Vital Surveillances

Relationships Between Meteorological Factors and Mongolian Gerbils and Its Flea Burdens — Xilingol League, Inner Mongolia Autonomous Region, China, 2012–2021

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ABSTRACT

Introduction: Plague is a significant global infectious disease, its spread is linked to host and flea populations. Meteorological conditions can impact flea populations and host densities, hence influencing plague outbreaks. Investigating the connection between meteorological factors, flea populations, and rodent densities in Inner Mongolia's natural plague foci can aid in predicting and managing plague outbreaks.

Methods: Monthly data on flea index, rodent density, meteorological factors, and normalized difference vegetation index (NDVI) were collected for the study area. Generalized additive modeling (GAM) was used to analyze the non-linear and lag effects of meteorological factors on flea index and rodent density. Structural equation modeling (SEM) was employed to investigate the relationships among meteorological factors, NDVI, flea index, and rodent density.

Results: GAM analysis revealed that temperature, precipitation, relative humidity, and NDVI had significant linear, non-linear, and time-lagged impacts on the density of Mongolian gerbils and the flea index. SEM analysis indicated that meteorological factors could directly influence the density and flea index of Mongolian gerbils, or indirectly impact NDVI, subsequently influencing gerbil density and the flea index.

Conclusions: Meteorological factors primarily influence gerbil density and flea index indirectly by affecting NDVI and the relationship between flea index and gerbil density. This study offers additional support for the significance of meteorological factors and NDVI in influencing the vector-rodent system, offering valuable insights for predicting and managing plague outbreaks.

Plague, responsible for millions of deaths globally across three pandemics, is caused by the bacterium *Yersinia pestis* (*Y. pestis*). The Mongolian gerbil (*Meriones unguiculatus*) is the primary host of plague in the natural focus in the Inner Mongolian Plateau, carrying various pathogens, including *Y. pestis*. Recent plague cases in China have been mostly associated with Mongolian gerbils. Rodent and flea populations are crucial in plague outbreaks, and with climate change, vector-borne diseases like plague may have a more significant impact (*1*). Climate change influences vegetation, human activities, rodent populations, and fleas, affecting plague transmission dynamics. Meteorological factors impact rodent populations, flea numbers, and their growth (*2*–*4*). The trophic cascade hypothesis (*5*) explains the relationship among climate, vegetation, host, vector, and pathogen. Monitoring data from Mongolian gerbils in the Xilingol League, Inner Mongolia Autonomous Region, China were analyzed to study the effects of meteorological factors and vegetation on the vector-rodent system.

METHODS

The monthly density and body flea index of Mongolian gerbils for this study were extracted from the Plague Control Management Information System of China CDC covering 10 counties in the Xilingol League from 2012 to 2021. Monthly cumulative precipitation, average temperature, and average relative humidity data were sourced from the China Meteorological Service Center (https://data.cma.cn/). The normalized difference vegetation index (NDVI) was used to evaluate vegetation conditions, offering insights into food availability and survival conditions for Mongolian gerbils. Monthly NDVI data were obtained from the Moderate Resolution Imaging

Spectroradiometer (MODIS) dataset, available via EarthData (https://search.earthdata.nasa.gov/search). All data were analyzed monthly. To account for the delayed impact of meteorological factors on Mongolian gerbils and their fleas, a lag of 0–2 months was applied to the meteorological data and NDVI in this study.

Generalized additive modeling (GAM) and structural equation modeling (SEM) were utilized to assess the impact of meteorological factors on the density and body flea index of Mongolian gerbils. In SEM, theoretical assumptions guided the exploration of direct and indirect causal relationships between variables. Initially, GAM was employed to develop two models incorporating Mongolian gerbil density and body flea index as response variables, alongside meteorological data lagged from 0–2 months and NDVI as explanatory variables. Model selection criteria prioritized maximizing Deviance explained and minimizing generalized cross-validation (GCV), favoring models with a lower GCV and a higher Deviance explained. Subsequently, SEM was employed, focusing on path analysis due to the absence of latent variables in the study. Monthly models were created using climate, rodent, flea, and NDVI data. Thirty-six time-lagged SEM combinations were evaluated to assess the delayed effects of meteorological factors and NDVI on rodent density and flea parasitism. The analysis was conducted using the "mgcv" package in R (version 4.2.2, R Core Team, Vienna, Austria) for GAM, and with AMOS (version 28.0, IBM Corporation, Armonk, NY, USA) for SEM.

RESULTS

The table presented the densities, flea index, meteorological factors, and NDVI of Mongolian gerbils in the Xilingol League from 2012 to 2021. Over this period, 23,396 Mongolian gerbils were captured, resulting in 17,809 fleas, of which 6,521 were found on rodents, indicating a flea rate of 27.87% and a flea index of 0.76. The research revealed a negative linear correlation between gerbil density and the flea index. Moreover, meteorological factors and NDVI demonstrated significant effects on the gerbil density/flea index relationship, showing non-linear patterns and lag effects. The impact of meteorological factors on this relationship was influenced by NDVI and the reciprocal flea index/gerbil density.

The GAM analysis using rodent density as the response variable showed a negative linear relationship with the flea index (F=5.155, P<0.05; Figure 1A). Rodent densities exhibited a cyclic pattern with peaks in 2014 and 2019 (F=5.391, P<0.001; Figure 1B). Additionally, a negative linear correlation was observed between rodent density and NDVI, possibly due to Mongolian gerbils' preference for desert grasslands with sparse vegetation (F=9.378, P<0.01; Figure 1C). Furthermore, rodent densities were positively correlated with temperature with a 2-month lag (F=5.143, P<0.05; Figure 1D), with precipitation in a linear fashion (F=4.895, P<0.05; Figure 1E), and with relative humidity in a nonlinear manner (F=3.222, P<0.05; Figure 1F). The GAM analysis using the flea index as the response variable revealed a negative linear correlation between body flea index in Mongolian gerbils and rodent density (F=5.759, P<0.05; Figure 2A) and NDVI (F=13.342, P<0.001; Figure 2C). The flea index decreased over time (F=7.145, P<0.001; Figure 2B) and was positively correlated with average temperature with a one-month lag (F=8.357, P<0.01; Figure 2D). Moreover, a nonlinear correlation was observed between the flea index and precipitation (F=2.864, P<0.05; Figure 2E) and average relative humidity with a one-month lag (F=3.773, P<0.01; Figure 2F).

The influence of meteorological factors on gerbil density occurs primarily through two indirect pathways (Figure 3A): meteorological factors (positive) → vegetation (negative) → rodent, and meteorological factors (positive) → vegetation (negative) → flea (negative) → rodent. These indirect pathways are well-supported by numerous models, whereas the direct pathway from meteorological factors to rodent density, meteorological factors → rodents, is less supported. This indicates that meteorological factors impact rodent density predominantly via NDVI and the flea index. Furthermore, in the SEM (Figure 3B) with the flea index as the final variable, the most supported model was meteorological factors (positive) → vegetation (negative) → flea, indicating that the influence of meteorological factors on the flea index is primarily mediated by NDVI.

