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Biology and morphometric relationship of gall inducers *Contarinia* sp. and corresponding parasitoids for swollen galls of *Nitraria sibirica* pall

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Abstract

Galls function as provide shelter for gall inducers, guarding them against their natural enemies. Previous research has illuminated the interactions between galls, gall inducers, and their corresponding parasitoids within various caltrop plants. However, less is known about these relationships within *Nitraria sibirica*, particularly regarding the efficacy of parasitism. Therefore, this study aimed to identify the morphometric relationships among the swollen galls, gall inducers, and their parasitoids. Two species of gall inducers and three species of parasitoids were obtained from the swollen galls of *N. sibirica*. The correlations of the parasitization indexes, the lifespan of gall inhabitants, and temperature and the morphometric relationships between the galls and their inhabitants were analyzed. The dominant gall inducer identified was *Contarinia* sp. (Diptera: Cecidomyiidae). Furthermore, it was observed that three solitary parasitoids attacked *Contarinia* sp. in the swollen galls, with only *Eupelmus gelechiphagus* acting as an idiobiont ectoparasitoid. The dominant parasitoids were *Platygaster* sp. and *Cheiloneurus elegans* at sites 1 and 2, respectively, with *Platygaster* sp. displaying greater abundance than *C. elegans* in the swollen galls. The lifespan of the gall inhabitants shortened gradually as the temperature increased. Moreover, the optimal number of gall chambers ranged from two to four per swollen gall with maximized fitness, which can be considered the optimal population density for the gall inducer *Contarinia* sp. Morphometric analysis exhibited a strong linear correlation between gall size and chamber number or the number of gall inhabitants, as well as a weak correlation between gall size and body size of the primary inhabitants of swollen galls. Our results highlight the importance of the biological investigation of parasitoids and gall inducers living in closed galls with multiple chambers and may pave the way for potential application in biological control.

Introduction

Galls, formed in response to irritation from inducing organisms, occur in most plants, with insects being the major producers of galls. Insects can cause abnormal growth of tissues and change the external morphology into diverse and complex structures (Stone and Schonrogge, 2003; Miller and Raman, 2019; Chauhan *et al.*, 2020). Approximately 21,100 species of galling insects have been recorded in numerous types of galls, which have unique shapes and a wide range of variation (Price *et al.*, 1987; Espirito-Santo and Fernandes, 2007). Different gall inducers can yield variant galls on related plant species, and the same gall inducers may produce different galls across various plants. Despite this variability, many gall inducers show high specialization toward their host plants, often belong to the same species or genus (Stone and Schonrogge, 2003; Wang *et al.*, 2010; Sevarika *et al.*, 2021).

Owing to the rich nutrients that are stored in most Zygophyllaceae plants (caltrops) as an adaptation to xeric environments, many insects prefer to produce galls in these plants to provide themselves with shelter and protection (Fernandes *et al.*, 2022). *Nitraria sibirica* Pall. (Zygophyllaceae) is a typical woody halophyte that is known as 'the king of desert vegetation' because of its cold and salt tolerance and strong adaptability to drought (Li *et al.*, 2017, 2020; Gu *et al.*, 2018). These characteristics make it a useful plant for wind prevention and sand fixation in deserts. Moreover, the ecological functions of *N. sibirica* plants, such as adjusting the local climate and increasing biodiversity, are irreplaceable (Ren and Lv, 2020). The leaves and fruits of *N. sibirica* have long been used as natural remedies for indigestion, irregular menses, and hypertension in the Middle East and Central Asia, indicating their ethnopharmacological relevance. In particular, in the northwest region of China, these plants are recommended for treating hypertension (Turghun *et al.*, 2020; Voronkova *et al.*, 2020). Therefore, conserving *N. sibirica* in natural ecosystems is imperative, not only for desertification control but also to ensure its medicinal availability.

There is broad consensus in the literature stating that gall midges are the most widespread gall-forming insects in caltrop plants. More than 20 species of gall midges belonging to six genera have been recorded in Zygophyllaceae. *Contarinia* Rondania is a large, cosmopolitan genus in the supertribe Cecidomyiidi, and many female midges of this genus oviposit in the shoots, buds, or leaves of host plants, where the larvae feed and develop (Uechi *et al.*, 2003; Kolesik and Gagné, 2020). *Contarinia nitrariae* Fedotova, *Contarinia nitrariagemmae* Fedotova (Diptera: Cecidomyiidae), and *Trilobophora nitrariae* Marikovskij (Diptera: Cecidomyiidae) have been collected on *Nitraria* spp. in Kazakhstan (Gagné and Jaschhof, 2021). Although more than 30 species of pests can damage *Nitraria* spp. in desert forests worldwide, only a few pests are associated with the galls on *Nitraria* (Li and Liu, 1993; Morse, 2003; Kravchenko *et al.*, 2006). *Diaspidiotus roseni* Danzig. (Hemiptera: Diaspididae) is considered to be a gall inducer of *Nitraria* in Israel (Danzig, 1999). In addition, five species (*Eremocampe nitrariae* Sugonjaev, *Mongolocampe bouceki* Sugonjaev, *M. kozlovi* Sugonjaev, *M. trjapitzini* Sugonjaev, and *M. zhaoningi* Yang) belonging to the subfamily Mongolocampinae (Hymenoptera: Chalcidoidea) have been reported to damage the leaves of *Nitraria* spp. (Sugonjaev, 1971; Yang, 1990; Sugonjaev and Voinovich, 2003). The parasite *Aphaniosoma* sp. (Chyromyidae) has been reported in gall-like swellings on the leaves of *Nitraria* spp. (Sugonjaev, 1971, 1974; Abrahamson *et al.*, 1983). However, previous studies have not provided convincing evidence to support that these insects were the induces of the swollen galls, and little information is available about the dominant species of gall inducers, especially gall midges.

Currently, efforts to control sheltered gall inducers have had limited success through the extensive application of insecticides (Stone and Schonrogge, 2003; Singh and Yadav, 2007; Bhandari and Cheng, 2016). Furthermore, insecticide use is not a sustainable control measure as it causes adverse effects on beneficial non-target organisms (Passos *et al.*, 2018; Soares *et al.*, 2019). Thus, a more effective and eco-friendly pest management method that uses fewer chemical insecticides is needed. Biological control is a vital component of integrated pest management, and utilizing parasitic natural enemies is a promising way to control pests in agricultural and forest ecosystems (Wang *et al.*, 2019; Masry and El-Wakeil, 2020; Harush *et al.*, 2021). Several studies have reported biological control using chalcidoid parasitoids, which were thought to be effective agents for the biological control of important forest pests worldwide (Tunca *et al.*, 2019; Haeussling *et al.*, 2021; Riaz *et al.*, 2021). Studies clarifying the host–parasite relationship between the Asian chestnut gall wasp *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae) and its natural enemy *Torymus sinensis* Kamijo (Hymenoptera: Torymidae) have provided convincing evidence to support biological control methods (Yara *et al.*, 2010; Quacchia *et al.*, 2013; Avtzis *et al.*, 2018; Ferracini *et al.*, 2019; Gil-Tapetado *et al.*, 2021). Increasing evidence has also indicated that the major factors affecting integrated pest management strategies include the entomic species composition, abundance of natural enemies, and host size (Dhawan *et al.*, 2009; Daniel and Grunder, 2012; Bhede *et al.*, 2014). Nevertheless, studies on the parasitoids of galls on *N. sibirica* have not been conducted.

