Host selection and influencing factors of parasitic fleas on the body surface of desert rodents, Inner Mongolia, China

Haiwen Yan [a,b,c,1], Fan Bu [a,b,c,1], Xinyu Wu [a,b,c], Haoting Zhang [a,b,c]
, Shanshan Sun [a,b,c], Wenke Bai [d], Xiaodong Wu [a,b,c], Shuai Yuan [a,b,c,**],
Heping Fu [a,b,c,*]

[a] College of Grassland and Resource Environment, Inner Mongolia Agricultural University, Hohhot, Inner Mongolia Autonomous Region, China
[b] Key Laboratory of Grassland Rodent Ecology and Rodent Pest Control, Hohhot, Inner Mongolia Autonomous Region, China
[c] Key Laboratory of Grassland Resources, Ministry of Education, Hohhot, Inner Mongolia Autonomous Region, China
[d] Key Laboratory of Southwest China Wildlife Resources Conservation, China West Normal University, Nanchong, 637009, China

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ABSTRACT

Fleas frequently parasitize rodents and serve as major vectors for many zoonotic diseases. The Alxa Desert in Inner Mongolia, China, is a typical arid region in Asia, which is suitable for the coexistence of a variety of rodents in this environment. Understanding the host selection of fleas among these rodents and the factors influencing this selection is crucial for comprehending rodent-borne diseases and the vector roles of fleas. This study utilized live-trap methods to capture rodents coexisting in the Alxa Desert from April to October 2022. Body surface fleas were collected and analyzed for abundance across different hosts, sexes, and reproductive statuses. The results indicated that: (1) there were significant differences in the species and abundance of parasitic fleas on different rodent species, with *Ophthalmopsylla kiritschenkoi* and *Mesopsylla hebes* preferring the *Dipus sagitta* and *Orientallactaga sibirica* as their hosts, and *Xenopsylla conformis* preferring *Meriones meridianus* as its host. (2) Fleas exhibited sex-preferential host selection, showing a greater preference for male hosts. (3) Among rodents of different reproductive states, most fleas prefer to parasitize individuals in non-reproductive periods. (4) The mean abundance of fleas varied significantly between seasons ($P < 0.05$), with spring and autumn being the peak periods for flea parasitism. (5) Factors influencing the mean abundance of fleas included host species, sex, reproductive status, and season, with host species having the greatest impact.

1. Introduction

Rodents are vital components of grassland ecosystems and serve as major hosts for fleas. The parasitic relationship between rodents and fleas is unique in ecology, as rodents provide both a food source and habitat for fleas (Sanchez and Lareschi, 2019). As in many host-parasite relationships, a single rodent can host various flea species on its body, and a single flea species can parasitize multiple rodent species (Xia et al., 1997; Kang, 2017). As primary ectoparasites on rodents, fleas can significantly impact their hosts' growth and development, and they are vectors for various zoonotic diseases such as murine typhus, rabbit fever, and plague (Xia et al., 2011), posing substantial threats to human health (Zhang, 2021).

Host animals provide fleas with a place to live, feed, reproduce, and engage in other activities. Different hosts offer varied conditions for flea survival and transmission. Consequently, fleas are influenced by multiple factors in their host selection (Smith et al., 2021). Research indicates that fleas evaluate the advantages and disadvantages of individual hosts to secure an environment conducive to their survival and reproduction (Balaz et al., 2019, 2021). For instance, differences in host species, sex, age, reproductive status, and physical condition can result in significant variations in the types and numbers of fleas parasitizing the host's body

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* Corresponding author. College of Grassland and Resource Environment, Inner Mongolia Agricultural University, Hohhot, Inner Mongolia Autonomous Region, China.
** Corresponding author. College of Grassland and Resource Environment, Inner Mongolia Agricultural University, Hohhot, Inner Mongolia Autonomous Region, China.
E-mail addresses: yanhaiwen@emails.imau.edu.cn (H. Yan), bufanimau@163.com (F. Bu), yuanshuai2020@163.com (S. Yuan), fuheping@126.com (H. Fu).
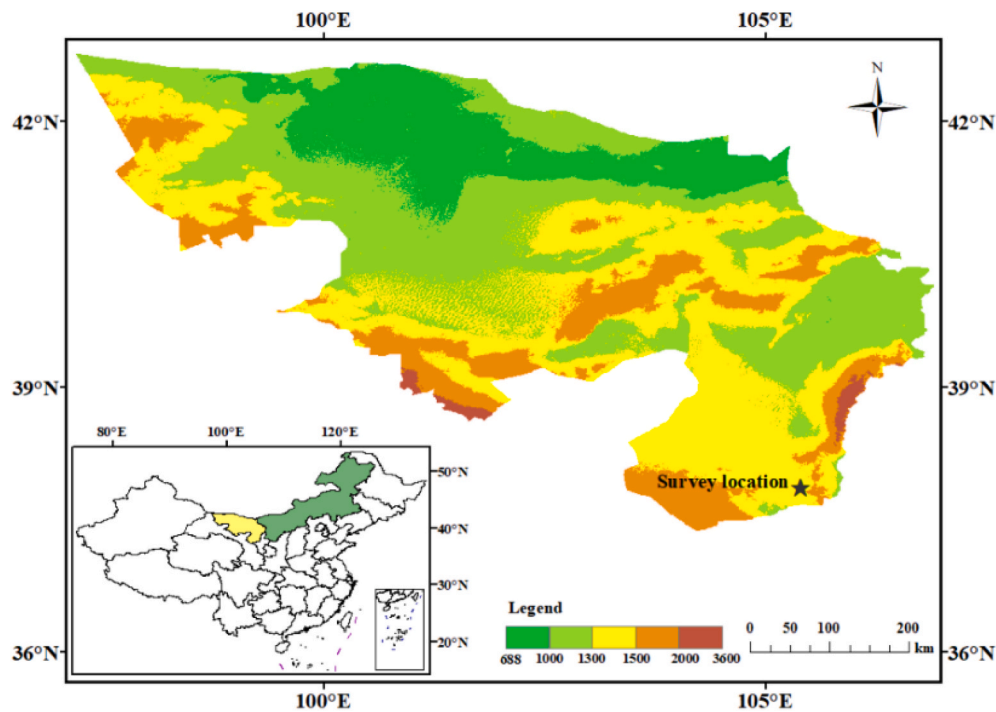[1] representing co-first authors.

Fig. 1. Map of the Alxa League, Inner Mongolia Autonomous Region, China. Note: The color indicates the altitude, the green area is 688~1300 m above sea level, the yellow area is 1300~1500 m, and the red area is above 1500 m. ★ Represent the survey location.

Table 1
Body size characteristics of five rodent species in the Alxa desert area.

Host species	Mass±SD	Length ±SD	Tail±SD	Ear Length ±SD	Hindfoot Length±SD
D. sagitta	83.63 ± 2.21	134.33 ± 2.14	125.66 ± 3.73	20.18 ± 0.97	51.52 ± 0.85
O. sibirica	93.79 ± 1.91	139.55 ± 1.82	177.30 ± 5.26	41.36 ± 1.05	61.64 ± 0.96
M. meridianus	56.07 ± 4.37	114.24 ± 4.35	90.65 ± 3.39	14.46 ± 1.48	27.41 ± 0.58
P. roborovksii	36.20 ± 6.00	83.15 ± 6.21	14.28 ± 2.08	13.85 ± 1.74	14.93 ± 1.26
S. alaschanicus	154.24 ± 5.05	180.63 ± 3.41	57.81 ± 2.58	6.15 ± 0.50	33.67 ± 0.84

Table 2
Rodent and flea catches and related variables.