CONCLUSIONS

GAM and SEM were employed to examine the intricate relationships between biotic and abiotic factors in natural plague foci. A decade of surveillance data from 10 counties in the Xilingol League was utilized for the analysis. The findings highlight the influence of meteorological conditions on gerbil density and flea index, mediated by NDVI and the

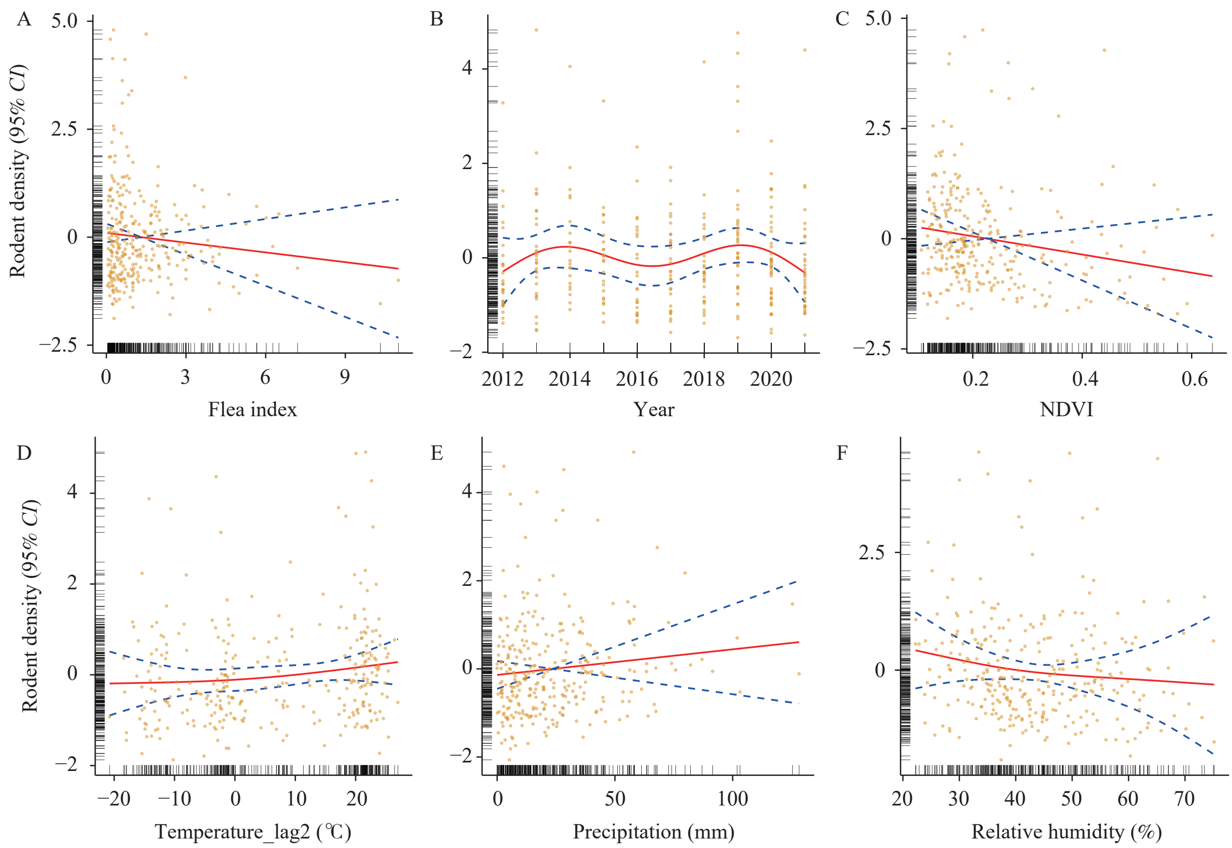

FIGURE 1. Analysis of factors influencing the density of Mongolian gerbils in Xilingol League from 2012 to 2021 using generalized additive modeling. (A) The correlation between flea index and rodent density; (B) The association between time trend (year) and rodent density; (C) The link between NDVI and rodent density; (D) The connection between monthly average temperature with a 2-month lag and rodent density; (E) The correlation between monthly cumulative precipitation and rodent density; (F) The relationship between monthly average relative humidity and rodent density.
Abbreviation: NDVI=normalized difference vegetation index; *CI*=confidence interval.

reciprocal impact of flea index on gerbil density.

A negative correlation was observed between gerbil density and their body flea index, aligning with similar patterns found in Utah prairie dogs (*6*). The higher flea infestation likely impacted the survival and reproduction of gerbils by affecting immunity, behavior, and reproduction, ultimately contributing to decreased gerbil populations. Research on North American red squirrels revealed that flea-infected females gave birth to offspring with lower body weight and survival rates (*7*), while studies on voles demonstrated that flea-infected voles had notably reduced average lifespans (*8*). Furthermore, as fleas serve as vectors for various pathogens, elevated flea indices facilitate pathogen transmission among gerbils, consequently lowering gerbil densities.

Temperature was found to have a positive correlation with gerbil density and flea index, aligning with a previous study on Rattus norvegicus in Ningbo (*2*). Temperature affects gerbil density through factors like metabolism, reproduction, activity, and food availability. Low temperatures can hinder oocyte development in female gerbils and lead to testicular atrophy in males, reducing sperm production and hindering gerbil reproduction. Flea larvae and pupae are sensitive to temperature, as higher temperatures can speed up their development and shorten the reproductive cycle, ultimately increasing flea populations (*9*). Consequently, warmer temperatures contribute to higher flea parasitism rates in gerbils due to increased flea numbers.

The study found a positive relationship between precipitation, gerbil density, and the flea index. Research in Hebei Province indicated a direct link between flea prevalence and precipitation (*3*). However, studies in Inner Mongolia demonstrated a curvilinear association among gerbil density, flea index, and precipitation (*4*). The increased precipitation and relative humidity likely created ideal conditions for flea survival and reproduction in gerbil burrows (*6*).