The gall–inducer–natural enemy system is an excellent model to study the nutritional relationships among plants, insects, and their natural enemies. Such study may provide a strong theoretical basis for the biological control of gall inducers and help to unravel the complex web of their interactions (Price *et al.*, 1987; Stone and Schonrogge, 2003; Compton *et al.*, 2018; Martini *et al.*, 2021; Michell and Nyman, 2021). To date, no agreement has been reached about gall formation and its relation to gall inducers (Diamond *et al.*, 2008; Bannerman *et al.*, 2012; Laszlo and Tothmeresz, 2013; Miller and Raman, 2019; Ramos *et al.*, 2019). Generally, the gall inducers seem to control gall development by affecting the articulated metabolic pathway of the plants, creating a protective and beneficial structure to serve as shelter and food, in which they are defended against natural enemies and spend most of their preimaginal instars (Price *et al.*, 1987; Cooper and Rieske, 2010; Tooker and Giron, 2020). As a result, the gall inducers may evolve highly specialized nutritional dependencies on their host plants. The relationships between the gall characteristics (gall volume, chamber number, and chamber density) and gall inhabitants (emerged gall inducers, parasitoids, and body length) were found to have a canonical correlation (Weis, 1993; Ozaki, 2000; Laszlo *et al.*, 2014; Aguirrebengoa *et al.*, 2022). In addition, the interactions between galling insects and their parasitoids are complex, and the principal factor influencing gall inducer mortality is parasitoid attacks. Successful attacks from parasitoids on gall inducers depend on the gall size, chamber number, and chamber density (Laszlo *et al.*, 2014; Hernandez-Lopez *et al.*, 2021). Despite the potential of insect galls as model systems, gall induction and the species richness of galls on *N. sibirica* are still poorly understood.

A preliminary survey was performed in north Xinjiang in 2016, and the galls on *N. sibirica* induced by the gall midge *Contarinia* sp. were investigated. However, limited information was obtained about the relationships among the galls, gall inducers, and corresponding parasitoids. In the present study, we hypothesized that closed galls with limited space limit the quantity and size of inhabitants of *N. sibirica* galls. We aimed to evaluate the occurrence and degree of damage by swollen galls on *N. sibirica* and determine the potential resources of gall inducers and their parasitoids. This allowed us to identify the morphometric relationships among the swollen galls, gall inducers, and their parasitoids and to clarify the biological characteristics of the parasitoids. We anticipate that our findings could contribute to the development of a novel strategy for safeguarding the desert ecosystem in which *N. sibirica* predominates.

Materials and methods

Study sites and sampling collections

Two collecting sites (table 1) with different habitat types where *N. sibirica* are naturally found with galls were selected to study the biological properties of the gall inducers and their parasitoids in Wujiaqu city (S1) and Jinghe county (S2) in Xinjiang during 2018–2021. The five-point sampling method was used by randomly selecting 3–5 trees from five sub-samples of the trees (Zhao *et al.*, 2021; Kang *et al.*, 2022). For each sampling date from March to October, five shrubs from five subsamples of 70–90 galls each were randomly selected and taken to the laboratory for rearing and dissection.

Laboratory rearing of the galls

The field-collected galls were placed individually in glass vials (diameter 1.5 cm and length 10.0 cm) to monitor their development in the insect laboratory of the College of Life Sciences and

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Table 1. Survey sites of *Nitraria sibirica* in Xinjiang in 2018–2021

Study site	Coordinates	Altitude	Habitat type	Main vegetation
S1: Nine company, 103rd regiment, Wujiaqu city of Xinjiang	87.514978°E 44.496674°N	363.87 m	Saline-alkali desertification (farmland around)	*N. sibirica* *Lycium* sp. *Haloxylon* sp. *Sophora alopecuroides* *Halimodendron* sp. *Alhagi* sp. *Salsola* sp. *Tamarix* sp.
S2: Mangding township, Jinghe county, Bortala Mongolian autonomous prefecture of Xinjiang	83.162365°E 44.620329°N	172.29 m	Saline-alkali desertification (natural conservation area)	*N. sibirica* *Haloxylon* sp. *Hedysarum* sp. *Salsola* sp. *Tamarix* sp.

Technology, Xinjiang University (ICXU). The galls were divided into three groups containing 20 galls each and were reared in 2018–2021 in climate-controlled chambers at 26°C and 65 ± 5% relative humidity, with a fluorescent lighting regime of 14:10 h (L:D). Furthermore, additional swollen galls were dissected to identify the morphological characteristics and life history of the dominant gall inducers and parasitoids.

The galls were checked every day for the emergence of gall inducers and the corresponding parasitoid adults. The insects were then separated according to their taxonomy and sex. The sex ratio was calculated as the mean percentage of female offspring for each type of parasitoid from the pest species that emerged in the laboratory. The emerged gall inducers and the corresponding parasitoids were reared individually in glass vials with gauze under four different temperatures (20, 26, 32, and 38°C). The gall inducers and parasitoids were fed with absorbent cotton soaked with water and 15% honey water. Next, the lifespan of the gall inducers and parasitoids was recorded every day until they all died, and the number of adults that emerged from the galls which were collected on each sampling date was counted. The dead gall inducers and parasitoids were stored in 100% ethanol for further morphological identification and molecular analyses. Then, the genomic DNA was extracted, and sequence amplification (*COI* and the D2 domain of *28S*) was conducted following the method of Zhao *et al.* (2021). All the specimens were deposited at ICXU.

Emergence periods and parasitization indexes of the insects in the swollen galls of N. sibirica

After emergence, all the collected swollen galls were inspected and dissected under a Nikon stereo microscope with a magnification of up to 100× to count the total number of gall inducers and parasitoids including the un-emerged insects. The percentage of emerged insects was used to calculate the different emergence periods among the gall inducers and parasitoids. The emergence periods of the gall inducers and corresponding parasitoids were determined, and the four parasitization indexes for each parasitoid species were calculated using the following formulae (Costi *et al.*, 2019; Zhao *et al.*, 2021).

The index discovery efficiency (DE) was used to describe the ability of the parasitoids to find galls in the field and was calculated as:

$$\mathrm{DE} = \frac{\text{Number of swollen galls with parasitoids}}{\text{Number of collected swollen galls}} \times 100. \tag{1}$$

The index exploitation efficiency (EE) was used to evaluate the ability of the parasitoids to exploit their hosts and was calculated as:

$$\mathrm{EE} = \frac{\begin{array}{c}\text{Number of parasitized gall inducers}\\ \text{in the swollen galls}\end{array}}{\begin{array}{c}\text{Total number of the gall inducers and}\\ \text{parasitoid in the parasitized swollen galls}\end{array}} \times 100. \tag{2}$$

The parasitism rate (PR) was used to describe the efficacy of a parasitoid in reducing gall inducers and was calculated as:

$$\mathrm{PR} = \frac{\text{Number of parasitoids in swollen galls}}{\begin{array}{c}\text{Total number of the gall inducers and}\\ \textit{parasitoid} \text{ in the swollen galls}\end{array}} \times 100. \tag{3}$$

The index relative importance (RI) was calculated as DE × PR × 100 (Virla *et al.*, 2019), which was used to describe the integrated capability of a parasitoid to reduce the gall inducers, and RI > 10, 9.99 ≥ RI > 1.0, 1 ≥ RI ≥ 0.09, and RI < 0.09 were considered 'very frequent', 'frequent', 'scarce or occasional species', and 'rare', respectively.

Morphometric relationship between the galls and insects in the swollen galls of N. sibirica

The swollen galls that were collected in 2019–2021 and dissected were used to explore the morphometric relationship between the galls and the inhabitants of the swollen galls of *N. sibirica*. Based on the different species of inhabitants in the swollen galls, we calculated the frequency of insect types in the different chambers at S1 and S2. For each gall on these survey dates, we measured the frequency of the number of chambers, the parasitism rate corresponding to the different number of gall chambers, and the gall size and body length of the major insects after all the gall inhabitants had emerged. In addition, the gall volume and chamber density were calculated using the following formulae:

$$\text{Gall volume (GV)} = \pi \times \left(\frac{1}{2} \times \text{gall length}\right) \times \left(\frac{1}{2} \times \text{gall width}\right)^2 \times \frac{3}{4}, \tag{4}$$

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$$\text{Chamber density (CD)} = \frac{\text{Gall volume of each gall}}{\text{Total number of chambers in each gall}} \times 100. \quad (5)$$

Statistical analysis

All the analyses were performed using Prism 8.0 (GraphPad Software, San Diego, CA, USA) and Origin 2021 (OriginLab, Northampton, MA, USA), and data were assessed for normality (Shapiro–Wilk test) and variance (*F*-test), when appropriate. The sample sizes were selected according to standard practice in the field (Sopow and Quiring, 2001; Zhao *et al.*, 2021; Kang *et al.*, 2022). Additionally, a two-tailed Student's *t*-test was used to determine the significance between the two groups. For multiple comparisons, a one-way analysis of variance followed by Tukey's post hoc test was used. The significance level was set at $P < 0.05$, and the data are presented as the mean ± standard error of at least three independent experiments. In addition, the relationships between the gall morphological characteristics (chamber number, gall volume, and chamber density) and the body size of the dominant insects were analyzed through logistic regression (binomial generalized linear model) which was performed using R version 3.4.1.