Rodents	Flea species	MA	Prevalence (%)
Dipus sagitta 195: ♂142 ♀53	*O. kiritschenkoi*	1.02	32.82
	Mesopsylla hebes	0.55	25.64
	X.conformis	0.21	12.82
	N. laiveceps	0.09	5.64
	O. praefecta	0.07	5.13
	C. tesquorum mongolicus	0.01	0.81
Orientallactaga sibirica 94: ♂61 ♀33	*M. hebes*	0.89	35.11
	O. kiritschenkoi	0.41	25.53
	X.conformis	0.12	6.38
	O. praefecta	0.11	7.44
	N. laiveceps	0.01	1.06
Phodopus roborovksii 61: ♂36 ♀25	*O. kiritschenkoi*	0.84	31.15
	S. formozovi	0.20	4.92
	M. hebes	0.10	3.28
	N. laiveceps	0.03	1.64
	X.conformis	0.02	1.64
Meriones meridianus 37: ♂19 ♀18	*X.conformis*	3	70.27
	O. kiritschenkoi	0.43	18.92
	M. hebes	0.19	2.70
	N. laiveceps	0.14	8.11
Spermophilus alaschanicus 27: ♂15 ♀12	*C. tesquorum mongolicus*	1.63	40.74
	O. kiritschenkoi	0.33	7.40
	M. hebes	0.19	7.40
	X.conformis	0.07	3.70

surface (Abu-Madi et al., 2005; Warburton et al., 2021). Further, studies have demonstrated that flea distribution between juvenile and adult hosts is uneven, with adult hosts harboring more parasitic flea species and higher numbers than juveniles (Hawlena et al., 2005). Additionally, the mean abundance of flea species on male hosts' body surfaces is greater than that on female hosts (Krasnov et al., 2011; Kowalski et al., 2015; Hamidi and Bueno-Marí, 2021). In addition to host characteristics, host-specific selection by fleas is also influenced by factors such as changes in external environmental conditions (Gao et al., 2014). There are seasonal differences in the mean abundance and prevalence of different flea species, and such differences are due to their different adaptations to the environment. For example, studies have shown that the survival and reproductive abilities of different flea species vary with temperature, and their mean abundance is primarily influenced by temperature and humidity (Gong et al., 2005; Krasnov, 2008). Similarly, López-Pérez et al. (2018) found that the mean abundance of *Echidnophaga gallinacea* and *Pulex irritans* was significantly higher in spring than in autumn, whereas the mean abundance of *Pulex simulans* was significantly higher in autumn than in spring.

The Alxa Desert, part of the Afro-Asian desert belt, is a significant center for biodiversity in the arid regions of Eurasia (Pei et al., 2011;

Yan, 2012). The region has a typical plateau continental climate, characterized by sparse precipitation and long daylight hours, creating a high-temperature, low-humidity environment conducive to fleas. The rodent species in this area, mainly adapted to extreme arid desert habitats, provide a diverse parasitic environment for fleas. The primary rodent species include *Dipus sagitta*, *Orientallactaga sibirica*, *Meriones meridianus*, *Phodopus roborovksii*, and *Spermophilus alaschanicus* (Wu
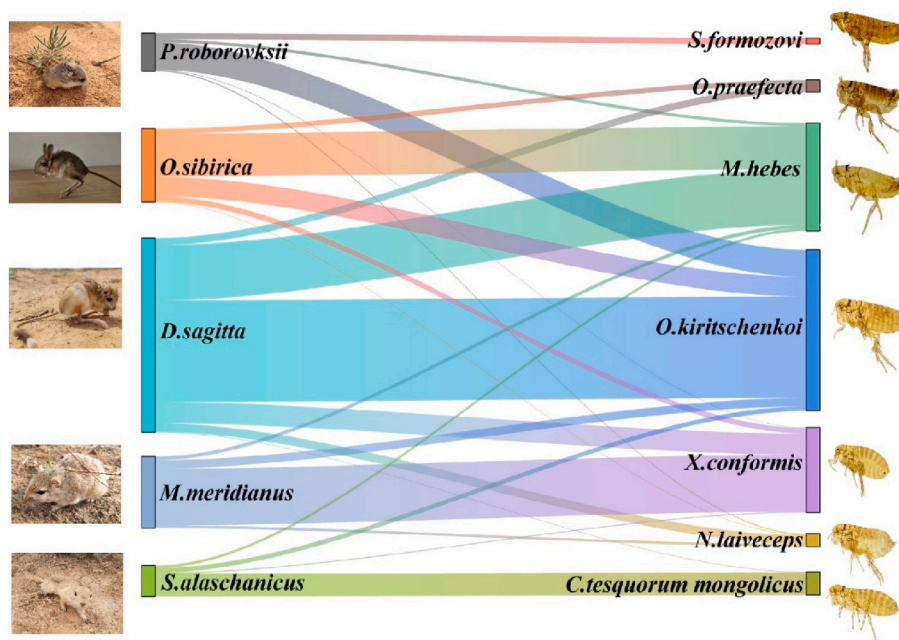
Fig. 2. Parasitic selection of rodents by fleas in desert areas. Note: There are five rodents on the left and seven fleas on the right. The connecting lines indicate the host-flea relationships, with thicker lines representing a greater number of fleas parasitizing the rodent's body surface.
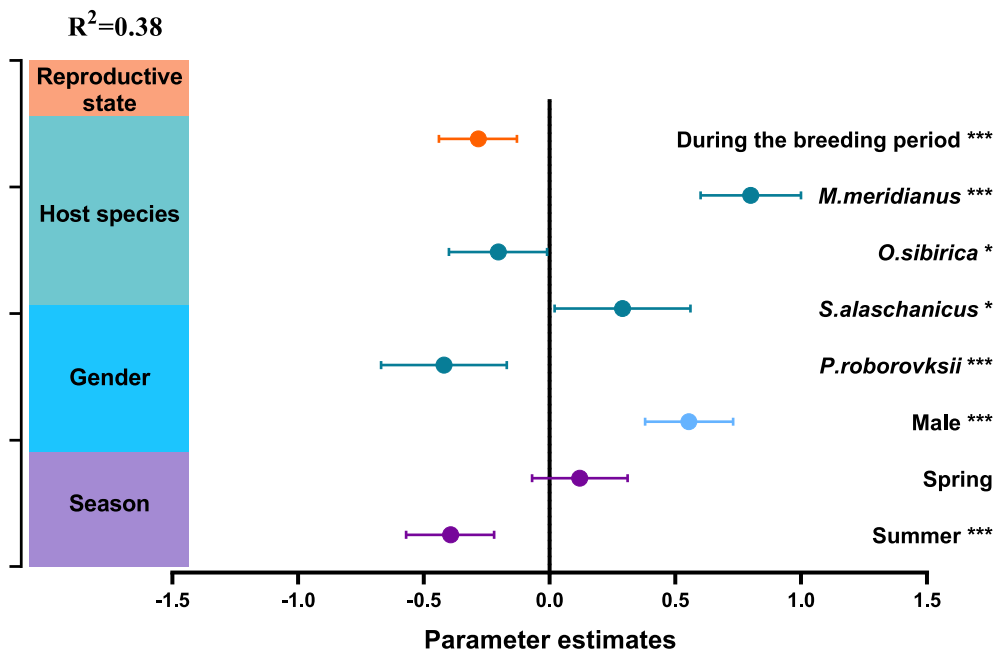

Fig. 3. Results of the GLMM showed multiple predictors affecting the MA of fleas. Note: The mean parameter estimates (standardized regression coefficients) of the model predictors and their associated 95% confidence intervals, as well as the relative importance of each predictor, are expressed as percentages of explanatory variance. The figure represents the best model (Table S1) selected based on AICc and model's Wi. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

et al., 2003).