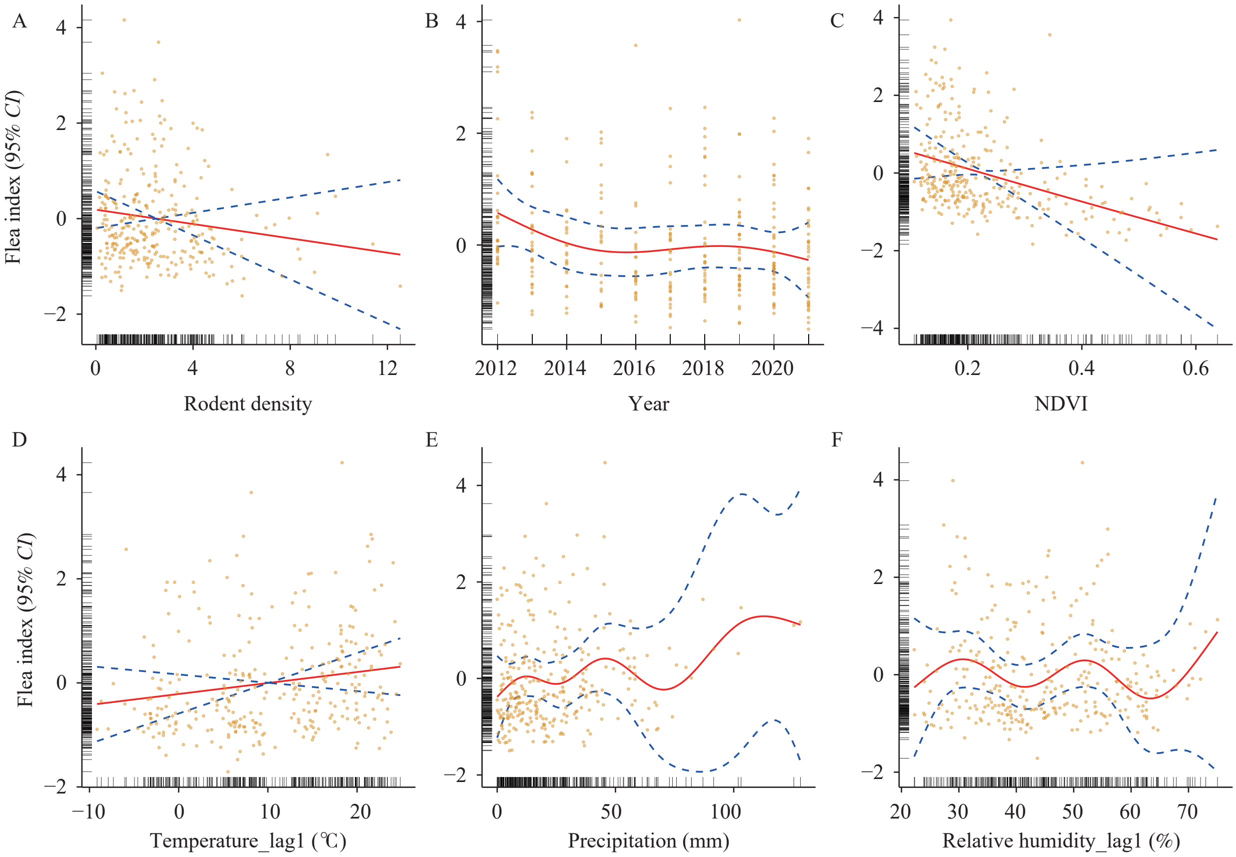

FIGURE 2. Analysis of factors influencing the flea index of Mongolian gerbils in Xilingol League from 2012 to 2021 using generalized additive modeling. (A) The correlation between rodent density and the flea index; (B) The association between flea time trend (year) and the flea index; (C) The link between flea NDVI and the flea index; (D) The connection between monthly average temperature with a 1-month lag and the flea index; (E) The correlation between monthly cumulative precipitation and the flea index; (F) The relationship between monthly average relative humidity with a 1-month lag and the flea index.

Abbreviation: NDVI=normalized difference vegetation index; *CI*=confidence interval.

Adequate precipitation boosts vegetation growth, providing more food for gerbils. Relative humidity displayed a non-linear negative correlation with gerbil density and an erratic upward trend with the flea index, possibly due to the arid environment of desert grasslands preferred by gerbils. Conversely, relative humidity can impact flea reproduction and abundance by influencing the female ratio, developmental rate, and life cycle of the fleas (*10*–*11*).

A multitude of studies have established a significant link between the NDVI and the distribution, abundance, and density of small mammal populations (*12*–*13*). Contrary to the trophic cascade hypothesis, our research in the Xilingol League has shown that as temperature, precipitation, and relative humidity increase, NDVI values rise, but the density of Mongolian gerbil populations and the flea index decrease, a finding that echoes those of Xu et al. (*14*). This inverse trend may be due to gerbils' preference for desert grassland ecosystems, where the NDVI reflects vegetation cover rather than the actual availability of food resources. Moreover, host habitat significantly shapes the composition and prevalence of fleas; variations in vegetation density and structure can alter flea populations and their movements. Furthermore, the diversity of flea parasites found on rodent hosts changes with the ecological terrain (*15*). Within our study, a negative correlation was observed between the gerbil flea index and NDVI, suggesting that less dense vegetation may be more conducive to host survival, and thus, the relationship between the flea index and NDVI correlates inversely with host distribution patterns.

This study is subject to some limitations. First, the lack of continuous data on Mongolian gerbil densities and flea index may have impacted the accuracy of model predictions. Second, the analysis focused solely on the ecological aspects of the vector-rodent system,

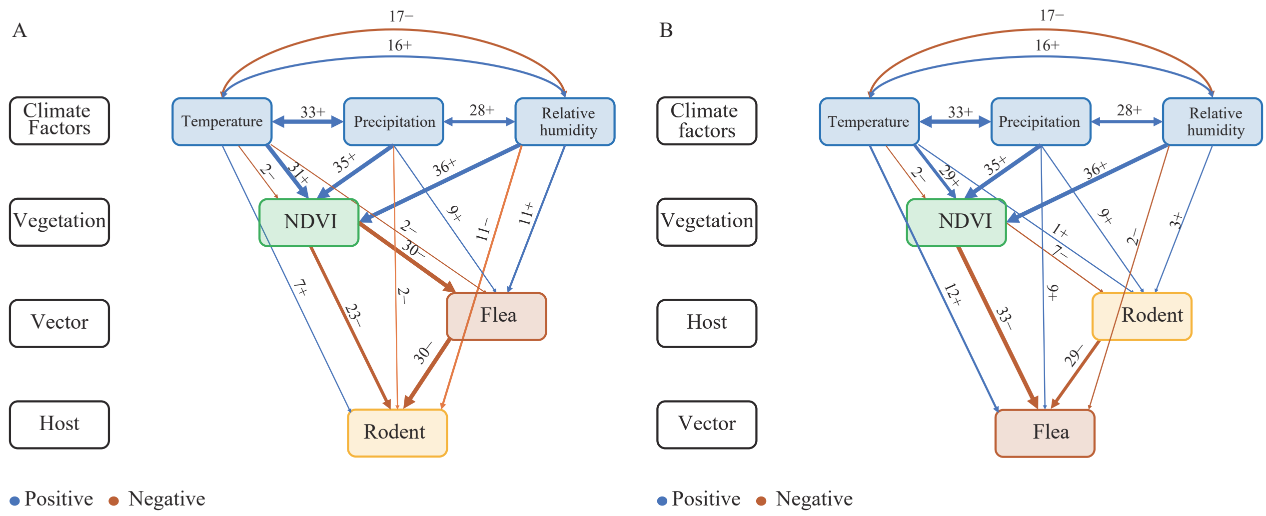

FIGURE 3. The results of SEM for meteorological factors and vegetation on the vector-rodent system in Xilingol League, 2012–2021. (A) SEM with Mongolian gerbils' density as the final variable; (B) SEM with Mongolian gerbils' flea index as the final variable.

Note: Thirty-six monthly model combinations were developed by considering time-lagged relationships between the current month and the two preceding months. The width and quantity of lines in the diagram reflect the statistical significance ($P<0.05$) and level of support for each pathway. Positive correlations are indicated by blue lines marked with a "+," while negative correlations are represented by orange lines marked with a "–". The arrows show the direction of influence within the model.