Results

Occurrence of swollen galls on N. sibirica

We collected a total of 215 and 565 swollen galls from the branches of *N. sibirica* at S1 and S2, respectively, during the period from 2018 to 2021 in northern Xinjiang. However, no galls were collected at S1 in 2018. The galls were conical and swollen when compared to the normal branches, and they were characterized by the lignification and thickening of the epidermis.

The development of the swollen galls on *N. sibirica* occurred once a year and consisted of four stages (fig. 1). The early period was from late May to early August, and the growth period was from mid-June to late October. The mature period was from early September to mid-May of the next year. The emergence period was from late April to early July. Additionally, the emergence of the gall inducers was followed by the drying up of the swollen galls. The galls that occurred had overlapping generations.

Species of gall inducers and parasitoids in swollen galls on N. sibirica

Two species of gall inducers, *Contarinia* sp. and *Platyneurus gobiensis* Sugonjaev (Hymenoptera: Tetracampidae), were recorded from the swollen galls that were collected at both sites. All the gall inducers were mostly univoltine, and they overwintered at the mature larval stage in the galls. After dissecting the swollen galls collected from 2018 to 2021, 89.83% unisexual galls (53.39% female and 36.44% male) and 10.17% mixed galls were identified (fig. S1). The proportion of unisexual galls (90.48% at S1 and 89.47% at S2) and mixed galls (9.52% at S1 and 10.53% at S2) was similar at S1 and S2 and among the 3 years, except for in 2019. Furthermore, in the unisexual galls, the number of gall midges in each 'female' gall was averaged at 2.69 ± 2.14, whereas that in each 'male' gall was averaged at 2.31 ± 1.90. Furthermore, the sex ratio (female:male) was approximately 15:7 in the mixed galls.

The dominant gall inducer *Contarinia* sp. mainly lived in the galls from the larval to pupal stages. After mating, the female adult laid eggs on the leaf buds, new shoots, or young leaves of *N. sibirica*. Then, the hatched larvae bored into the twigs. Later, the larvae developed inside the galls to form gradually enlarged galls. With the development of the pupae, the gall inducers broke the epidermis of the swollen gall using the spines on their head and then emerged successfully (fig. 1).

In this survey, three solitary parasitoid species belonging to the genera *Platygaster* (Hymenoptera: Platygasteridae), *Cheiloneurus* (Hymenoptera: Encyrtidae), and *Eupelmus* (Hymenoptera: Eupelmidae) were recorded from the swollen galls (fig. 2). Among them, *Platygaster* sp. and *Cheiloneurus elegans* are solitary

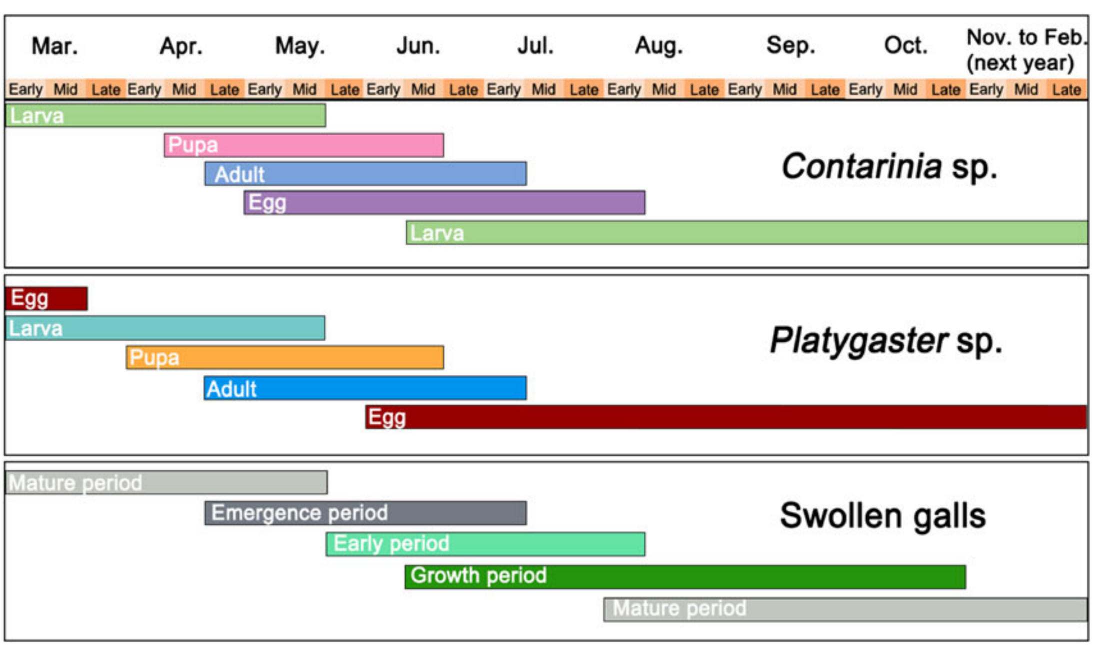

Figure 1. Phenological fitting based on the dynamic changes in the growth period of the swollen galls, *Contarinia* sp., and *Platygaster* sp. on *Nitraria sibirica*. The early period is labelled with light green, and the growth period is labelled with light white. The mature period is labelled with white lignification, and the emergence period is labelled with off-white.

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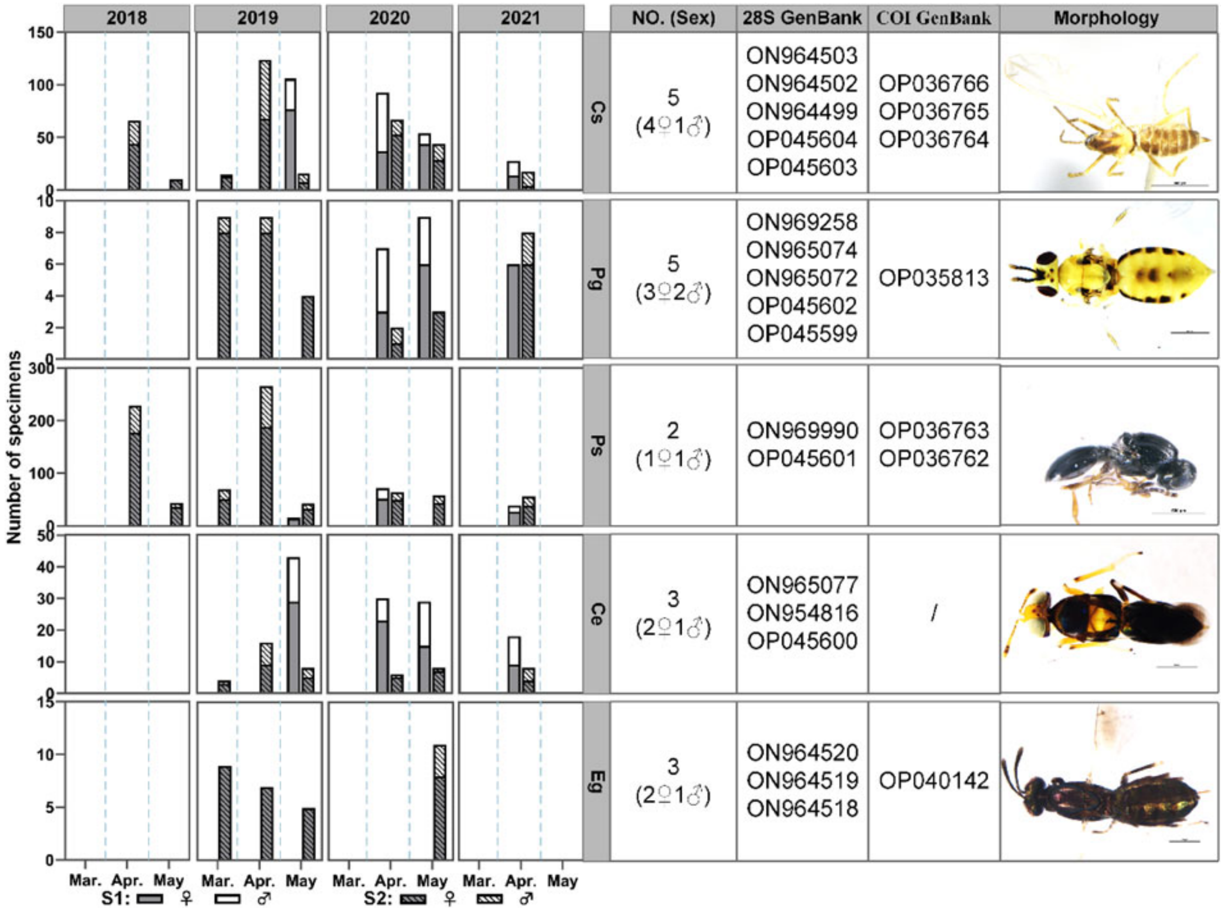