To this end, we hypothesize that (1) there are differences in the species and abundance of five rodent body surface parasitic flea species with sympatric distribution in the Alxa Desert Region; (2) host characteristics (species, sex, and reproductive status) and seasons differently affect the mean abundance of various flea species; and (3) seasonal differences in the abundance of rodent surface-parasitic fleas in desert areas are related to environmental factors (temperature, humidity, and precipitation). In this study, we measured the rate of flea infestation in rodents and the mean abundance of different flea species, analyzing host characteristics and seasonal changes in spring, summer, and autumn. This analysis aimed to elucidate the selective parasitism of fleas on rodents in the Alxa Desert Region and identify factors influencing flea cross-co-parasitism and host selectivity. This information will contribute
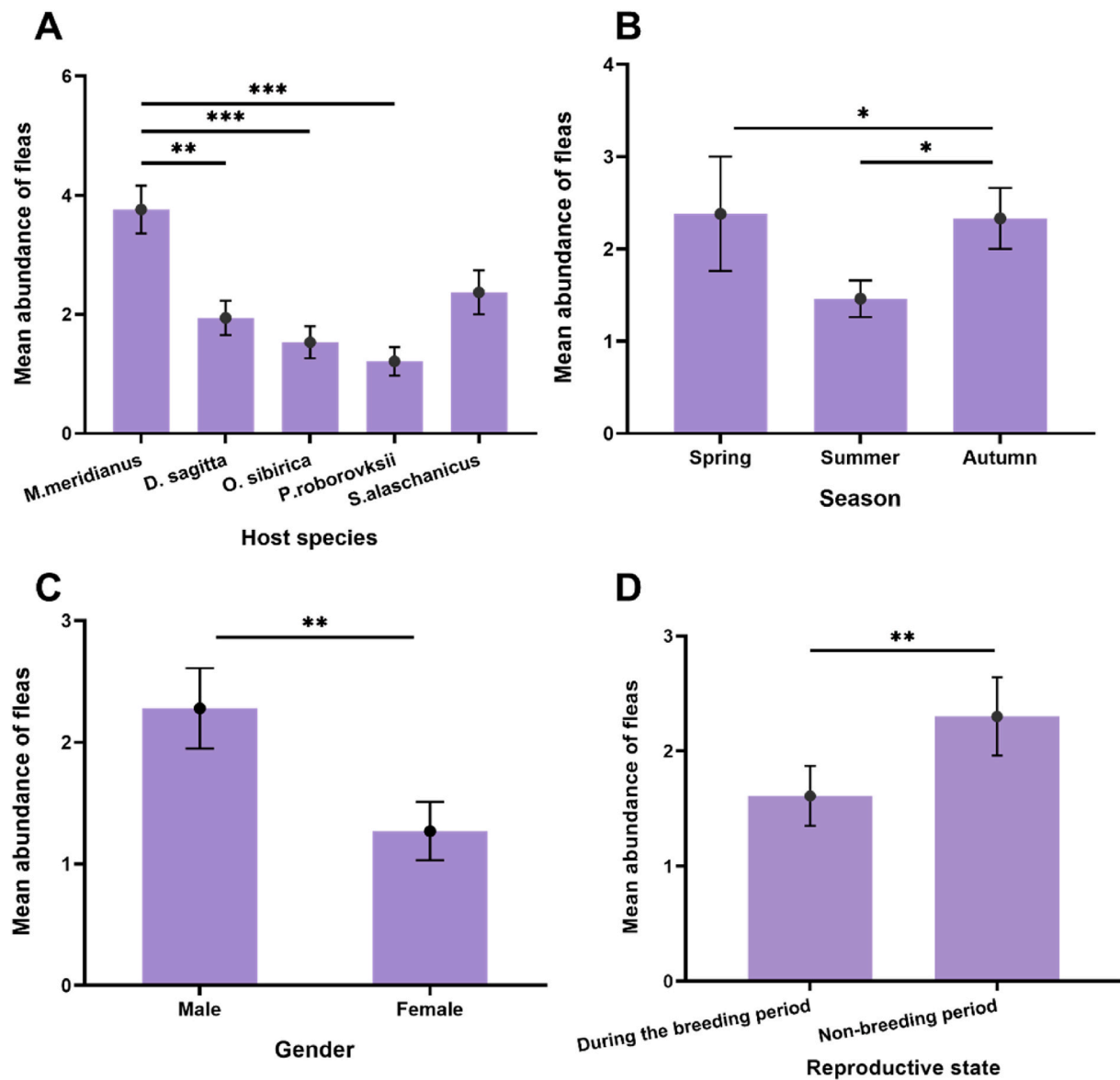
Fig. 4. The predictors analyzed for variance based on the results of the optimal model affecting the MA of fleas. Note: (A) Analysis of the mean abundance of fleas between different host species. (B) Analysis of the mean abundance of fleas between different seasons. (C) Analysis of the mean abundance of fleas between different sexes of the host. (D) Analysis of the mean abundance of fleas between different reproductive statuses of the host. $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

to regional rodent pest management, plague prevention, and control, reducing the risk of plague transmission.

2. Materials and methods

2.1. Study site

The study area (97°10′-105°30′E, 37°24′-38°25′N) is situated in the southern part of Alxa Left Banner, Inner Mongolia, at the eastern edge of the Tengger Desert, with an average elevation of 1050 m (Fig. 1). Annual precipitation ranges from 40 to 200 mm, while annual evaporation ranges from 3000 to 4700 mm, 15 to 117 times the precipitation. The vegetation is sparse and monotonous, with low coverage, generally only 1%–20%. Plant species are limited, primarily consisting of arid, super-arid, and saline shrubs, half-shrubs, small shrubs, and small half-shrubs, with fewer perennial grasses and leguminous pastures.

2.2. Data collection

From April to October 2022, five sample plots were randomly selected each month, with each plot spaced more than 500 m apart. Rodents were captured using a 7×8 grid-format cage deployment method, conducted in April–May (spring), June–August (summer), and September–October (autumn). One cage was placed at each grid point, resulting in 56 cages with 15-m spacing between them. Peanuts were used as bait, and the trapping was conducted over four days.

After recording the species and measuring the weights and other characteristics of the captured rodents, they were placed into a flea combing box ($50 \times 40 \times 40$ cm) and anesthetized with isoflurane. The rodents were then combed for fleas, and parasitic fleas were collected from their surfaces. The collected fleas were stored in 75% alcohol. After collecting all the fleas from the rodent's body, PITs (Passive Integrated Transponder tags) were injected subcutaneously into the neck for labeling, preventing recapture and subsequent experimental errors. Upon completion of these steps, the captured individuals were released in situ. Meteorological data were collected from an automatic weather station
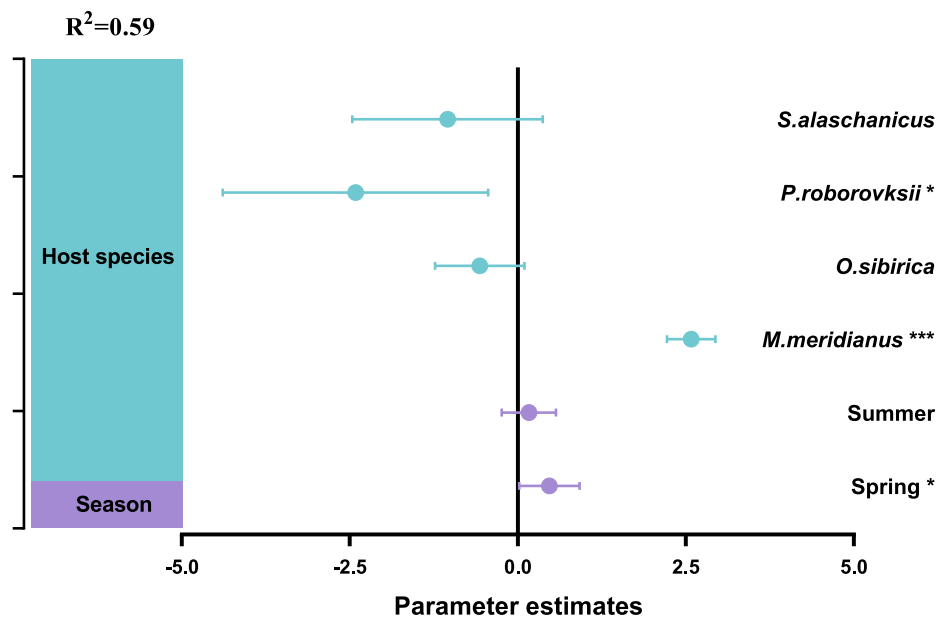
Fig. 5. Results of the generalized linear mixed-effects model showing multiple predictors affecting the MA of *X. conformis*. Note: The mean parameter estimates (standardized regression coefficients) of the model predictors and their associated 95% confidence intervals, as well as the relative importance of each predictor, are expressed as percentages of explanatory variance. The figure represents the best model (Table S1) selected based on AICc and model's Wi. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

(Campbell Scientific, CR1000) located 10 km from the sampling site.