Abbreviation: SEM=structural equation modeling; NDVI=normalized difference vegetation index.

TABLE 1. Monthly summary statistics for Mongolian gerbil density, flea index, and meteorological factors in Xilingol League, 2012–2021.

Variable	Mean	Standard deviation	Minimum	P25	P50	P75	Maximum
Rodent density (gerbils/hectare)	2.49	1.98	0.05	1.05	2.08	3.33	12.53
Flea index	1.31	1.50	0.04	0.33	0.77	1.79	11.00
Monthly average temperature (℃)	11.77	6.15	−8.01	6.78	12.97	15.81	22.81
Average temperature with 1-month lag (℃)	10.12	8.50	−9.15	3.73	9.42	17.98	24.85
Average temperature with 2-month lag (℃)	6.16	14.01	−20.76	−4.58	5.43	20.93	27.00
Monthly cumulative precipitation (mm)	23.62	21.69	0.00	7.50	16.90	33.80	128.20
Cumulative precipitation with 1-month lag (mm)	23.64	26.32	0.00	4.60	14.20	35.30	168.60
Cumulative precipitation with 2-month lag (mm)	26.22	37.38	0.00	2.60	9.20	40.30	271.20
Monthly average relative humidity (%)	43.37	11.49	22.23	34.97	41.42	51.60	75.17
Monthly average relative humidity with 1-month lag (%)	44.68	11.86	22.23	35.63	43.50	53.77	75.05
Monthly average relative humidity with 2-month lag (%)	49.95	11.75	22.30	41.05	51.58	58.55	75.52
NDVI	0.23	0.11	0.11	0.16	0.19	0.26	0.64
NDVI with 1-month lag	0.23	0.13	0.10	0.15	0.18	0.26	0.66
NDVI with 2-month lag	0.21	0.14	−0.01	0.13	0.16	0.25	0.63

Abbreviation: NDVI=normalized difference vegetation index.

without consideration of pathogens or plague cases. Consequently, drawing direct conclusions about pathogen transmission dynamics or mechanisms of plague outbreaks is not feasible.

In conclusion, meteorological factors influence gerbil density and flea index indirectly through their impact on NDVI and the interaction between fleas and gerbils. This suggests a complex mediating mechanism in the ecosystem, indicating the regulatory roles of NDVI and flea-gerbil interactions. Favorable temperature and precipitation conditions enhance Mongolian gerbil survival, leading to local rodent infestations and increasing the risk of plague outbreaks. Human activities like overgrazing contribute to grassland desertification, creating suitable habitats for Mongolian gerbils and further elevating the plague risk. Regular monitoring of meteorological conditions (temperature, humidity, precipitation) and NDVI is crucial to comprehend gerbil ecological dynamics and flea vectors. Local CDC departments should intensify rodent surveillance and control during warm temperatures, increased precipitation, and low NDVI. Implementing grazing reduction measures and grassland restoration can reduce gerbil plague risk. Developing predictive systems for gerbils and plague outbreaks should integrate ecological, meteorological, and human activity factors for effective management. Such a holistic approach can safeguard human and ecosystem health.

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SUPPLEMENTARY MATERIAL

SUPPLEMENTARY TABLE S1. Model selection process for analyzing factors affecting Mongolian gerbils density using generalized additive modeling.

Model	Model type	Formula	Significant factors	R-sq.(adj)	Deviance explained (%)	GCV
1	Year	$Y_{i,t}=f_1(year_{i,t})+\alpha_{i,t}$	year	0.0899	11.90	1.2908