Figure 2. Number of specimens of the gall inducers and their parasitoids in the swollen galls on *Nitraria sibirica* in 2018–2021, with the GenBank accession numbers for the deposited sequences that were generated from this study. Cs, *Contarinia* sp.; Pg, *Platyneurus gobiensis*; Ps, *Platygaster* sp.; Ce, *Cheiloneurus elegans*; Es, *Eupelmus gelechiphagus*.

primary koinobiont endoparasitoids, whereas *Eupelmus gelechiphagus* is an idiobiont ectoparasitoid of *Contarinia* sp. Only *Platygaster* sp. was an egg parasitoid, and the others were larval parasitoids (fig. S2). Moreover, the molecular analyses confirmed the identity of the gall inducers and corresponding parasitoids that emerged from the swollen galls. All obtained sequences of the *28S* and *COI* genes were deposited in the GenBank database (fig. 2).

Emergence of gall inducers and their parasitoids from swollen galls on N. sibirica

The highest number of emerged gall inducers (♀107, ♂70) and parasitoids (♀312, ♂118) from the swollen galls of *N. sibirica* was observed in 2019 at S2 (figs 2 and 3). For the gall inducers, the number of *Contarinia* sp. recorded at S1 was significantly higher than that at S2 ($F = 6.348$, df = 30, $P < 0.0001$). In addition, there were slightly more female adults than male adults for each species of gall inducers and corresponding parasitoids that emerged from the swollen galls (fig. 2).

The emergence of both the gall inducers and parasitoids obtained from the swollen galls showed an initial increasing tendency before decreasing from April to June. *Contarinia* sp. emerged earlier than *P. gobiensis*, which rarely emerged in the 4 years (fig. 3). Moreover, the parasitoid *Platygaster* sp. emerged earlier than the other parasitoids, and *C. elegans* emerged earlier than *E. gelechiphagus* (fig. 3).

Parasitization indexes of parasitoids recorded from swollen galls on N. sibirica

The parameters of the parasitization indexes for the different parasitoid species showed significant differences (fig. 4). All the parasitization indexes of *Platygaster* sp. were significantly higher than those of *C. elegans* ($F = 2.097$, df = 31, $P = 0.0431$) and *E. gelechiphagus* ($F = 10.28$, df = 31, $P < 0.0001$). The parasitoid impact and relative importance of *Platygaster* sp. were 17.70% and 6.73 at S1 and 57.46% and 28.88 at S2, respectively. The relative importance of *Platygaster* sp. peaked at 41.68 at S2 in 2018, whereas the maximum was 15.40 and 0.87 for *C. elegans* at S1 in 2019 and *E. gelechiphagus* at S2 in 2020, respectively. The results indicated that *Platygaster* sp. and *C. elegans* were the dominant parasitoids of the swollen galls at S1 and S2, respectively.

Among the indexes, the EE was higher than the DE in most cases, with the exception of *Platygaster* sp. and *C. elegans* in 2019 at S1 and *Platygaster* sp. in 2020 at S2. In general, the EE did not reach 100% since few parasitized gall midges were reared from one gall with more than one gall inducer. The swollen galls of *N. sibirica* collected in 2019 at S1 and in 2020 at S2 had lower EE.

Effect of temperature on the lifespan of adult parasitoids recovered from swollen galls on N. sibirica

There were differences in lifespan between the gall inducers and parasitoids, and they were affected by temperature and sites

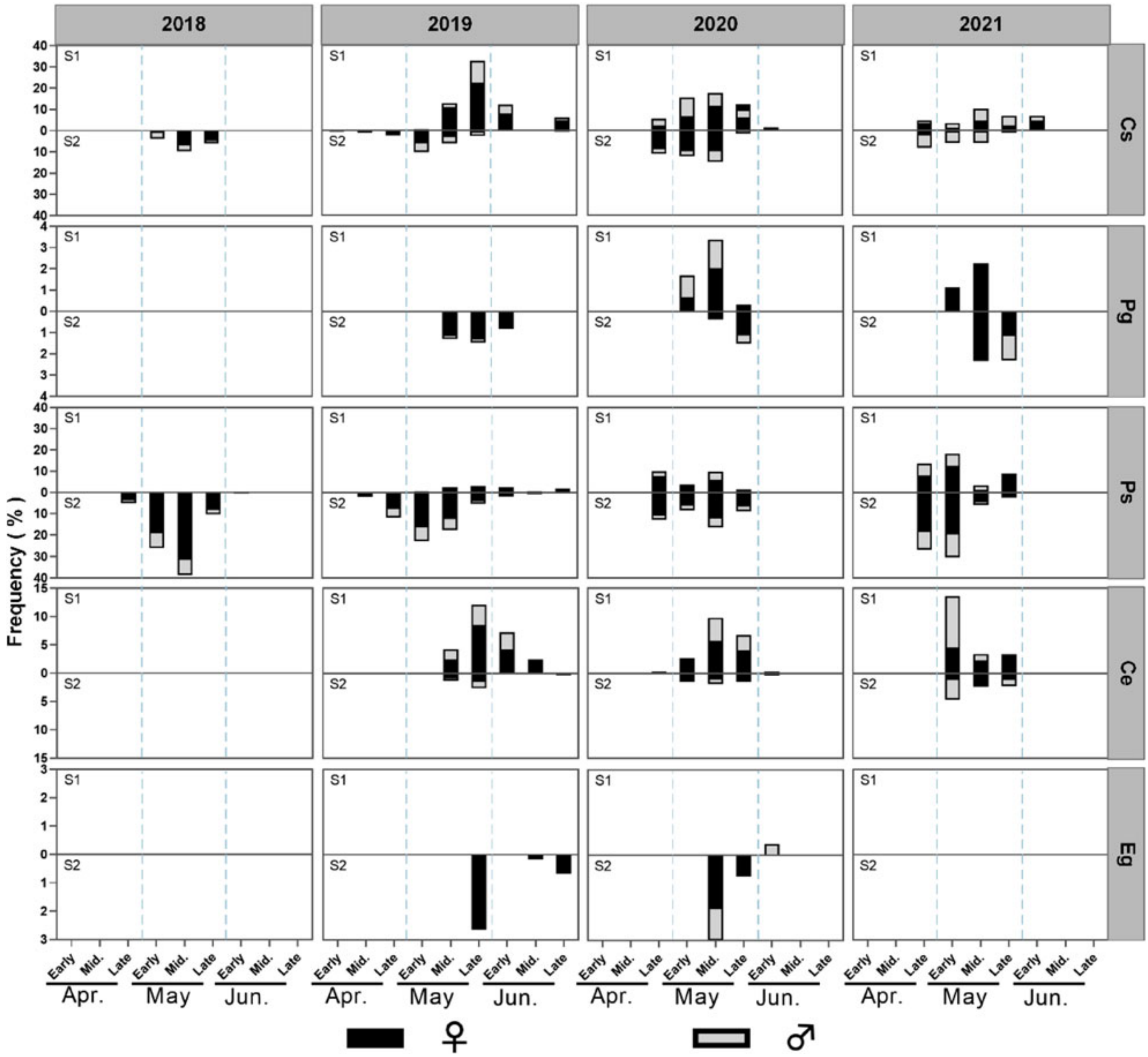

Figure 3. Emergence periods of the gall inducers and their parasitoids from the swollen galls on *Nitraria sibirica* in 2018–2021. The emergence of the individuals from the swollen galls was investigated daily under laboratory conditions at sites 1 and 2. Cs, *Contarinia* sp.; Pg, *Platyneurus gobiensis*; Ps, *Platygaster* sp.; Ce, *Cheiloneurus elegans*; Es, *Eupelmus gelechiphagus.*