2.3. Parasitic flea identification

In the laboratory, body surface parasitic fleas preserved in 75% alcohol were washed with distilled water and placed in a 10% sodium hydroxide solution to degrease and increase the transparency of the specimens. The fleas were then dehydrated using ethanol solutions at concentrations of 30%, 50%, 75%, 90%, 95%, and anhydrous ethanol, and sealed to make permanent specimens using neutral gum dissolved in xylene as a sealing solution. The samples were identified one by one using a compound microscope and following according to Insecta. Siphonaptera (Wu, 2007).

2.4. Data analysis

From the data obtained above, the prevalence and the mean abundance of each rodent species were calculated separately using the following formulae: Prevalence (%) = $A_i/A \times 100\%$; Mean abundance (MA) = B/A. where Prevalence is the flea-infestation rate, which represents the proportion of flea-infected rodents to the total number of rodents captured; A_i is the total number of flea-infested rodents, A is the total number of rodents captured, B is the total number of fleas on the body surface of the rodent, and MA is the mean abundance, which represents the density of parasitic fleas on the body surface of the rodent.

A generalized linear mixed effects model (GLMM) was used to fit the factors affecting the overall flea class and the mean abundance of dominant fleas, using the 'lme 4′ package in R. The "glmm" function in R to statistically analyze the data, with season, host species, sex and reproductive status (descending testes in male rodents were judged to be reproductive, vaginal openings and visible nipples in females were judged to be reproductive, and rodents without any of these characteristics were considered to be non-reproductive status (Lavrinienko et al., 2018; Manzano Nieves et al., 2019)). In the model, the mean abundance

of fleas collected throughout the year was used as the response variable for model group 1. The mean abundance of the dominant fleas was used as the response variable for the other model groups. Based on Akaike's information criterion, modified for small sample sizes, the best candidate model among all possible combinations of explanatory variables was determined using the "model.sel" function of the R package "MuMIn" (Perrin et al., 2023). Individual effects of predictors in the model were calculated using the 'glmm.hp' package (Lai et al., 2023). Multiple comparisons of mean flea abundance between seasons, host species, sex, and breeding status in linear mixed-effects models were conducted using the 'ghlt' function in the 'multcomp' package (Hothorn et al., 2008). Meteorological factors were correlated with mean flea abundance using the 'correlated' function in the 'Humisc' package and finally plotted using the 'ggplot 2′ package.

3. Results

3.1. Host selection results for parasitic fleas

In this study, we captured coexisting rodents belonging to five species from four families: *D. sagitta* (195 individuals) and *O. sibirica* (94 individuals) from the Dipodidae family, *P. roborovksii* (61 individuals) from the Circetidae family, *M. meridianus* (37 individuals) from the Muridae family, and *S. alaschanicus* (27 individuals) from the Sciuridae family, totaling 414 individuals. There were significant differences in body weight, body length, ear length, and hindfoot length among the five rodent species captured. *S. alaschanicus* was the largest, followed by *O. sibirica*, and the smallest was *P. roborovksii* (Table 1).

A total of seven flea species from 4 families were collected from the body surface of the captured rodents: *Mesopsylla hebes* (Leptopsyllidae Baker, Amphipsyllinae Ioff), *Ophthalmopsylla kiritschenkoi* (Leptopsyllidae Baker, Amphipsyllinae Ioff), *Xenopsylla conformis* (Pulicinae Billberg), *Ophthalmopsylla praefecta* (Leptopsyllidae Baker, Amphipsyllinae Ioff), *Nosopsyllus laeviceps* (Ceratophyllidae Dampf), *Citellophilus*
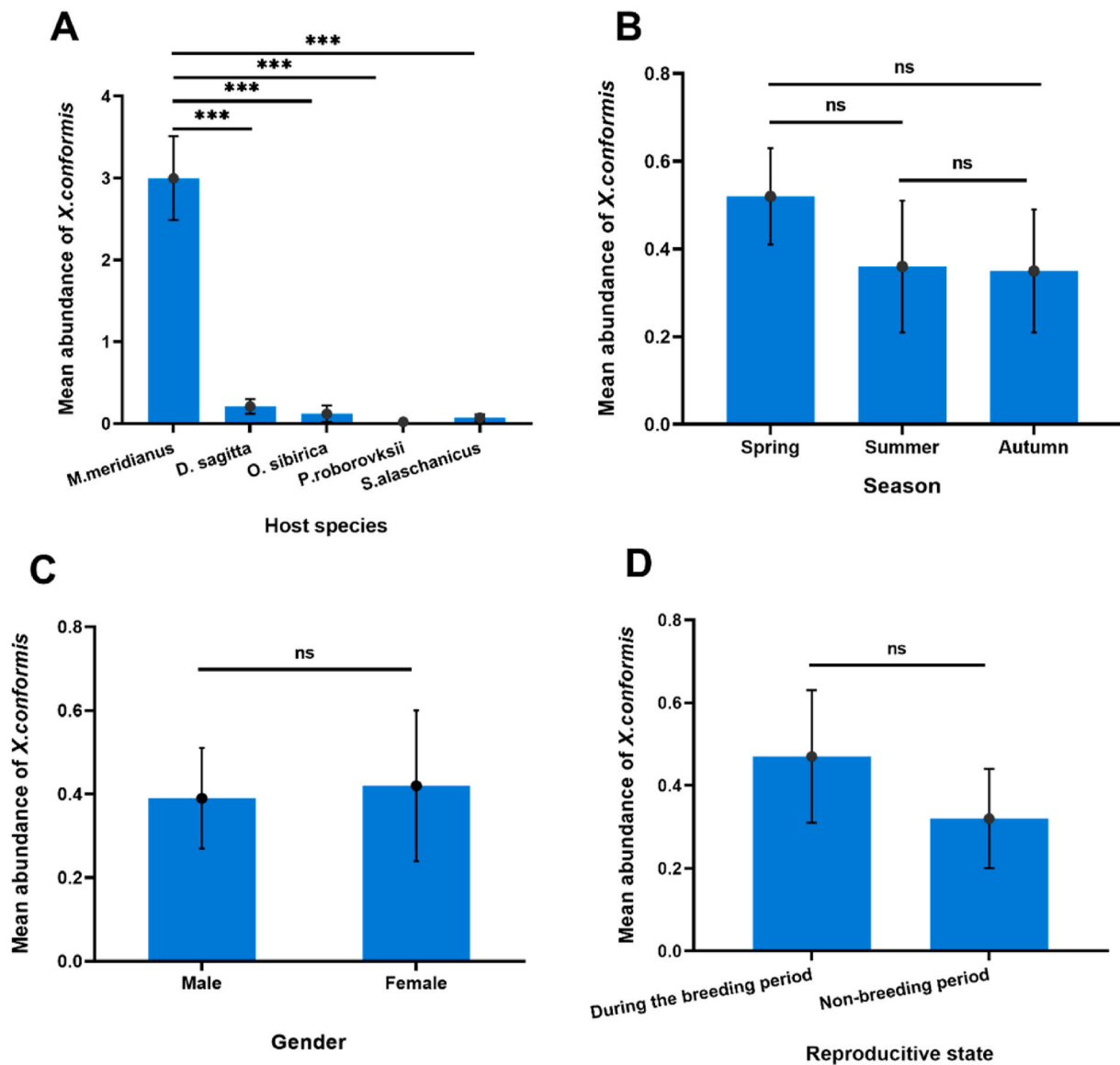
Fig. 6. The predictors analyzed for variance based on the results of the optimal model affecting the MA of *X. conformis*. Note: (A) Analysis of the mean abundance of *X. conformis* between different host species. (B) Analysis of the mean abundance of *X. conformis* between different seasons. (C) Analysis of the mean abundance of *X. conformis* between different sexes of the host. (D) Analysis of the mean abundance of *X. conformis* between different reproductive statuses of the host. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

tesquorum mongolicus (Ceratophyllidae Dampf), and *Stenoponia for-mozovi* (Ctenophthalmidae Rothschild, Stenoponiinae Cunha), amount-ing to 800 fleas (Table 2).