2	Flea	$Y_{i,t}=f_1(flea_{i,t})+\alpha_{i,t}$	NAN	0.0024	1.06	1.3985
3	NDVI	$Y_{i,t}=f_1(NDVI_{i,t})+\alpha_{i,t}$	NDVI	0.0340	4.45	1.3462
3.lag1		$Y_{i,t}=f_1(NDVI_{i,t-1})+\alpha_{i,t}$	NAN	0.0088	1.47	1.3883
3.lag2		$Y_{i,t}=f_1(NDVI_{i,t-2})+\alpha_{i,t}$	NAN	0.0050	1.40	1.3986
4	Tmp	$Y_{i,t}=f_1(Tmp_{i,t})+\alpha_{i,t}$	NAN	0.0037	1.10	1.4013
4.lag1		$Y_{i,t}=f_1(Tmp_{i,t-1})+\alpha_{i,t}$	NAN	0.0342	6.56	1.3729
4.lag2		$Y_{i,t}=f_1(Tmp_{i,t-2})+\alpha_{i,t}$	NAN	−0.0034	0.00	1.4089
5	Pre	$Y_{i,t}=f_1(Pre_{i,t})+\alpha_{i,t}$	NAN	0.0007	0.46	1.4025
5.lag1		$Y_{i,t}=f_1(Pre_{i,t-1})+\alpha_{i,t}$	NAN	0.0055	1.01	1.3946
5.lag2		$Y_{i,t}=f_1(Pre_{i,t-2})+\alpha_{i,t}$	NAN	0.0009	0.54	1.4014
6	Rhu	$Y_{i,t}=f_1(Rhu_{i,t})+\alpha_{i,t}$	Rhu	0.0346	5.38	1.3596
6.lag1		$Y_{i,t}=f_1(Rhu_{i,t-1})+\alpha_{i,t}$	Rhu	0.0329	4.10	1.3512
6.lag2		$Y_{i,t}=f_1(Rhu_{i,t-2})+\alpha_{i,t}$	NAN	0.0176	3.38	1.3881
7	Flea+Tmp	$Y_{i,t}=f_1(flea_{i,t})+f_2(Tmp_{i,t})+\alpha_{i,t}$	NAN	0.0060	2.03	1.4010
7.lag1		$Y_{i,t}=f_1(flea_{i,t-1})+f_2(Tmp_{i,t-1})+\alpha_{i,t}$	NAN	0.0375	7.28	1.3730
7.lag2		$Y_{i,t}=f_1(flea_{i,t-2})+f_2(Tmp_{i,t-2})+\alpha_{i,t}$	NAN	−0.0014	0.91	1.4090
8	Flea+Pre	$Y_{i,t}=f_1(flea_{i,t})+f_2(Pre_{i,t})+\alpha_{i,t}$	NAN	0.0023	1.26	1.4028
8.lag1		$Y_{i,t}=f_1(flea_{i,t-1})+f_2(Pre_{i,t-1})+\alpha_{i,t}$	NAN	0.0092	2.03	1.3916
8.lag2		$Y_{i,t}=f_1(flea_{i,t-2})+f_2(Pre_{i,t-2})+\alpha_{i,t}$	NAN	0.0036	1.43	1.4001
9	Flea+Rhu	$Y_{i,t}=f_1(flea_{i,t})+f_2(Rhu_{i,t})+\alpha_{i,t}$	Rhu	0.0472	7.00	1.3486
9.lag1		$Y_{i,t}=f_1(flea_{i,t-1})+f_2(Rhu_{i,t-1})+\alpha_{i,t}$	Rhu	0.0435	5.60	1.3399
9.lag2		$Y_{i,t}=f_1(flea_{i,t-2})+f_2(Rhu_{i,t-2})+\alpha_{i,t}$	NAN	0.0216	4.33	1.3844
10	Flea+Tmp+ year	$Y_{i,t}=f_1(flea_{i,t})+f_2(Tmp_{i,t})+f_3(year_{i,t})+\alpha_{i,t}$	Year	0.0938	13.20	1.2977
10.lag1		$Y_{i,t}=f_1(flea_{i,t})+f_2(Tmp_{i,t-1})+f_3(year_{i,t})+\alpha_{i,t}$	Year	0.1010	15.50	1.2968
10.lag2		$Y_{i,t}=f_1(flea_{i,t})+f_2(Tmp_{i,t-2})+f_3(year_{i,t})+\alpha_{i,t}$	Year	0.0863	12.20	1.3031
11	Flea+Pre+ year	$Y_{i,t}=f_1(flea_{i,t})+f_2(Pre_{i,t})+f_3(year_{i,t})+\alpha_{i,t}$	Year	0.0874	12.00	1.3008
11.lag1		$Y_{i,t}=f_1(flea_{i,t})+f_2(Pre_{i,t-1})+f_3(year_{i,t})+\alpha_{i,t}$	Year	0.0882	12.30	1.3004
11.lag2		$Y_{i,t}=f_1(flea_{i,t})+f_2(Pre_{i,t-2})+f_3(year_{i,t})+\alpha_{i,t}$	Year	0.3230	40.70	1.0058
12	Flea+Rhu+ year	$Y_{i,t}=f_1(flea_{i,t})+f_2(Rhu_{i,t})+f_3(year_{i,t})+\alpha_{i,t}$	Rhu, year	0.1260	17.90	1.2667
12.lag1		$Y_{i,t}=f_1(flea_{i,t})+f_2(Rhu_{i,t-1})+f_3(year_{i,t})+\alpha_{i,t}$	Rhu, year	0.1180	15.00	1.2559
12.lag2		$Y_{i,t}=f_1(flea_{i,t})+f_2(Rhu_{i,t-2})+f_3(year_{i,t})+\alpha_{i,t}$	Year	0.0891	12.50	1.2960
13	Flea+NDVI+ year	$Y_{i,t}=f_1(flea_{i,t})+f_2(NDVI_{i,t})+f_3(year_{i,t})+\alpha_{i,t}$	NDVI, year	0.1200	15.70	1.2486
13.lag1		$Y_{i,t}=f_1(flea_{i,t})+f_2(NDVI_{i,t-1})+f_3(year_{i,t})+\alpha_{i,t}$	NDVI, year	0.1310	18.10	1.2708
13.lag2		$Y_{i,t}=f_1(flea_{i,t})+f_2(NDVI_{i,t-2})+f_3(year_{i,t})+\alpha_{i,t}$	year	0.0897	12.40	1.2996
14	Flea+Tmp+Pre+ Rhu+NDVI+year	$Y_{i,t}=f_1(flea_{i,t})+f_2(year_{i,t})+f_3(Tmp_{i,t-2})+$ $f3(Pre_{i,t})+f3(Rhu_{i,t})+f4(NDVI_{i,t})+\alpha_{i,t}$	Flea, year, Tmp, RHU, pre, NDVI	0.1350	18.80	1.2216