(fig. 5). The lifespans of the adult gall inducers and parasitoids that emerged from the swollen galls showed a shortened trend with an increasing temperature. The minimum number and shortest lifespan of gall inducers and parasitoids were recorded at 38°C. The average expected lifespan of the gall inducers *Contarinia* sp. and *P. gobiensis* was 3.08 and 14.63 days at 20°C and 0.83 and 2.29 days at 38°C, respectively.

The average expected lifespan of *Platygaster* sp., *C. elegans*, and *E. gelechiphagus* was 9.96, 21.48, and 20.00 days at 20°C and 2.03, 4.94, and 5.25 days at 38°C, respectively. However, there was a small difference in the average lifespans of the gall inducers between the two sites. The average lifespan of *E. gelechiphagus* was 13.54 days at S2, whereas no living *E. gelechiphagus* were observed at S1. Moreover, the adults of *C. elegans* recorded from the swollen galls had longer lifespans than those of *Platygaster* sp. at the given temperatures (20℃: $\chi^2 = 47.06$, $P < 0.0001$; 26℃: $\chi^2 = 75.45$, $P < 0.0001$; 32℃: $\chi^2 = 75.72$, $P < 0.0001$; 38℃: $\chi^2 = 24.93$, $P < 0.0001$). Additionally, no significant differences were observed in the lifespans of the parasitoids recorded from the swollen galls between S1 and S2 and between the females and males of each parasitoid species at all the given temperatures (fig. 5).

Number, parasitism rate, and insect composition types of swollen gall chambers on N. sibirica

The frequency of gall chamber numbers in the swollen galls on *N. sibirica* is illustrated in fig. 6a. The chamber numbers of the swollen galls ranged from 1 to 34. The maximum number of gall chambers was 22 at S2 ($N = 200$) and 35 at S1 ($N = 500$). The distribution of the number of gall chambers was approximately bell-shaped with extended tails (fig. 6a), and it was similar among the given years with a few subtle differences. In 2018 and 2019, the percentages of gall chambers with fewer than five chambers

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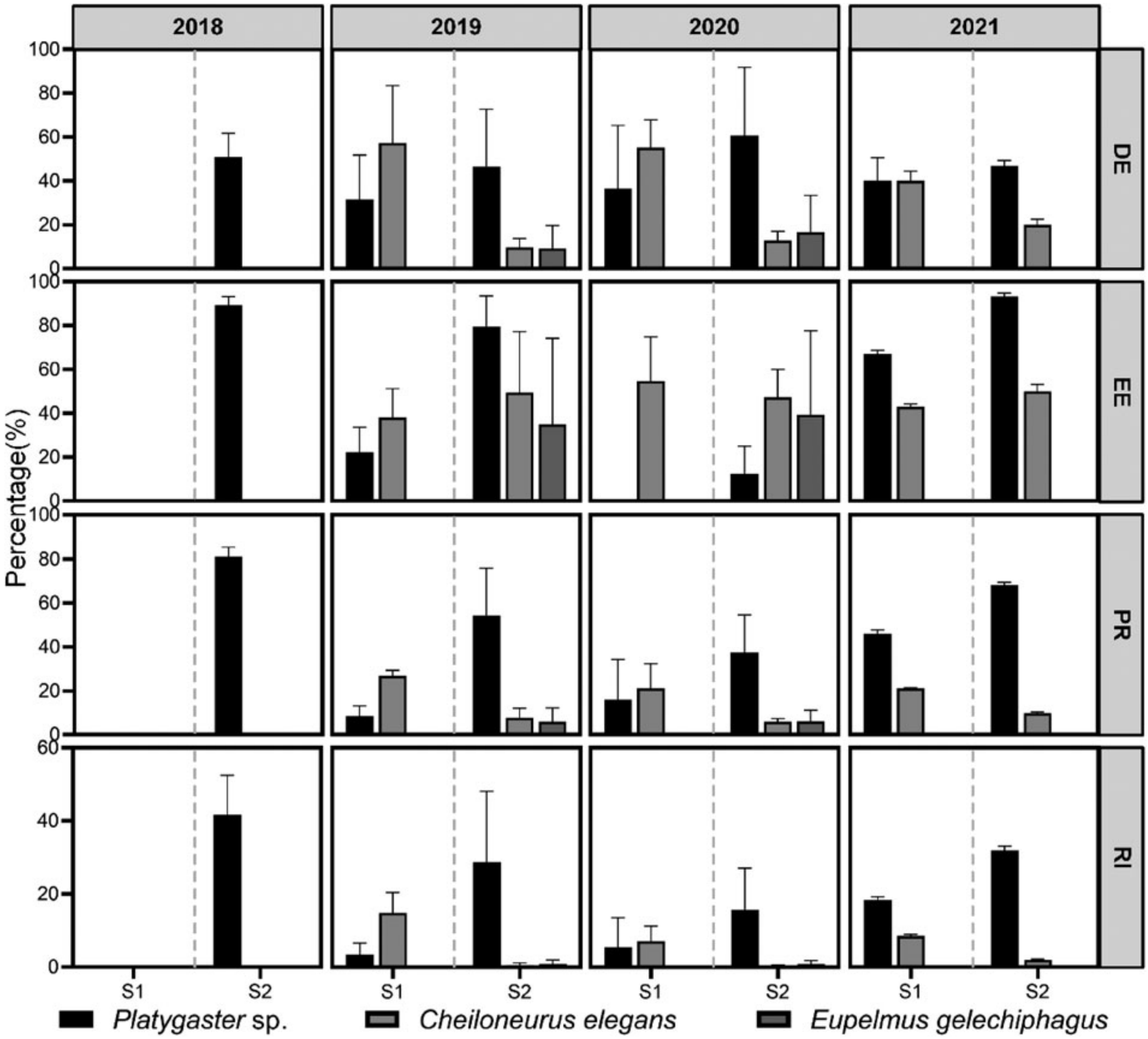

Figure 4. Parasitization indexes and relative importance of the parasitoid species that were recorded from the swollen galls on *Nitraria sibirica*. RI > 10, very frequent; 9.99 ≥ RI ≥ 1.0, frequent; 1.0 ≥ RI ≥ 0.09, scarce or occasional species; RI < 0.09, rare.

were 82.80 and 79.27%, whereas those in 2020 and 2021 were 72.03 and 62.85%, respectively. In addition, the percentage of gall chambers with fewer than 5 and 10 chambers were 65.05 and 89.56% at S1, whereas those at S2 were 78.98 and 97.87%, respectively. In general, the highest frequency of gall chamber number ranged from two to four.

The average probability of parasitoid attack for all parasitoids was 0.41 (SE = 0.40, $N = 111$) at S1 and 0.58 (SE = 0.52, $N = 187$) at S2. The probability of a parasitoid attack was similar for the swollen galls at S1 and S2. The parasitoid attack rates showed a bimodal distribution, with peaks at both low and high values. In most cases, the parasitoids were either absent or attacked almost all inhabitants (fig. 6b). When the gall chamber numbers ranged from one to eight, the probability of a parasitoid attack fell in the interval of 0.8–1.0, whereas an extremely low attack probability or even no attacks were found when the gall chamber number was greater than eight.