The species abundance and population distribution of rodent surface parasitic fleas coexisting in the Alxa Desert region are shown in Fig. 2. *O. kiritschenkoi*, *M. hebes*, and *X. conformis* are co-parasitic on the body surface of rodents. *O. kiritschenkoi* primarily parasitized *D. sagitta*, *O. sibirica*, and *P. roborovksii*. *M. hebes* was found on *D. sagitta* and *O. sibirica*, while *X. conformis* was found on *M. meridianus*. *S. formozovi* was only collected from *P. roborovksii*. *C. tesquorum mongolicus* primarily parasitized *S. alaschanicus*. A small number of *O. praefecta* were collected from Dipodidae family rodents, and a small number of *N. laeviceps* were collected from *D. sagitta*, *O. sibirica*, *M. meridianus*, and *P. roborovksii*.

3.2. Factors affecting the mean abundance of fleas

After selecting the optimal GLMM for the factors influencing the overall mean abundance of fleas (Table S1), the results indicated that host species, season, host sex, and host reproductive status all

significantly affected the mean abundance of fleas ($P < 0.05$) (Fig. 3). Contribution analysis of variables with significant effects revealed that host species was the primary factor influencing flea abundance (Fig. 3). The effects of different host species on flea abundance varied. *M. meridianus* and *S. alaschanicus* showing a significant positive corre-lation ($P < 0.05$), while *O. sibirica* and the lesser *P. roborovksii* showed a significant negative correlation ($P < 0.05$) (Fig. 3).

The mean abundance of fleas on the body surface of the *M. meridianus* was significantly higher than that on *D. sagitta*, *O. Sibirica*, and *P. roborovksii* ($P < 0.001$) (Fig. 4A). The mean abundance of flea species was significantly negatively correlated with summer (Fig. 3), being significantly lower in summer compared to spring and autumn ($P < 0.05$) (Fig. 4B). Comparing the flea abundance on male and female hosts, it was found that males had a significantly higher mean abun-dance of fleas than females ($P < 0.01$) (Fig. 4C). Interestingly, a signif-icant negative correlation ($P < 0.001$) was observed between reproductive status and mean flea abundance (Fig. 3). Hosts in repro-ductive status had a significantly lower mean abundance of fleas compared to non-reproductive hosts ($P < 0.01$) (Fig. 4D).
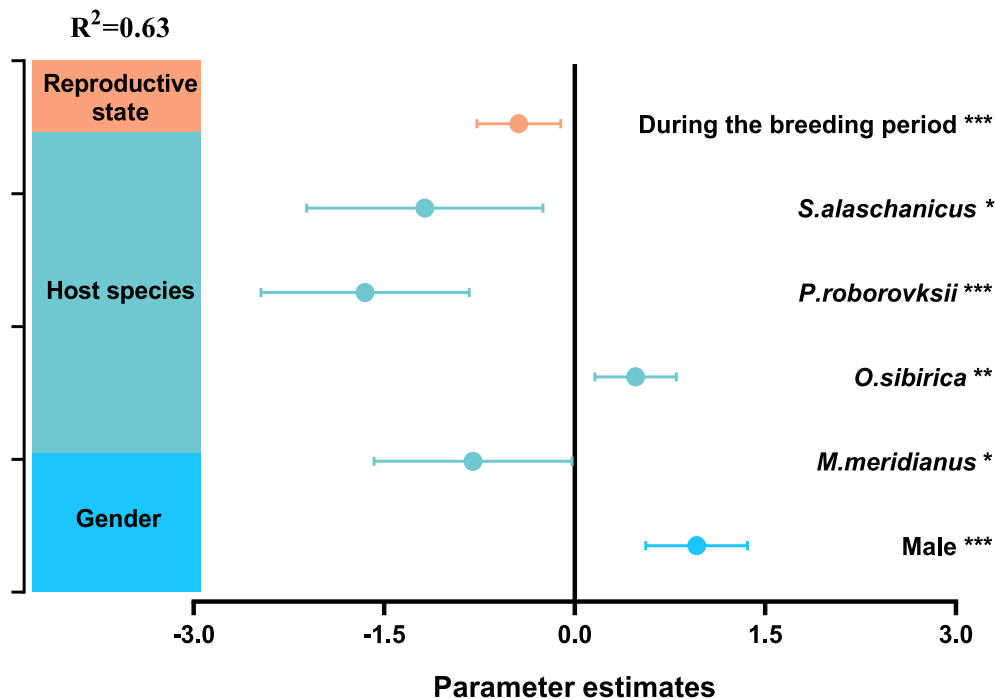
Mean abundance of *M.hebes*

Fig. 7. The results of the generalized linear mixed-effects model showed multiple predictors affecting the MA of *M. hebes*. Note: The mean parameter estimates (standardized regression coefficients) of the model predictors and their associated 95% confidence intervals, as well as the relative importance of each predictor, are expressed as percentages of explanatory variance. The figure represents the best model (Table S1) selected based on AICc and model's Wi. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

After selecting the optimal GLMM for the factors affecting the mean abundance of *X. conformis* (Table S1), the results showed that host species and season significantly influenced flea abundance ($P < 0.05$) (Fig. 5). Contribution analysis revealed that host species was the main factor influencing the mean abundance of *X. conformis* (Fig. 5). There was a significant positive correlation between the mean abundance of *X. conformis* and *M. meridianus* ($P < 0.001$) (Fig. 5).

Analysis of the mean abundance of *X. conformis* among different hosts showed that *M. meridianus* had a significantly higher mean abundance of *X. conformis* on its body surface compared to the other four rodent species ($P < 0.001$) (Fig. 6A). The mean abundance of *X. conformis* was higher in spring than in summer and autumn, but the difference was not significant (Fig. 6B). There were no significant differences in the mean abundance of *X. conformis* on the body surface of hosts of different sexes and reproductive statuses (Fig. 6C and D).

GLMM analysis showed that host species, sex, and reproductive status significantly affected the mean abundance of *M. hebes* ($P < 0.05$). Contribution analysis revealed that host species was the primary factor influencing the mean abundance of *M. hebes* (Fig. 7). There was a significant positive correlation between the mean abundance of *O. sibirica* and *M. hebes* ($P < 0.01$) (Fig. 7).

Analysis showed that the mean abundance of *M. hebes* on the body surfaces of *O. sibirica* was significantly higher than that on the body surfaces of *M. meridianus*, *P. roborovksii*, and *S. alaschanicus* ($P < 0.05$) (Fig. 8A). Mean abundance of *M. hebes* was highest in autumn, but there was no significant difference between seasons (Fig. 8B). The mean abundance of *M. hebes* on the body surface of male rodents was significantly higher than that on females ($P < 0.01$) (Fig. 8C). The mean abundance of *M. hebes* on the body surface of non-breeding hosts was significantly higher than that on breeding hosts (Fig. 8D).