Note: Models were selected using the coefficient of determination (R-sq.) and GCV.Models withlarger R-sq. and lower GCV values had higherout-of-sample predictive power. Therefore, Model 14 is the final model withthe highest R-sq. value and the lowest GCV value.
Abbreviation:GCV=Generalized cross-validation.

SUPPLEMENTARY TABLE S2. Results of generalized additive modeling to analyze factors affecting Mongolian gerbils density.

Factors	edf	F	*P* value
s(flea)	1	5.155	0.0239*
s(year)	3.922	5.391	0.0003***
s(NDVI)	1	9.378	0.0024**
s(pre)	1	4.895	0.0277*
s(RHU_Avg)	1.839	3.222	0.0461*
s(TEM_Avg_2)	1.561	5.143	0.0173*

* $P<0.05$.
** $P<0.01$.
*** $P<0.001$.

SUPPLEMENTARY TABLE S3. Model selection process for analyzing factors affecting Mongolian gerbils flea index using generalized additive modeling.

Model	Model type	Formula	Significant factors	R-sq.(adj)	Deviance explained (%)	GCV
1	Year	$Y_{i,t}=f_1(year_{i,t})+\alpha_{i,t}$	Year	0.0507	7.00	1.2118
2	Rodent	$Y_{i,t}=f_1(rodent_{i,t})+\alpha_{i,t}$	NAN	0.0117	3.26	1.2607
3		$Y_{i,t}=f_1(NDVI_{i,t})+\alpha_{i,t}$	NDVI	0.0425	6.81	1.1967
3.lag1	NDVI	$Y_{i,t}=f_1(NDVI_{i,t-1})+\alpha_{i,t}$	NDVI	0.0412	8.32	1.208
3.lag2		$Y_{i,t}=f_1(NDVI_{i,t-2})+\alpha_{i,t}$	NDVI	0.0438	9.51	1.2064
4		$Y_{i,t}=f_1(Tmp_{i,t})+\alpha_{i,t}$	NAN	0.00328	0.95	1.2719
4.lag1	Tmp	$Y_{i,t}=f_1(Tmp_{i,t-1})+\alpha_{i,t}$	NAN	−0.00334	0.00	1.2841
4.lag2		$Y_{i,t}=f_1(Tmp_{i,t-2})+\alpha_{i,t}$	NAN	0.0013	0.64	1.276
5		$Y_{i,t}=f_1(Pre_{i,t})+\alpha_{i,t}$	NAN	0.00545	3.21	1.2791
5.lag1	Pre	$Y_{i,t}=f_1(Pre_{i,t-1})+\alpha_{i,t}$	Pre	0.0147	2.78	1.2485
5.lag2		$Y_{i,t}=f_1(Pre_{i,t-2})+\alpha_{i,t}$	NAN	0.00608	1.49	1.265
6		$Y_{i,t}=f_1(Rhu_{i,t})+\alpha_{i,t}$	Rhu	0.0392	7.25	1.2244
6.lag1	Rhu	$Y_{i,t}=f_1(Rhu_{i,t-1})+\alpha_{i,t}$	Rhu	0.084	13.60	1.153
6.lag2		$Y_{i,t}=f_1(Rhu_{i,t-2})+\alpha_{i,t}$	Rhu	0.0105	1.86	1.2603
7		$Y_{i,t}=f_1(rodent_{i,t})+f_2(Tmp_{i,t})+\alpha_{i,t}$	NAN	0.0195	5.68	1.2547
7.lag1	Rodent+Tmp	$Y_{i,t}=f_1(rodent_{i,t-1})+f_2(Tmp_{i,t-1})+\alpha_{i,t}$	NAN	0.00825	3.28	1.2691
7.lag2		$Y_{i,t}=f_1(rodent_{i,t-2})+f_2(Tmp_{i,t-2})+\alpha_{i,t}$	NAN	0.013	4.08	1.2592
8		$Y_{i,t}=f_1(rodent_{i,t})+f_2(Pre_{i,t})+\alpha_{i,t}$	NAN	0.0165	6.07	1.2656
8.lag1	Rodent+Pre	$Y_{i,t}=f_1(rodent_{i,t-1})+f_2(Pre_{i,t-1})+\alpha_{i,t}$	Pre	0.0277	7.93	1.2495
8.lag2		$Y_{i,t}=f_1(rodent_{i,t-2})+f_2(Pre_{i,t-2})+\alpha_{i,t}$	NAN	0.0208	5.18	1.2461
9		$Y_{i,t}=f_1(rodent_{i,t})+f_2(Rhu_{i,t})+\alpha_{i,t}$	Rhu	0.0595	11.50	1.1972
9.lag1	Rodent+Rhu	$Y_{i,t}=f_1(rodent_{i,t-1})+f_2(Rhu_{i,t-1})+\alpha_{i,t}$	Rodent, Rhu	0.122	19.30	1.1133
9.lag2		$Y_{i,t}=f_1(rodent_{i,t-2})+f_2(Rhu_{i,t-2})+\alpha_{i,t}$	Rhu	0.0251	5.03	1.2462
10		$Y_{i,t}=f_1(rodent_{i,t})+f_2(Tmp_{i,t})+f_3(year_{i,t})+\alpha_{i,t}$	Year	0.0731	13.40	1.1877
10.lag1	Rodent+Tmp+year	$Y_{i,t}=f_1(rodent_{i,t})+f_2(Tmp_{i,t-1})+f_3(year_{i,t})+\alpha_{i,t}$	Year	0.0594	10.70	1.2065
10.lag2		$Y_{i,t}=f_1(rodent_{i,t})+f_2(Tmp_{i,t-2})+f_3(year_{i,t})+\alpha_{i,t}$	Year	0.0818	15.20	1.1888
11		$Y_{i,t}=f_1(rodent_{i,t})+f_2(Pre_{i,t})+f_3(year_{i,t})+\alpha_{i,t}$	Year	0.0971	15.60	1.1923
11.lag1	Rodent+Pre+year	$Y_{i,t}=f_1(rodent_{i,t})+f_2(Pre_{i,t-1})+f_3(year_{i,t})+\alpha_{i,t}$	Pre, year	0.084	13.60	1.1706
11.lag2		$Y_{i,t}=f_1(rodent_{i,t})+f_2(Pre_{i,t-2})+f_3(year_{i,t})+\alpha_{i,t}$	Pre,year	0.0726	12.40	1.1824
12		$Y_{i,t}=f_1(rodent_{i,t})+f_2(Rhu_{i,t})+f_3(year_{i,t})+\alpha_{i,t}$	Rhu, year	0.111	17.60	1.1542
12.lag1	Rodent+Rhu+year	$Y_{i,t}=f_1(rodent_{i,t})+f_2(Rhu_{i,t-1})+f_3(year_{i,t})+\alpha_{i,t}$	Rodent, Rhu, year	0.202	27.20	1.0458
12.lag2		$Y_{i,t}=f_{1(}rodent_{i,t})+f_2(Rhu_{i,t-2})+f_3(year_{i,t})+\alpha_{i,t}$	Rhu, year	0.0828	14.80	1.1692
13		$Y_{i,t}=f_1(rodent_{i,t})+f_2(NDVI_{i,t})+f_3(year_{i,t})+\alpha_{i,t}$	NDVI, year	0.112	17.00	1.1213
13.lag1	Rodent+NDVI+year	$Y_{i,t}=f_1(rodent_{i,t})+f_2(NDVI_{i,t-1})+f_3(year_{i,t})+\alpha_{i,t}$	NDVI, year	0.111	18.70	1.1267
13.lag2		$Y_{i,t}=f_1(rodent_{i,t})+f_2(NDVI_{i,t-2})+f_3(year_{i,t})+\alpha_{i,t}$	NDVI, year	0.114	19.60	1.1327
14	Rodent+Tmp+Pre+ Rhu+NDVI+year	$Y_{i,t}=f_1(rodent_{i,t})+f_2(year_{i,t})+f_3(Tmp_{i,t-1})+ f3(Pre_{i,t})+f3(Rhu_{i,t-1})+f4(NDVI_{i,t})+\alpha_{i,t}$	Rodent, year, Tmp, Pre, Rhu, NDVI	0.23	29.00	1.014

Note: Models were selected using the coefficient of determination (R-sq.) and GCV. Models withlarger R-sq. and lower GCV valueshadhigherout-of-samplepredictive power. Therefore, Model 14 is the final model withthe highest R-sq. value and the lowest GCV value.

Abbreviation: GCV=Generalized cross-validation;NDVI= normalized difference vegetation index.

SUPPLEMENTARY TABLE S4. Results of generalized additive modeling to analyze factors affecting Mongolian gerbils flea index.

Factors	edf	F	*P* value
s(rodent,bs='cr')	1	5.759	0.0171*
s(year,bs='cr')	3.055	7.145	0.0000487***
s(NDVI,bs='cr')	1.061	13.342	0.0002***
s(pre,bs='cr')	5.659	2.864	0.0096*
s(RHU_Avg_1,bs='cr')	4.892	3.773	0.0036**
s(TEM_Avg_1,bs='cr')	1	8.357	0.0041**

* $P<0.05$.
** $P<0.01$.
*** $P<0.001$.

SUPPLEMENTARY TABLE S5. SEM with Mongolian gerbils' density as the final variable.Red means statistically significant, black means not statistically significant, 0 current month, 1 previous month, 2 previous 2 months.