The insect composition of the swollen gall chambers was simpler at S1 than at S2; *Contarinia* sp. and *C. elegans* did not simultaneously emerge from the same galls at S1. Additionally, 28.13 and 17.11% of the galls produced only the dominant gall inducer *Contarinia* sp. at S1 and S2, respectively, whereas 28.13 and 44.74% of the galls produced only the dominant parasitoid *Platygaster* sp. (fig. 6c). Moreover, 48.96 and 28.95% of the galls produced both gall inducers and parasitoids at S1 and S2, respectively. It was shown that the insect composition of the swollen galls was similar over the 3 years with a slightly different percentage of gall inhabitants.

Morphometric relationship between galls and insects on swollen galls of N. sibirica

The gall size was positively correlated to the number of gall chambers and emerged insects (fig. 7a, c, d, f), and negatively correlated to the chamber density, except in 2021 ($R^2 = 0.03$, $P = 0.14$; fig. 7b, e). Among all parasitoids, for *Platygaster* sp. ($R^2 = 0.04$, $P = 0.079$), the relationship between the number of gall chambers and body length was stronger than that for *C. elegans* and *Contarinia* sp. ($R^2 = 0.01$, $P = 0.26$; $R^2 < 0.01$, $P = 0.43$) without evident linear correlation. However, the relationship between

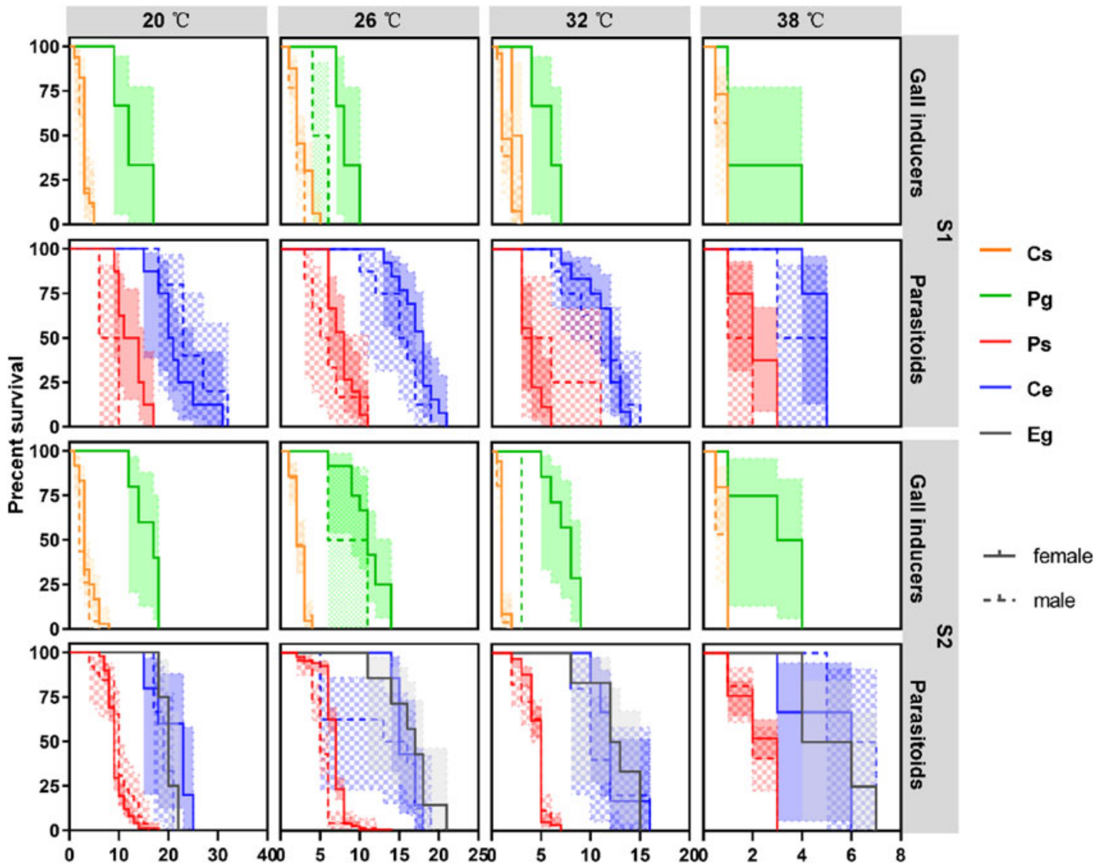

Figure 5. Survival curves of the gall inducers and their parasitoids from the swollen galls on *Nitraria sibirica* at four different temperatures, 20, 26, 32, and 38°C. The 95% confidence intervals are represented by shades of different colors. Cs, *Contarinia* sp.; Pg, *Platyneurus gobiensis*; Ps, *Platygaster* sp.; Ce, *Cheiloneurus elegans*; Es, *Eupelmus gelechiphagus*.

the chamber density and body length was stronger for both *C. elegans* and *Contarinia* sp. than that for *Platygaster* sp. The regression analysis showed a significant negative relationship between the chamber volume and body length for both *C. elegans* and *Contarinia* sp. ($R^2 = 0.19$, $P = 0.0043$; $R^2 = 0.13$, $P = 0.0013$), but not for *Platygaster* sp. ($R^2 < 0.01$, $P = 0.52$).

Discussion

Various gall inducers engender a myriad of gall types across different caltrop plants, yet only a single type of leaf gall has been reported on *Nitraria* (Sugonjaev, 1971; Yang, 1990; Sugonjaev and Voinovich, 2003). In the present study, we delineated the occurrence period of the swollen galls on *N. sibirica* for the first time. Some of the collected galls from previous years might have been in diapause, resulting in non-eclosion, which complicates the determination of the current generation of galls solely based on their appearance. It is noteworthy that the inhabitants in overwintering galls could emerge in the current year, indicating that overwintering diapause was broken and that the insects can resume normal development under favorable environmental conditions (Chen *et al*., 2013, 2015). In addition, anthropogenic interference and overgrazing at S1 have significantly diminished the populations of swollen galls and gall inhabitants compared to S2, a nature reserve with limited logging.

Although *Contarinia nitensis* and *C. nitrariae* (Diptera: Cecidomyiidae) have been documented on *N. sibirica* in Kazakhstan, and *T. nitrariae* (Diptera: Cecidomyiidae) on *Nitraria schoberi*, none were considered as gall inducers (Gagné and Jaschhof, 2021). In China, this study represents the first documentation of gall midge *Contarinia* sp. as a major gall inducer for swollen galls, specifically attacking the indigenous species *N. sibirica*. Only three species of this genus have been collected on caltrop plants (Gagné and Jaschhof, 2021). Another gall inducer, *P. gobiensis*, from the subfamily Mongolocampinae, was previously reported as a parasitoid of *N. sibirica* (Sugonjaev, 1971), but our findings suggest it to be an inquiline species, not a parasitoid. Furthermore, this study is also the first to report the male specimen of *P. gobiensis*, which will be described in detail in a subsequent paper.

This study indicated that the gall inducers *Contarinia* sp. exhibit monogeny – an unusual reproductive characteristic prevalent among gall midges, whereby female *Contarinia* sp. principally generated unisex galls on *N. sibirica*. Similar observations have been reported in several species of gall midges within the genera *Dasineura* (Murchie and Hume, 2003), *Asphondylia* (Park and Thompson, 2018), *Izeniola* (Dorchin and Freidberg, 2004), and *Aphidoletes* (Tabadkani *et al*., 2011), which produce predominantly male or female offspring, with only a sporadic mixed brood. We discovered a few mixed galls, significantly outnumbered by unisexual ones, among the swollen galls, potentially resulting from multiple female gall midges ovipositing on a single shoot to share the same gall due to nutritional limitations in arid areas. However, the sex-determination mechanism in gall midges remains unclear, and the monogenous *Contarinia* sp. pedigrees need to be further studied.

