in forecasting. However, this study only incorporates climatic factors to analyze their influence on the parasitic relationship between rodents and fleas. In addition, other research suggests that vegetation index, soil cover, and other factors also have certain effects on this parasitic relationship [37]. Therefore, more comprehensive ecological studies need to be conducted to ensure ecological relevance and practical value.

5. Conclusions

The flea index of the *M. unguiculatus* is mainly influenced by density, monthly average humidity, and monthly accumulated sunshine hours, with the latter having a lagged effect. For the *S. dauricus*, the flea index is predominantly influenced by density, and monthly aver-

age ground temperature. The GAM can predict the flea index of dominant rodent species reasonably well, advancing plague forecasting and early warning efforts. This provides a theoretical basis for the prevention and eradication of fleas in rodents.

Acknowledgements

This work was supported by the Major Program of National Natural Science Foundation of China (32090023). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. We thank the CDC from Xilingol League and the monitoring sites for their hard work, and the CRESO for data support. We are also grateful to the National Natural Science Foundation of China for its support of this study.

Conflict of interest statement

The authors declare that there are no conflicts of interest.

Author contributions

Lu Zhang: Writing – original draft, Writing – review & editing, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Zihao Wang:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Nan Chang:** Formal analysis, Data curation, Conceptualization. **Meng Shang:** Investigation, Funding acquisition, Formal analysis. **Xiaohui Wei:** Project administration, Methodology, Investigation. **Ke Li:** Software, Resources, Project administration. **Jinyu Li:** Resources, Project administration, Methodology. **Xinchang Lun:** Validation, Supervision, Software. **Haoqiang Ji:** Supervision. **Qiyong Liu:** Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