Time lag of RHU_Avg	Time lag of TEM_Avg	Time lag of pre	Time lag of NDVI	pre→ NDVI	RHU_Avg→ NDVI	TEM_Avg→ NDVI	pre→ flea	RHU_Avg→ flea	TEM_Avg→ flea	NDVI→ flea	NDVI→ rodent	flea→ rodent	RHU_Avg→ rodent	TEM_Avg→ rodent	pre→ rodent	RHU_Avg↔ pre	RHU_Avg↔ TEM_Avg	TEM_Avg↔ pre
0	0	0	0	0.088	0.671	0.265	0.165	0.087	−0.058	−0.286	−0.184	−0.131	−0.154	−0.073	0.164	0.578	−0.057	0.408
0	1	0	0	0.248	0.503	0.106	0.198	0.147	−0.175	−0.273	−0.242	−0.151	−0.169	0.151	0.111	0.578	0.570	0.428
0	1	1	0	0.443	0.482	−0.048	−0.065	0.189	−0.118	−0.174	−0.210	−0.136	−0.135	0.154	0.016	0.570	0.570	0.614
0	1	2	0	0.258	0.522	0.057	0.003	0.165	−0.119	−0.208	−0.220	−0.137	−0.147	0.144	0.058	0.591	0.570	0.558
0	2	0	0	0.271	0.521	0.046	0.232	0.109	−0.193	−0.256	−0.231	−0.149	−0.256	0.212	0.163	0.578	0.643	0.271
0	2	1	0	0.507	0.561	−0.222	−0.017	0.077	−0.093	−0.166	−0.166	−0.126	−0.183	0.185	−0.006	0.570	0.643	0.623
0	2	2	0	0.329	0.601	−0.138	0.032	0.056	−0.094	−0.187	−0.182	−0.127	−0.185	0.169	0.032	0.591	0.643	0.625
0	0	1	0	0.342	0.525	0.219	−0.002	0.155	0.029	−0.268	−0.209	−0.117	−0.087	−0.016	0.089	0.570	−0.057	0.217
0	0	2	0	0.273	0.563	0.301	0.084	0.166	0.006	−0.306	−0.210	−0.123	−0.097	0.006	0.103	0.591	−0.057	−0.024
1	0	0	0	0.374	0.622	0.223	0.144	0.112	0.009	−0.328	−0.156	−0.127	−0.139	−0.063	0.081	0.191	−0.181	0.408
1	1	0	0	0.398	0.528	0.198	0.151	0.100	−0.043	−0.318	−0.235	−0.140	−0.097	0.102	0.049	0.191	0.246	0.428
1	1	1	0	0.285	0.416	0.221	−0.025	0.132	−0.081	−0.204	−0.220	−0.135	−0.148	0.072	0.091	0.642	0.246	0.614
1	1	1	1	0.158	0.55	0.311	−0.053	0.145	−0.062	−0.189	0.018	−0.114	−0.246	0.016	0.027	0.642	0.246	0.614
1	1	2	0	0.154	0.494	0.291	0.019	0.115	−0.097	−0.213	−0.213	−0.136	−0.144	0.075	0.087	0.571	0.246	0.558
1	1	2	1	0.384	0.456	0.217	0.080	0.105	−0.091	−0.244	−0.011	−0.116	−0.241	0.014	0.059	0.571	0.246	0.558
1	2	0	0	0.451	0.517	0.126	0.167	0.039	−0.059	−0.285	−0.224	−0.136	−0.130	0.125	0.059	0.191	0.399	0.271
1	2	2	0	0.275	0.456	0.101	0.063	0.021	−0.131	−0.170	−0.195	−0.132	−0.166	0.099	0.069	0.571	0.399	0.625
1	2	2	1	0.414	0.421	0.178	0.101	0.041	−0.122	−0.205	−0.036	−0.117	−0.237	0.086	0.030	0.571	0.399	0.625
1	0	1	0	0.290	0.520	0.294	0.015	0.137	−0.028	−0.236	−0.154	−0.121	−0.233	−0.084	0.165	0.642	−0.181	0.217
1	2	1	0	0.430	0.360	0.043	0.041	0.033	−0.127	−0.168	−0.204	−0.131	−0.171	0.100	0.078	0.642	0.399	0.623
1	2	1	1	0.228	0.473	0.273	0.002	0.066	−0.117	−0.148	−0.017	−0.116	−0.234	0.095	−0.006	0.642	0.399	0.623
1	0	2	0	0.291	0.554	0.370	0.093	0.149	−0.045	−0.274	−0.156	−0.127	−0.186	−0.036	0.119	0.571	−0.181	−0.024
2	0	0	0	0.513	0.479	0.279	0.157	0.150	0.077	−0.362	−0.241	−0.125	−0.054	−0.045	0.092	−0.089	−0.470	0.408
2	1	0	0	0.441	0.453	0.428	0.178	0.126	0.049	−0.390	−0.334	−0.138	0.024	0.119	0.083	−0.089	−0.260	0.428
2	1	1	0	0.477	0.334	0.292	−0.066	0.157	0.002	−0.241	−0.284	−0.129	0	0.114	0.015	0.093	−0.260	0.614
2	1	1	1	0.391	0.494	0.431	−0.074	0.205	0.058	−0.276	−0.094	−0.106	−0.046	0.070	−0.079	0.093	−0.260	0.614
2	1	2	0	0.199	0.353	0.480	−0.024	0.146	0.011	−0.270	−0.283	−0.129	−0.022	0.092	0.046	0.374	−0.260	0.558
2	1	2	1	0.377	0.390	0.434	0.051	0.164	0.048	−0.340	−0.162	−0.105	−0.057	0.026	0.053	0.374	−0.260	0.558

Continued

Time lag of RHU_Avg	Time lag of TEM_Avg	Time lag of pre	Time lag of NDVI	pre→ NDVI	RHU_Avg→ NDVI	TEM_Avg→ NDVI	pre→ flea	RHU_Avg→ flea	TEM_Avg→ flea	NDVI→ flea	NDVI→ rodent	flea→ rodent	RHU_Avg→ rodent	TEM_Avg→ rodent	pre→ rodent	RHU_Avg↔ pre	RHU_Avg↔ TEM_Avg	TEM_Avg↔ pre
2	2	0	0	0.521	0.396	0.364	0.185	0.033	0.004	−0.332	−0.328	−0.132	0.008	0.110	0.099	−0.089	−0.129	0.271
2	2	1	0	0.587	0.264	0.123	−0.008	0.017	−0.056	−0.193	−0.260	−0.121	−0.023	0.095	0.013	0.093	−0.129	0.623
2	2	1	1	0.410	0.432	0.405	−0.040	0.074	−0.020	−0.201	−0.122	−0.104	−0.038	0.113	−0.088	0.093	−0.129	0.623
2	2	2	0	0.369	0.197	0.250	0.083	−0.034	−0.088	−0.216	−0.265	−0.123	−0.043	0.072	0.050	0.374	−0.129	0.625
2	2	2	1	0.396	0.321	0.398	0.111	0.020	−0.043	−0.271	−0.187	−0.104	−0.032	0.082	0.026	0.374	−0.129	0.625
2	2	2	2	0.307	0.249	0.520	0.067	0.019	−0.079	−0.205	0.022	−0.086	−0.095	−0.003	−0.054	0.374	−0.129	0.625
2	0	1	0	0.580	0.402	0.326	0.012	0.175	0.047	−0.277	−0.230	−0.117	−0.063	−0.029	0.062	0.093	−0.470	0.217
2	0	2	0	0.489	0.319	0.425	0.080	0.183	0.034	−0.314	−0.241	−0.121	−0.086	−0.021	0.096	0.374	−0.470	−0.024

SUPPLEMENTARY TABLE S6. SEM with Mongolian gerbils' flea index as the final variable. Red means statistically significant, black means not statistically significant, 0 current month, 1 previous month, 2 previous 2 months.