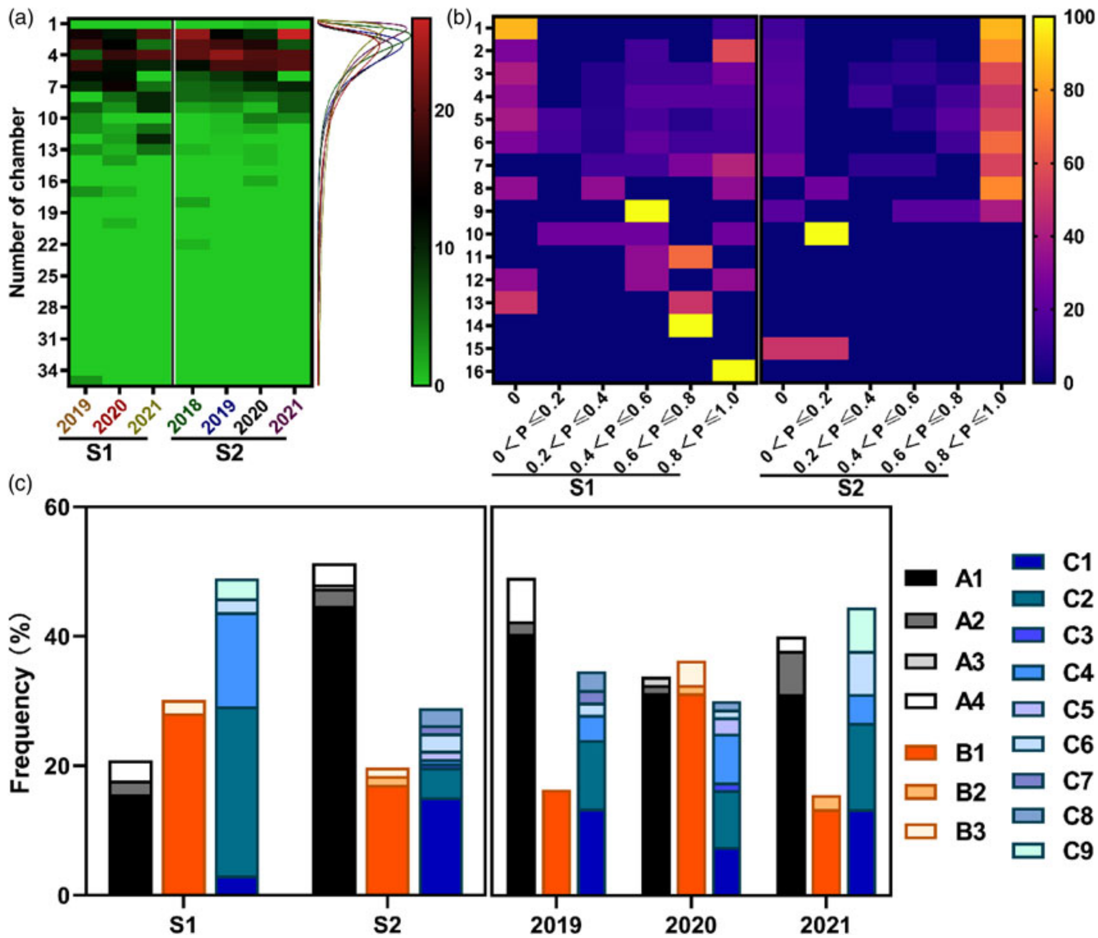

Figure 6. Frequency of the number of gall chambers (a), the parasitism rate corresponding to the different numbers of gall chambers (b) in the swollen galls on *Nitraria sibirica*, and the frequency of the insect composition types in the different chambers (c) at S1 and S2 in 2019–2021. The color of the year corresponds to the color of the curve in (a). A–C indicate 16 insect composition types recorded in swollen galls on *N. sibirica*. A: only parasitoids in the galls, A1: *Platygaster* sp., A2: *Cheiloneurus elegans*, A3: *Eupelmus gelechiphagus*, A4: *Platygaster* sp. and *C. elegans*; B: only gall inducers in the galls, B1: *Contarinia* sp., B2: *P. gobiensis*, B3: *Contarinia* sp. and *Platyneurus gobiensis*; C: both parasitoids and gall inducers in the galls, C1: *Platygaster* sp. and *Contarinia* sp., C2: *C. elegans* and *Contarinia* sp., C3: *E. gelechiphagus* and *Contarinia* sp., C4: *Platygaster* sp. and *C. elegans* and *Contarinia* sp., C5: *E. gelechiphagus* and *C. elegans* and *Contarinia* sp., C6: *Platygaster* sp. and *P. gobiensis*, C7: *Platygaster* sp. and *C. elegans* and *P. gobiensis*, C8: *Platygaster* sp. and *Contarinia* sp. and *P. gobiensis*, C9: *C. elegans* and *Contarinia* sp. and *P. gobiensis*.

Interestingly, we observed two species of gall inducers, *Contarinia* sp. and *P. gobiensis*, coexisting sympatrically with the same gall on *N. sibirica*. This finding is unusual as gall inducers inhabiting the same host plant typically exploit different ecological niches or make different types of galls (Sardon-Gutierrez *et al.*, 2021). Considering the numerical superiority and the extent of damage inflicted by these species, *Contarinia* sp. was the dominant gall inducer of the swollen galls, while *P. gobiensis* was likely an inquiline species.

Cheiloneurus elegans has been recorded in association with several species of scale insects in Europe and was perceived as a hyperparasitoid of *Mayetiola destructor* Say, which is parasitized by *Platygaster zosinae* Walker in the USA (Gahan, 1933). However, our study demonstrated that *C. elegans*, similar to *Platygaster* sp., was the primary parasitoid of *Contarinia* sp. It was also observed that the emergence time of an unreported parasitoid, *Eurytomidae* sp., coincided with that of *P. gobiensis*, although we detected no evidence of parasitism. Consequently, investigations are warranted to elucidate these observations.

Parasitization indexes have been extensively utilized to evaluate the parasitic efficacy of egg parasitoids (Virla *et al.*, 2019; Moraglio *et al.*, 2020; Zhao *et al.*, 2021). In the present study, we adapted these indexes to evaluate the overall efficiency of parasitoids from swollen galls – a methodology yet to be reported in the literature. In most cases, the exploitation efficiency (EE) exceeded the discovery efficiency (DE). In general, the EE rarely achieved 100% due to the scarcity of parasitized gall midges reared from galls with multiple gall inducers. Moreover, the swollen galls collected in 2019 at S1 and in 2020 at S2 exhibited a lower EE, likely due to the abundant occurrence of both the gall inducers and galls during these periods. Some galls contained only non-parasitized gall midges, whereas others harbored both parasitoid (s) and gall midges.

The RI, which measures the frequency of parasitoids recorded from galls (Virla *et al.*, 2019; Zhao *et al.*, 2021), was used to determine the dominant parasitoid species in the different galls. *Platygaster* sp. and *C. elegans* were the dominant parasitoids of the swollen galls at S1 and S2, respectively. However, dissecting the swollen galls showed that it was difficult for the gall midges to develop from young larvae into adults under laboratory conditions. Furthermore, determining whether young larvae have been parasitized based only on their external appearance is difficult,