The results of the optimal model analysis for the factors affecting the mean abundance of *O. kiritschenkoi* showed that host species, season, and sex all significantly influenced the mean abundance of this flea ($P < 0.05$) (Fig. 9). *O. sibirica*, *M. meridianus*, *P. roborovksii*, and *S. alaschanicus* were significantly negatively correlated with the mean abundance of *O. kiritschenkoi* ($P < 0.05$) (Fig. 9). Analysis of variance showed no significant differences in the mean abundance of *O. kiritschenkoi* among the different hosts (Fig. 10A). There was a significant negative correlation between spring and the mean abundance of *O. kiritschenkoi* ($P < 0.001$) (Fig. 9). The mean abundance of *O. kiritschenkoi* was significantly higher in spring and autumn than in summer ($P < 0.05$) (Fig. 10B). The mean abundance of *O. kiritschenkoi* on the body surface of male rodents was significantly higher than that on females ($P < 0.001$) (Fig. 9). There was no significant difference in the mean abundance of *O. kiritschenkoi* on the body surface of hosts with different reproductive statuses (Fig. 10D).

3.3. Analysis of meteorological factors affecting the mean abundance of fleas

Due to seasonal differences in the mean abundance of fleas, Spearman's correlation analysis was conducted to examine the relationship between the mean abundance of fleas and meteorological factors such as ambient temperature, humidity, wind speed, precipitation, and solar radiation (Fig. 11). The results showed that the overall mean abundance (MA) of fleas was significantly negatively correlated with ambient temperature and humidity (r = 0.17, P < 0.05; r = 0.11, P < 0.05). Conversely, the mean abundance of fleas was significantly positively correlated with wind speed (r = 0.13, P < 0.05), indicating that an increase in ambient temperature and humidity within a certain range
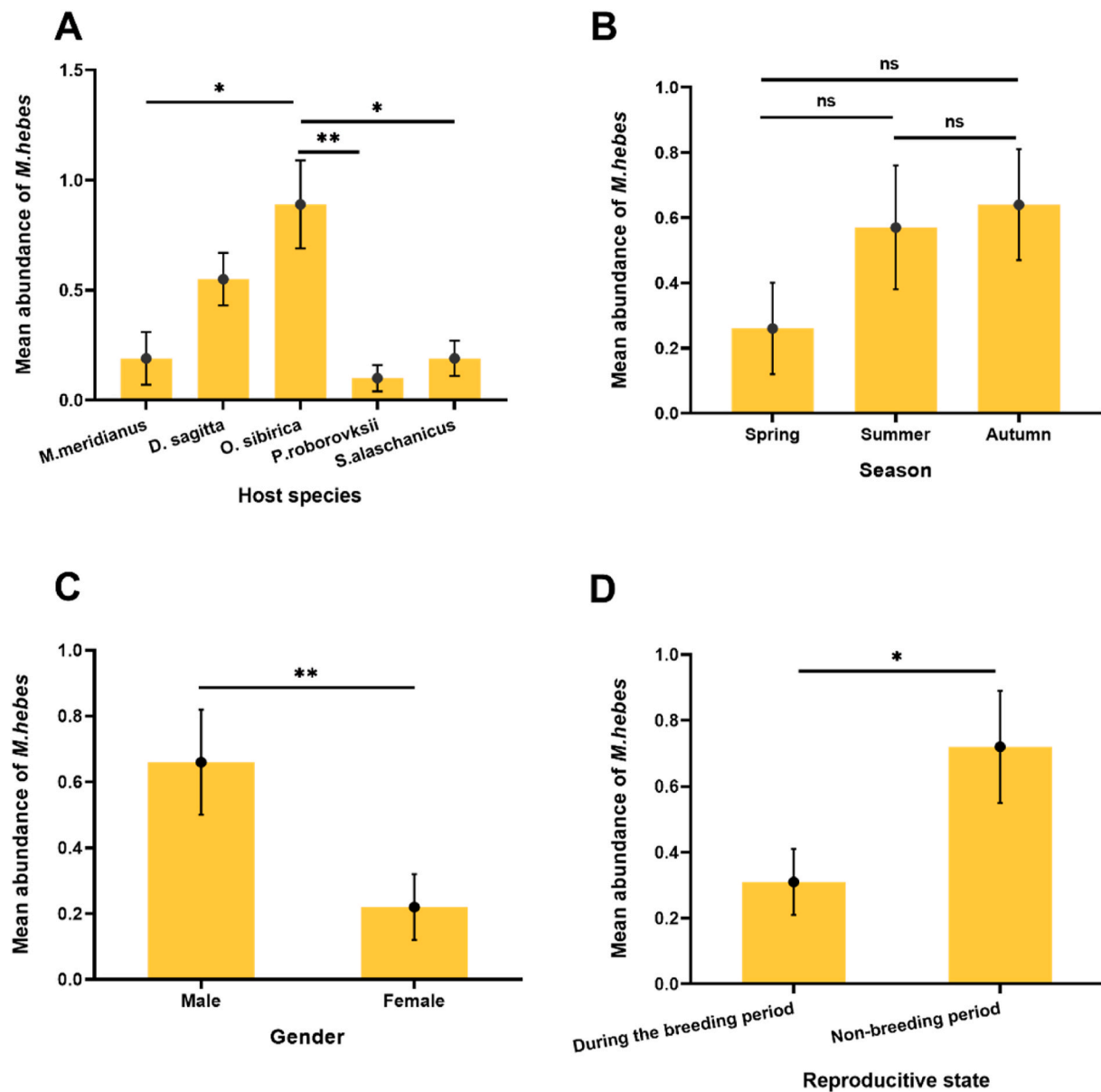
Fig. 8. The predictors were analyzed for variance based on the results of the optimal model affecting the MA of *M. hebes*. Note: (A) Analysis of the mean abundance of *M. hebes* between different host species. (B) Analysis of the mean abundance of *M. hebes* between different seasons. (C) Analysis of the mean abundance of *M. hebes* between different sexes of the host. (D) Analysis of the mean abundance of *M. hebes* between different reproductive statuses of the host. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

decreases the mean abundance of overall fleas, while an increase in wind speed increases the abundance of parasitic fleas on rodents' body surfaces. The correlations between the mean abundance of *X. conformis* and temperature and humidity, wind speed, rainfall and sunshine duration were not significant ($P \geq 0.05$). The mean abundance of *M. hebes* was significantly positively correlated with wind speed ($r = 0.12$, $P < 0.05$), while correlations with other meteorological factors did not reach significance ($P \geq 0.05$). This suggests that higher wind speed increases the mean abundance of *M. hebes* on rodents' body surfaces. The mean abundance of *O. kiritschenkoi* was significantly negatively correlated with temperature and humidity ($r = 0.17$, $r = 0.13$, $P < 0.05$). Correlations with other meteorological factors did not reach significance ($P \geq 0.05$). The abundance of *O. kiritschenkoi* on rodent body surfaces declined when ambient temperature and humidity increased within a certain range.