Time lag of RHU_Avg	Time lag of TEM_Avg	Time lag of pre	Time lag of NDVI	pre→ NDVI	RHU_Avg→ NDVI	TEM_Avg→ NDVI	NDVI→ rodent	RHU_Avg→ rodent	TEM_Avg→ rodent	pre→ rodent	pre→ flea	TEM_Avg→ flea	RHU_Avg→ flea	NDVI→ flea	rodent→ flea	RHU_Avg↔ pre	RHU_Avg↔ TEM_Avg	TEM_Avg↔ pre
0	0	0	0	0.088	0.671	0.265	−0.147	−0.147	−0.084	0.142	0.183	0.077	−0.077	−0.305	−0.127	0.578	−0.057	0.408
0	1	0	0	0.248	0.503	0.106	−0.201	−0.142	0.129	0.082	0.210	0.165	−0.196	−0.302	−0.146	0.578	0.570	0.428
0	1	1	0	0.443	0.482	−0.048	−0.187	−0.119	0.128	0.025	−0.061	0.206	−0.134	−0.199	−0.134	0.570	0.570	0.614
0	1	2	0	0.258	0.522	0.057	−0.192	−0.131	0.121	0.057	0.010	0.182	−0.137	−0.234	−0.135	0.591	0.570	0.558
0	2	0	0	0.271	0.521	0.046	−0.193	−0.227	0.196	0.128	0.250	0.138	−0.227	−0.285	−0.147	0.578	0.643	0.271
0	2	1	0	0.507	0.561	−0.222	−0.146	−0.171	0.175	−0.004	−0.017	0.099	−0.115	−0.184	−0.127	0.570	0.643	0.623
0	2	2	0	0.329	0.601	−0.138	−0.158	−0.173	0.162	0.028	0.035	0.077	−0.116	−0.207	−0.128	0.591	0.643	0.625
0	0	1	0	0.342	0.525	0.219	−0.178	−0.091	−0.034	0.089	0.009	0.152	0.019	−0.289	−0.115	0.570	−0.057	0.217
0	0	2	0	0.273	0.563	0.301	−0.173	−0.097	−0.014	0.093	0.095	0.164	−0.006	−0.326	−0.120	0.591	−0.057	−0.024
1	0	0	0	0.374	0.622	0.223	−0.115	−0.140	−0.077	0.062	0.151	0.103	−0.008	−0.342	−0.123	0.191	−0.181	0.408
1	1	0	0	0.398	0.528	0.198	−0.190	−0.091	0.088	0.028	0.155	0.112	−0.056	−0.344	−0.136	0.191	0.246	0.428
1	1	1	0	0.285	0.416	0.221	−0.192	−0.137	0.054	0.095	−0.012	0.139	−0.099	−0.230	−0.133	0.642	0.246	0.614
1	1	1	1	0.158	0.550	0.311	0.040	−0.239	−0.001	0.034	−0.049	0.145	−0.088	−0.184	−0.112	0.642	0.246	0.614
1	1	2	0	0.154	0.494	0.291	−0.184	−0.131	0.060	0.084	0.031	0.123	−0.115	−0.238	−0.135	0.571	0.246	0.558
1	1	2	1	0.384	0.456	0.217	0.018	−0.230	0.002	0.049	0.086	0.106	−0.118	−0.242	−0.114	0.571	0.246	0.558
1	2	0	0	0.451	0.517	0.126	−0.186	−0.122	0.120	0.037	0.172	0.055	−0.075	−0.310	−0.134	0.191	0.399	0.271
1	2	2	0	0.275	0.456	0.101	−0.172	−0.149	0.096	0.061	0.071	0.034	−0.151	−0.193	−0.132	0.571	0.399	0.625
1	2	2	1	0.414	0.421	0.178	−0.011	−0.223	0.081	0.018	0.103	0.050	−0.148	−0.206	−0.116	0.571	0.399	0.625

Continued

Time lag of RHU_Avg	Time lag of TEM_Avg	Time lag of pre	Time lag of NDVI	pre→ NDVI	RHU_Avg→ NDVI	TEM_Avg→ NDVI	NDVI→ rodent	RHU_Avg→ rodent	TEM_Avg→ rodent	pre→ rodent	pre→ flea	TEM_Avg→ flea	RHU_Avg→ flea	NDVI→ flea	rodent→ flea	RHU_Avg↔ pre	RHU_Avg↔ TEM_Avg	TEM_Avg↔ pre
1	0	1	0	0.290	0.520	0.294	−0.125	−0.230	−0.100	0.163	0.034	0.124	−0.056	−0.251	−0.120	0.642	−0.181	0.217
1	2	1	0	0.430	0.360	0.043	−0.182	−0.154	0.096	0.072	0.050	0.046	−0.147	−0.192	−0.132	0.642	0.399	0.623
1	2	1	1	0.228	0.473	0.273	0	−0.220	0.088	−0.006	0.001	0.076	−0.143	−0.148	−0.115	0.642	0.399	0.623
1	0	2	0	0.291	0.554	0.370	−0.122	−0.180	−0.054	0.107	0.106	0.142	−0.067	−0.289	−0.125	0.571	−0.181	−0.024
2	0	0	0	0.513	0.479	0.279	−0.196	−0.064	−0.064	0.072	0.166	0.142	0.069	−0.386	−0.120	−0.089	−0.470	0.408
2	1	0	0	0.441	0.453	0.428	−0.28	0.017	0.102	0.059	0.186	0.140	0.051	−0.427	−0.134	−0.089	−0.260	0.428
2	1	1	0	0.477	0.334	0.292	−0.253	0	0.094	0.024	−0.063	0.169	0.002	−0.273	−0.127	0.093	−0.470	0.217
2	1	1	1	0.391	0.494	0.431	−0.065	−0.053	0.048	−0.071	−0.081	0.210	0.053	−0.283	−0.102	0.093	−0.470	0.217
2	1	2	0	0.199	0.353	0.480	−0.249	−0.023	0.073	0.049	−0.018	0.155	0.008	−0.301	−0.127	0.374	−0.260	0.558
2	1	2	1	0.377	0.390	0.434	−0.126	−0.062	0.009	0.048	0.055	0.165	0.042	−0.352	−0.101	0.374	−0.260	0.558
2	2	0	0	0.521	0.396	0.364	−0.284	0.007	0.106	0.075	0.195	0.046	0.005	−0.369	−0.130	−0.089	−0.129	0.271
2	2	1	0	0.587	0.264	0.123	−0.236	−0.017	0.093	0.014	−0.007	0.028	−0.058	−0.221	−0.121	0.093	−0.129	0.623
2	2	1	1	0.410	0.432	0.405	−0.101	−0.035	0.105	−0.084	−0.048	0.085	−0.024	−0.211	−0.102	0.093	−0.129	0.623
2	2	2	0	0.369	0.197	0.250	−0.238	−0.032	0.076	0.040	0.088	−0.025	−0.092	−0.245	−0.122	0.374	−0.129	0.625
2	2	2	1	0.396	0.321	0.398	−0.159	−0.028	0.079	0.015	0.113	0.028	−0.046	−0.287	−0.101	0.374	−0.129	0.625
2	2	2	2	0.307	0.249	0.520	0.039	−0.089	−0.004	−0.060	0.062	0.019	−0.087	−0.202	−0.083	0.374	−0.129	0.625
2	0	1	0	0.580	0.402	0.326	−0.198	−0.068	−0.050	0.061	0.019	0.170	0.040	−0.299	−0.114	0.093	−0.470	0.217
2	0	2	0	0.489	0.319	0.425	−0.203	−0.091	−0.044	0.087	0.090	0.178	0.023	−0.338	−0.118	0.374	−0.470	−0.024