References

- [1] Q. Liu, X. Liu, N. Chang, L. Zhang, Advances and achievements in the surveillance and control of vectors and vector-borne diseases in China, 2012–2021, *Chin. J. Vector Biol. Control* 33 (5) (2022) 613–621, <https://doi.org/10.11853/j.issn.1003.8280.2022.05.001>.
- [2] Q. Liu, W. Xu, S. Lu, J. Jiang, J. Zhou, Z. Shao, X. Liu, L. Xu, Y. Xiong, H. Zheng, et al., Landscape of emerging and re-emerging infectious diseases in China: impact of ecology, climate, and behavior, *Front. Med.* 12 (1) (2018) 3–22, <https://doi.org/10.1007/s11684-017-0605-9>.
- [3] J. Semenza, B. Menne, Climate change and infectious diseases in Europe, *Lancet Infect. Dis.* 9 (6) (2009) 365–375, [https://doi.org/10.1016/S1473-3099\(09\)70104-5](https://doi.org/10.1016/S1473-3099(09)70104-5).
- [4] R. Yue, H. Lee, Pre-industrial plague transmission is mediated by the synergistic effect of temperature and aridity index, *BMC Infect. Dis.* 18 (1) (2018) 134, <https://doi.org/10.1186/s12879-018-3045-5>.
- [5] N. Stenseth, N. Samia, H. Viljugrein, K. Kausrud, M. Begon, S. Davis, H. Leirs, V. Dubyanskiy, J. Esper, V. Ageyev, et al., Plague dynamics are driven by climate variation, *Proc. Natl. Acad. Sci. U. S. A.* 103 (35) (2006) 13110–13115, <https://doi.org/10.1073/pnas.0602447103>.
- [6] B. Krasnov, I. Khokhlova, The effect of behavioural interactions on the transfer of fleas (Siphonaptera) between two rodent species, *J. Vector Ecol.* 26 (2) (2002) 181–190.
- [7] R. Yue, H. Lee, C. Wu, Navigable rivers facilitated the spread and recurrence of plague in pre-industrial Europe, *Sci. Rep.* 6 (2016) 34867, <https://doi.org/10.1038/srep34867>.
- [8] K. Kreppel, C. Caminade, S. Telfer, M. Rajerison, L. Rahalison, A. Morse, M. Baylis, A non-stationary relationship between global climate phenomena and human plague incidence in Madagascar, *PLoS Negl. Trop. Dis.* 8 (10) (2014) e3155, <https://doi.org/10.1371/journal.pntd.0003155>.
- [9] L. Xu, Q. Liu, L. Stige, T. Ari, X. Fang, K. Chan, S. Wang, N. Stenseth, Z. Zhang, Nonlinear effect of climate on plague during the third pandemic in China, *Proc. Natl. Acad. Sci. U. S. A.* 108 (25) (2011) 10214–10219, <https://doi.org/10.1073/pnas.1019486108>.
- [10] Z. Li, W. Zhang, Analysis on the relation between population of *Meriones unguiculatus* and factors of meteorological phenomena, *Acta Theriol. Sin.* 13 (2) (1993) 131.
- [11] C. Shu, M. Jiang, M. Yang, J. Xu, S. Zhao, X. Yin, B. Wang, J. Sheng, Y. Wang, Flea surveillance on wild mammals in northern region of Xinjiang, northwestern China, *Int. J. Parasitol. Parasites Wildl.* 11 (2019) 12–16, <https://doi.org/10.1016/j.ijppaw.2019.11.004>.
- [12] I. Bitam, K. Dittmar, P. Parola, M. Whiting, D. Raoult, Fleas and flea-borne diseases, *Int. J. Infect. Dis.* 14 (8) (2010) e667–e676, <https://doi.org/10.1016/j.ijid.2009.11.011>.
- [13] V. Guernier, E. Lagadee, G. LeMinter, S. Licciardi, E. Balleydier, F. Pagès, A. Laudisoit, K. Dellagi, P. Tortosa, Fleas of small mammals on Reunion Island: diversity, distribution and epidemiological consequences, *PLoS Negl. Trop. Dis.* 8 (9) (2014) e3129, <https://doi.org/10.1371/journal.pntd.0003129>.
- [14] S. Qosamah, A. Adriansyah, D. Handayani, Analysis of rat demand with fleas index in class work area I Tanjung Perak Surabaya Port, *Proceeding Surabaya International Health Conference* 1 (2020) 304–310.
- [15] L. Zhang, X. Wei, N. Chang, H. Li, X. Si, X. Bai, J. Wang, Q. Liu, Composition of parasitic fleas on rodents and spatiotemporal distribution of flea index in Xilin Gol League, Inner Mongolia Autonomous Region, China, 2012–2021, *Chin. J. Vector Biol. Control* 34 (1) (2023) 82–90, <https://doi.org/10.11853/j.issn.1003.8280.2023.01.015>.
- [16] Chinese Academy of Sciences, Editorial Committee of Fauna Sinica, Fauna Sinica (Insecta, Siphonaptera), Science Press, Beijing, 2007.
- [17] L. Čepelka, J. Šipoš, J. Suchomel, M. Heroldová, Can we detect response differences among dominant rodent species to climate and acorn crop in a Central European forest environment?, *Eur. J. Res.* 139 (4) (2020) 539–548, <https://doi.org/10.1007/s10342-020-01267-7>.