4. Discussion

Parasitic fleas on the body surfaces of five rodent species coexisting in the desert region differed significantly. *M. hebes*, *O. kiritschenkoi*, and *X. conformis* are widely distributed on the body surfaces of these five rodent species. However, significant differences were observed in the mean abundance of these three flea species on different host body surfaces. The mean abundance of *M. hebes* was highest on *O. sibirica*, indicating a preference for this host. The mean abundance of *O. kiritschenkoi* was highest on the body surfaces of *D. sagitta* and *P. roborovksii*, suggesting a preference for these two rodents. *M. meridianus* had the highest mean abundance of homomorphic passenger fleas on its body surface, indicating a greater preference for this host. *C. tesquorum mongolicus* is highly selective for *S. alaschanicus*, and *S. formozovi* was found only on *P. roborovksii*, demonstrating the obvious selectivity of fleas for their host species. These observations are consistent with observations that flea populations can be determined by host
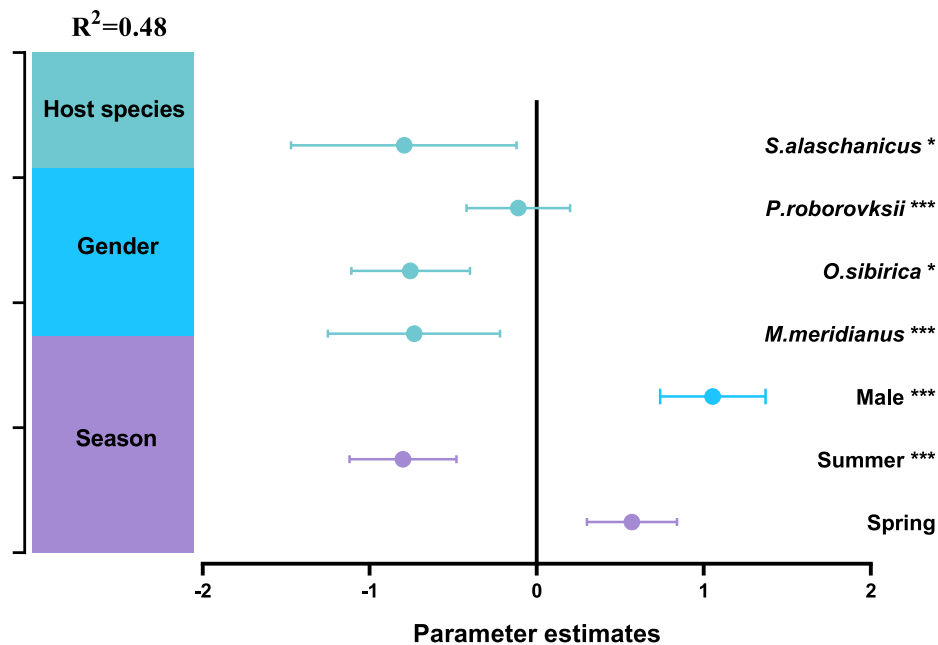
Fig. 9. Results of GLMMs showed multiple predictors affecting the MA of *O. kiritschenkoi*. Note: The mean parameter estimates (standardized regression coefficients) of the model predictors and their associated 95% confidence intervals, as well as the relative importance of each predictor, are expressed as percentages of explanatory variance. The figure represents the best model (Table S1) selected based on AICc and model's Wi. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

species. Vashchenok (2006) also showed that the species composition of parasitic fleas on rodent body surfaces is correlated with the host species. These results indicate significant differences in the attractiveness of different hosts to fleas (Acosta-Gutiérrez, 2014; Escalante et al., 2014), with fleas typically choosing host species that are suitable for their survival and reproduction. By examining the variation in abundance-prevalence relationships among 17 different flea-host combinations and between different species of hosts and fleas in the Negev Desert, it was found that the prevalence, mean abundance, and abundance variance of host-specific fleas were significantly higher than those of host-opportunistic fleas (Krasnov et al., 2005b).

In this study, we found that *D. sagitta* hosted the largest number of flea species on its body surface, with a total of six species. Previous studies have shown that *D. sagitta* in Inner Mongolia can be parasitized by up to nine flea species simultaneously (Yang et al., 2008). Among these, *N. laeviceps* and *X. conformis* have been proven to transmit plague (Yang et al., 1994; Li et al., 2000; Li et al., 2002). Individual fleas can migrate from one host to another through host-to-host interactions, host burrow replacement, or free dispersal (Balaz et al., 2021). Therefore, we believe the high flea density is related to the life habits of *D. sagitta*, which typically lives in a wide range without a fixed nest, choosing burrows opportunistically to hide or rest during predation (Zhao, 1964). Often, this opportunistic behavior means that *D. sagitta*'s body surface can be contaminated with parasitic fleas from other rodent species in the same area (Fu et al., 2005; Wang et al., 2020). Thus, In the event of an inter-rat plague, *D. sagitta* is more susceptible to plague infection than other rodent species, resulting in the spread of plague over long distances (Li et al., 2005). The high rate of flea infestation and mean flea abundance in *M. meridianus* observed in this study is largely related to the fact that *M. meridianus* are gregarious rodents that often congregate in small habitat patches, resulting in high inter-individual contact that provides favorable conditions for the transmission of fleas and thus, plague (Song and Liu, 1984). Additionally, the five rodent species captured differed significantly in characteristics such as body weight, body length, and ear length (Table 1). We believe this contributes to the

significant differences in parasitic flea abundance among rodents. Studies have shown that larger body weight in hosts is associated with higher flea abundance (Zduniak et al., 2023). Larger host body size can also reduce competition, create more ecological niches, and allow better resource partitioning, thereby providing a suitable environment for parasitic fleas to survive (Kiffner et al., 2014). Krasnov et al. (2003) studied the survival status of body fleas in a wide range of rodent species coexisting in the desert and found that a number of physiological and biochemical differences between hosts can lead to significant ecological differences in host-parasite relationships.

Both host sex and reproductive status can influence flea parasitism. Male rodents significantly and positively affected the mean abundance of overall fleas, *M. hebes*, and *O. kiritschenkoi*, suggesting that fleas prefer male hosts. Male rodents are reported to be more active and have a wider range of activities than females, resulting in higher flea infestation rates and mean flea abundance in males (Herrero-Cófreces et al., 2021), which increases the risk of disease transmission. It has been suggested that the reproductive status of the host may differentially affect flea dynamics based on the host's sex (Klein, 2004). In the present study, we also found a negative correlation between the reproductive status of the host and the mean abundance of fleas, suggesting that fleas do not prefer to parasitize the body surface of reproductive hosts, which is in line with the findings of Klein et al. Klein et al. (1999), that reproduction is an energy-demanding activity in mammals, and that during pregnancy, and especially during lactation, energy requirements increase, thus failing to meet the energy needs of the body surface parasites, leading to a decrease in parasite infestation rates. It is also possible that changes in sex hormone levels and immune status of the host during reproduction negatively affect flea infestation (Romano et al., 2015).