- [18] Z. Li, W. Zhang, Analysis on the relation between population of *Meriones unguiculatus* and factors of meteorological phenomena, *Acta Theriol. Sin.* 13 (1993) 131–135, <https://doi.org/10.16829/j.slxb.1993.02.008>.
- [19] W. Liu, X. Wan, W. Zhong, Population dynamics of the Mongolian gerbils: seasonal patterns and interactions among density, reproduction and climate, *J. Arid Environ.* 68 (3) (2007) 383–397, <https://doi.org/10.1016/j.jaridenv.2006.07.002>.
- [20] B. Krasnov, G. Shenbrot, L. van der Mescht, Khokhlova, Drivers of compositional turnover are related to species' commonness in flea assemblages from four biogeographic realms: zeta diversity and multi-site generalised dissimilarity modelling, *Int. J. Parasitol.* 50 (4) (2020) 331–344, <https://doi.org/10.1016/j.ijpara.2020.03.001>.
- [21] L. Xu, B. Schmid, J. Liu, X. Si, N. Stenseth, Z. Zhang, The trophic responses of two different rodent-vector-plague systems to climate change, *Proc. R. Soc. B* 2015 (282) (1800) 20141846, <https://doi.org/10.1098/rspb.2014.1846>.
- [22] P. Stapp, Trophic cascades and disease ecology, *EcoHealth* 4 (2) (2007) 121–124, <https://doi.org/10.1007/s10393-007-0099-z>.
- [23] B. Krasnov, Functional and evolutionary ecology of fleas: a model for ecological parasitology, Cambridge University Press, Cambridge, UK, 2008.
- [24] J. Wimsatt, D. Biggins, A review of plague persistence with special emphasis on fleas, *J. Vector Borne Dis.* 46 (2) (2009) 85.
- [25] D. Eads, D. Biggins, D. Long, K. Gage, M. Antolin, Droughts may increase susceptibility of prairie dogs to fleas: incongruity with hypothesized mechanisms of plague cycles in rodents, *J. Mammal.* 97 (4) (2016) 1044–1053, <https://doi.org/10.1093/jmammal/gyw035>.
- [26] H. Pham, D. Dang, N. Tran, D. Nguyen, T. Nguyen, Correlates of environmental factors and human plague: an ecological study in Vietnam, *Int. J. Epidemiol.* 38 (6) (2009) 1634–1641, <https://doi.org/10.1093/ije/dyp244>.
- [27] Z. Li, D. Chen, Studies on relationships among parasitic flea index of *Meriones unguiculatus* and meteorological factors, *Acta Entomol. Sin.* 42 (3) (1999) 284–290, <https://doi.org/10.16380/j.kcxb.1999.03.009>.
- [28] D. Eads, Swabbing prairie dog burrows for fleas that transmit *Yersinia pestis*: influences on efficiency, *J. Med. Entomol.* 54 (5) (2017) 1273–1277, <https://doi.org/10.1093/jme/tjx090>.
- [29] B. Blagburn, M. Dryden, Biology, treatment, and control of flea and tick infestations, *Vet. Clin. North. Am. Small Anim. Pract.* 39 (6) (2009) 1173–1200, <https://doi.org/10.1016/j.cvsm.2009.07.001>.
- [30] B. Krasnov, I. Khokhlova, G. Shenbrot, The effect of host density on ectoparasite distribution: an example of a rodent parasitized by fleas, *Ecology* 83 (1) (2002) 164–175, <https://doi.org/10.2307/2680129>.
- [31] L. van der Mescht, C. le Roux Peter, A. Matthee Conrad, J. Raath Morgan, S. Matthee, The influence of life history characteristics on flea (Siphonaptera) species distribution models 178 *Parasit. Vectors* 9 (1) (2016) 1–10, <https://doi.org/10.1186/s13071-016-1466-9>.
- [32] R. MacArthur, Fluctuations of animal populations and a measure of community stability, *Ecology* 36 (3) (1955) 533–536, <https://doi.org/10.2307/1929601>.
- [33] R. MacArthur, *Geographical Ecology*, Princeton University Press, Princeton, 1972.
- [34] D. Eads, J. Hoogland, Factors that affect parasitism of black-tailed prairie dogs by fleas, *Ecosphere* 7 (7) (2016) e01372, <https://doi.org/10.1002/ecs2.1372>.
- [35] L. Shuai, L. Wang, J. Wang, Y. Xia, B. Zhai, W. Xu, X. Chen, X. Yang, F. Zhang, Ecological correlates of ectoparasite load in a rodent: Complex roles of seasonality, *Int. J. Parasitol. Parasites Wildl.* 18 (2022) 244–248, <https://doi.org/10.1016/j.ijppaw.2022.06.006>.
- [36] M. Denny, K. Jürgen, B. Julia, R. Dania, M. Janina, M. Franz-Rainer, H. Susanne, V. Georg, Factors associated with diversity, quantity and zoonotic potential of ectoparasites on urban mice and voles, *PLoS One* 13 (6) (2018) e0199385, <https://doi.org/10.1371/journal.pone.0199385>.
- [37] L. Xu, G. Li, X. Si, X. Fang, Q. Liu, Nonlinear effects of climate driven plague in *M. unguiculatus* natural foci in Inner Mongolia, *Chin. J. Vector Biol. Control* 27 (4) (2016) 321–325, <https://doi.org/10.11853/j.issn.1003.8280.2016.04.002>.