Mean abundance and species of fleas varied between seasons (Krasnov et al., 2005a; Gálvez et al., 2017). Our study found that the overall mean abundance of fleas was highest in spring and autumn, while lowest in summer. The decreasing seasonal trend between June and September in mites and fleas may result from biological properties, the study period ranging from the decline following the first peak in
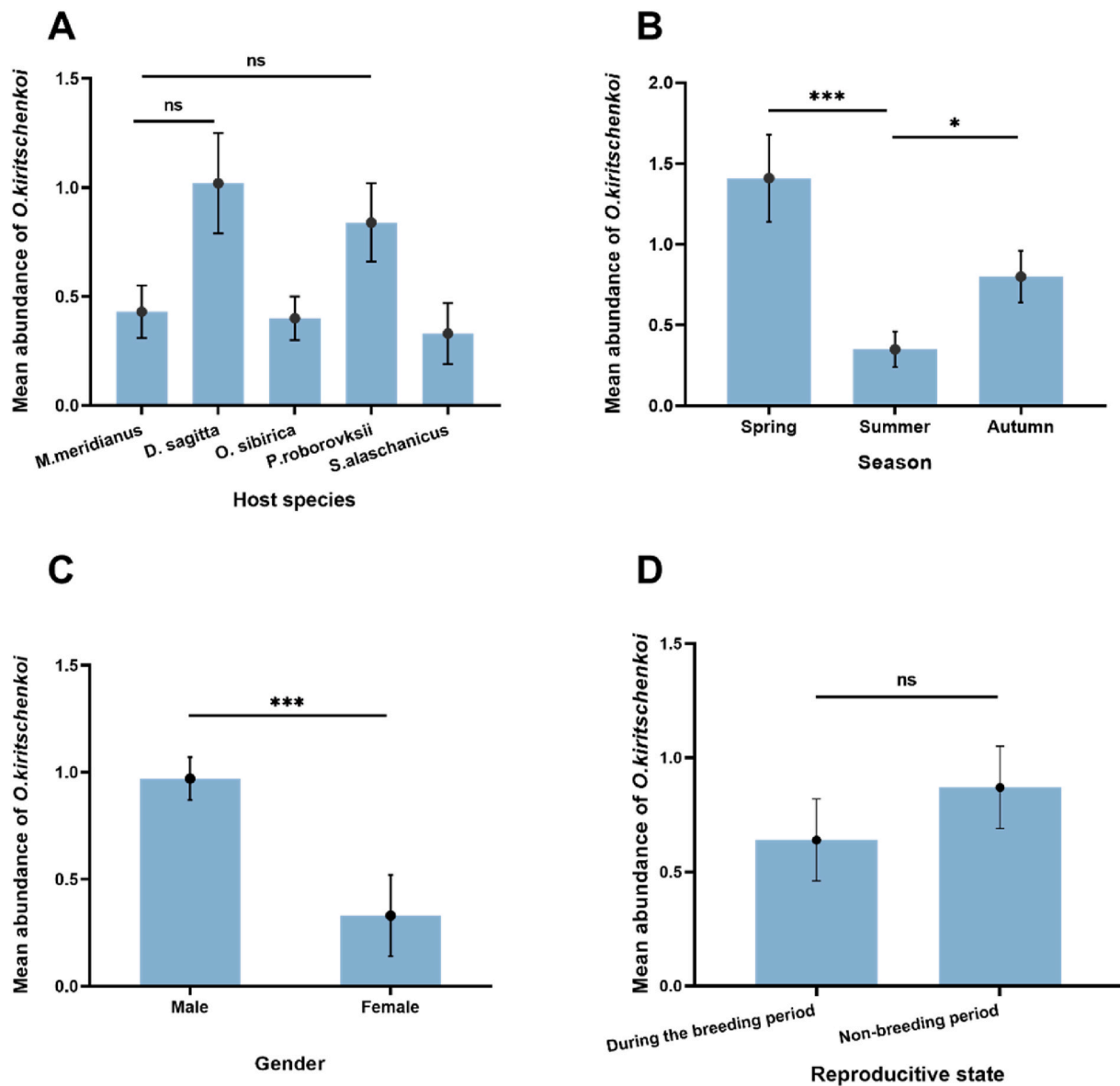
Fig. 10. The predictors were analyzed for variance based on the results of the optimal model affecting the MA of *O. kiritschenkoi*. Note: (A) Analysis of the mean abundance of *O. kiritschenkoi* between different host species. (B) Analysis of the mean abundance of *O. kiritschenkoi* between different seasons. (C) Analysis of the mean abundance of *O. kiritschenkoi* between different sexes of the host. (D) Analysis of the mean abundance of *O. kiritschenkoi* between different reproductive status of the host. $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

spring to the second peak in autumn (Benedek et al., 2024). Studies by many others have similarly found that the average abundance of fleas on the animal's body surface is at a low peak during the summer (Durden et al., 2005; Gálvez et al., 2017; Hamidi and Bueno-Marí, 2021). This is related to flea habits, as an increase in temperature within a certain range (15–20 °C) increases the number of parasitic fleas on the host's body surface, enhancing their survival (Moore et al., 2015). The survival rate of parasitic fleas will increase under suitable temperature. Liu (1986) suggests that the peak activity of fleas on animal bodies occurs in the warm season. However, excessively high temperatures are unfavorable for flea survival, consistent with this study's finding of a significant positive correlation between mean flea abundance and temperature. This is consistent with the literature - the survival and reproductive abilities of different fleas vary under different temperatures and humidity. The survival rate of *X. cheopis* is highest at 24 °C and 85% relative humidity (Kang et al., 2020), while *Leptopsylla segnis* shows high survival at 19.4 ± 2.5 °C and 75.9 ± 5.9% relative humidity, with peak reproduction occurring in winter (He et al., 1996).

It was found that the abundance of fleas was higher in the wet season compared to the dry season (Laudisoit et al., 2009). Ming et al. (2023) also found temperature, and humidity are key factors influencing flea abundance on small mammal. The Alxa Desert has four distinct seasons, with mean temperatures of 16.8 ± 5.5 °C in spring and autumn, and 25.05 ± 4.2 °C in summer, with maximum temperatures of up to 40 °C (Liu, 2023). The high summer temperatures exceed optimal conditions for flea survival and reproduction, and consistent with this, we observed the lowest mean abundance of overall fleas, *O. kiritschenkoi*, and *X. conformis* during the summer. Wind speed was significantly and positively correlated with mean abundance of parasitic fleas, Martínez-de la Puente et al. (2009) found a significant negative correlation between wind speed and the abundance of parasites in bird nests, supporting our hypothesis that higher external wind speeds are unfavorable for flea survival in nests. Consequently, fleas prefer to parasitize the host's body surface to obtain a safer and more stable environment. Current studies on the effect of wind speed on flea abundance have mainly focused on birds, with few studies on fleas parasitizing rodents.
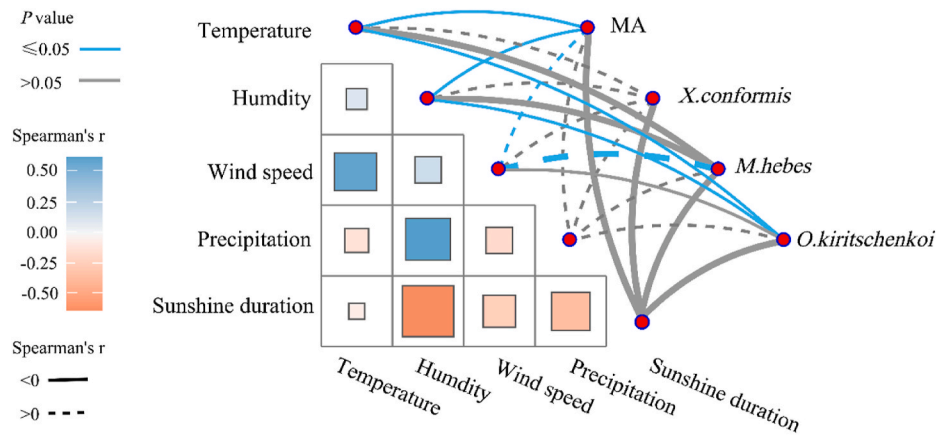
Fig. 11. Correlation plot of mean abundance of fleas with climatic factors. Note: The different tones represent the relevant values for Spearman. The boundary hue represents the level of statistical relevance. use a solid line for a positive correlation, a dashed line for a negative correlation, a blue line for a significant correlation, and a grey line for a non-significant correlation.

Our findings suggest that spring and autumn in the Alxa Desert are more favorable for flea survival, potentially increasing the risk of plague transmission during these seasons.

This study on the selective parasitism of desert rodent body fleas and the factors influencing their parasitism provides an important ecological baseline for future research and the prevention of rodent-borne diseases in the region. Host sex, reproductive status, and species can all influence flea richness and abundance. Additionally, the abundance of parasitic fleas on rodents' surfaces rises during the summer months. The presence of five species of co-parasitic fleas on the body surfaces of five rodent species coexisting in the same area, including *X. conformis*, *N. laeviceps*, and *C. tesquorum mongolicus*, which have been shown to transmit the plague bacillus, poses a potential epidemic risk. This indicates that cross-infection between rodents and fleas is likely in this area. Although there have been no reports of plague in this area, close monitoring is necessary to prevent the spread of the disease.

CRediT authorship contribution statement

Haiwen Yan: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation. **Fan Bu:** Writing – original draft, Supervision, Methodology, Investigation. **Xinyu Wu:** Supervision, Methodology, Investigation. **Haoting Zhang:** Visualization, Software, Methodology, Conceptualization. **Shanshan Sun:** Resources, Investigation. **Wenke Bai:** Funding acquisition. **Xiaodong Wu:** Supervision, Project administration, Funding acquisition. **Shuai Yuan:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Heping Fu:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

All authors disclosed no relevant relationships.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijppaw.2024.100993.

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