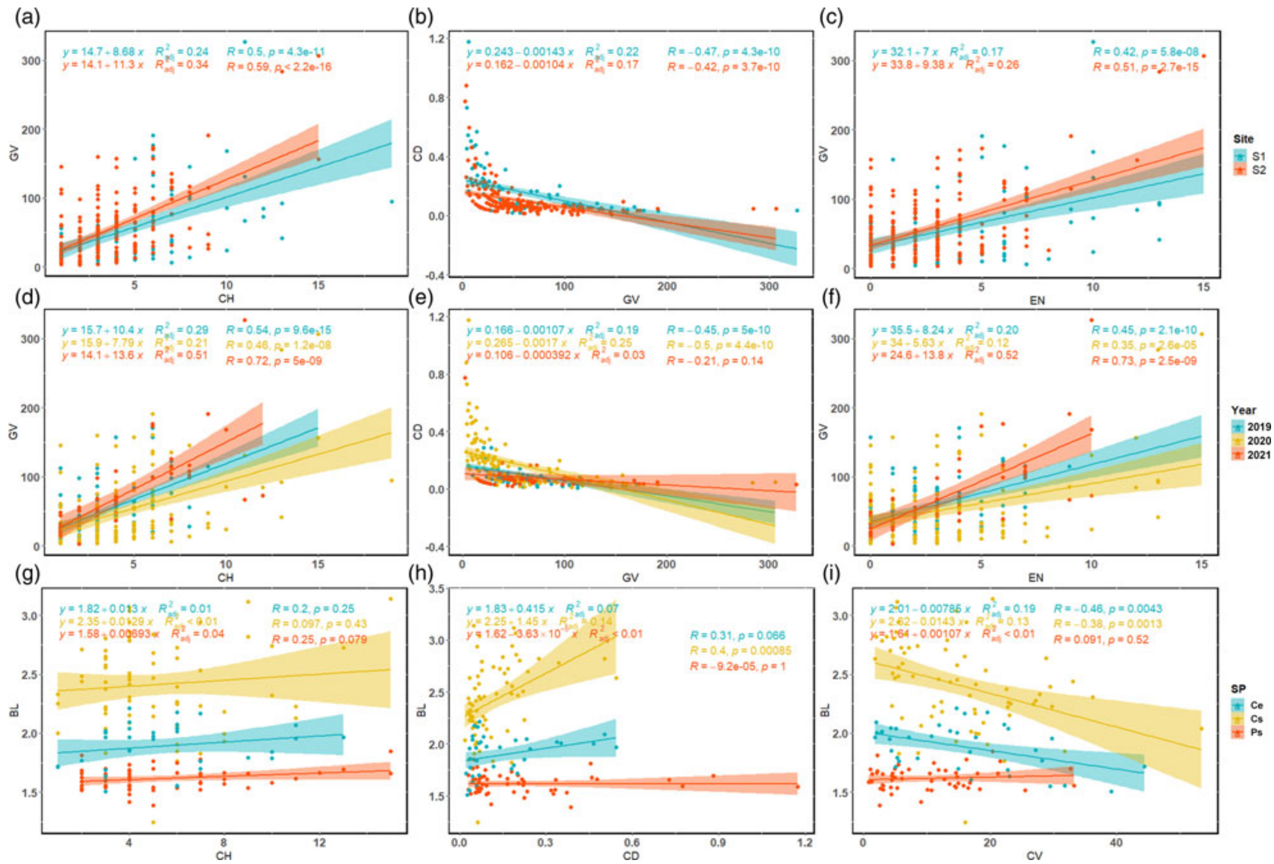

Figure 7. Morphometric relationship between the galls and the major insects in the swollen galls of *Nitraria sibirica* at S1 and S2 in 2019–2021. (a) Relationships between chamber (CH) and gall volume (GV) at S1 and S2. (b) Relationships between GV and chamber density (CD) at S1 and S2. (c) Relationships between emerged insects (EN) and GV at S1 and S2. (d) Relationships between CH and GV in 2019–2021. (e) Relationships between GV and CD in 2019–2021. (f) Relationships between EN and GV in 2019–2021. (g) Relationships between CH and body length (BL) of major insects. (h) Relationships between CD and BL of major insects. (i) Relationships between chamber volume (CV) and BL of major insects. Note differences in scales of axes. Cs, *Contarinia* sp.; Pg, *Platyneurus gobiensis*; Ps, *Platygaster* sp.; Ce, *Cheiloneurus elegans*; Es, *Eupelmus gelechiphagus*.

potentially leading to an underestimation of the actual parasitic rate in the wild. The parasitization indexes of the three species of parasitoids remained consistent in both 2019 and 2020. In addition, for S1, the indexes of *Platygaster* sp. were significantly lower than those of *C. elegans* in both 2019 and 2020, whereas in 2021, they demonstrated an opposite trend. This could be attributed to a shorter survey period and fewer swollen galls in 2021 compared to 2019 and 2020. An increased parasitism rate of *Platygaster* sp. may also account for these results.

Temperature stands as a significant environmental factor influencing the life activities of insects (Wang *et al.*, 2018; Gopko *et al.*, 2020). The present study demonstrated that the lifespan of gall inducers and parasitoids fluctuate in response to escalating temperature. Specifically, when temperatures ranged from 20 to 38°C, the lifespan of these insects showed a steady decline. This was consistent with the composition of the *Psyllaephagus* parasitoid complex that was reported in the flower-like galls of *Haloxylon* spp. and other similar wasps that parasitize gall inducers (Picciau *et al.*, 2017; Zhao *et al.*, 2021). However, it is important to conduct further evaluations to understand the impact of multiple factors on the biological characteristics (life cycle, sex ratio, and longevity) of the gall midges and dominant wasps documented in this study (Quacchia *et al.*, 2008; Dang Hoa *et al.*, 2012; Bari *et al.*, 2015).

The galls provide shelter for the gall inducers and make it more difficult for parasitic natural enemies to parasitize the hosts (Stone and Schonrogge, 2003). The galls represent a changing resource for the natural enemies. As the gall develops, the community of parasitoids that can exploit the gall also changes. Generally, small species with short ovipositors attack their host at an early stage of development, whereas larger species with long ovipositors attack at a later stage (Craig *et al.*, 1990; Stone *et al.*, 2002; Laszlo and Tothmeresz, 2013). In the present study, the gall midges laid eggs on the surface rather than in the young branches of *N. sibirica*. Thus, the egg parasitoid *Platygaster* sp., which has a shorter ovipositor, could successfully parasitize the gall midges. In contrast, when the larvae of the gall midges induced the swollen galls of *N. sibirica*, they developed inside the galls. Then, only the larval parasitoids with longer ovipositors, i.e. *C. elegans* and *E. gelechiphagus*, could successfully lay eggs on or inside the larvae of the hosts. Moreover, considering the location of the gall inducers in the swollen galls and the ovipositor length of the parasitoids, we noted that larvae of the gall midges parasitized by *Platygaster* sp. were primarily found in the inner center of the galls. Conversely, those parasitized by *C. elegans* and *E. gelechiphagus* were predominantly located near the epidermis, facilitated by their ability to pierce through the bracts of the galls more readily. Nonetheless, the relationship between successful parasitism, the parasitoid's ovipositor length, and the size of swollen galls on *N. sibirica* remains unclear, warranting further investigation in future studies.

Ecological studies about the relationships between plant traits and the fitness of galling insects have assumed that the fitness of the gall inhabitants was directly related to gall size; however, fitness did not necessarily increase as the gall size increased (Honěk, 1993; McKinnon *et al.*, 1999; Freeman and Geoghgen, 2010). The number of chambers in the swollen galls on *N. sibirica* showed an asymmetric distribution that was bell-shaped with extended tails with predominantly smaller galls (the number of gall chambers ranged from two to four), and the gall size increased as the number of gall chambers increased. Previous studies have focused on other species, such as *Thecodiplosis japonensis*, *Dryocosmus kuriphilus*, and *Diplolepis rosae*, which showed similar gall size and gall chamber distributions (Bailey and Whitham, 2003; Laszlo and Tothmeresz, 2008; Mao *et al.*, 2017). Thus, there is an optimal gall chamber number that corresponds to the maximum fitness for some insects.

For many insect species, empirical evidence has suggested that the gall size is positively related to the number of gall inhabitants within the galls but negatively related to the chamber density (Honěk, 1993; Freeman and Geoghgen, 2010). Consistently, our results showed that the size of the swollen gall on *N. sibirica* was positively associated with the number of gall chambers or emerging insects, and inversely related to the chamber density of the swollen galls. Comparable findings have been reported for different types of galls (Ozaki, 1993; McKinnon *et al.*, 1999; Sopow and Quiring, 2001). For a solitary gall, the body size of the gall inhabitants escalates with increasing gall size and decreases with increasing chamber density (Sopow and Quiring, 2001). Nevertheless, no evident linear correlation was observed between the gall chamber number and body length for all species. However, a weak linear correlation was observed between chamber density and body length for *Contarinia* sp. Contrary to previous reports, our results showed a negative correlation between the chamber volume and body length for both *C. elegans* and *Contarinia* sp. The unidentified thickness of both the inner and outer walls and the irregular distribution of the swollen gall chambers may explain this phenomenon. Thus, more morphometric parameters (thickness of both the inner walls and out walls of the galls, ovipositor length of the parasitoids, and chamber volume) and their relationships need to be evaluated.

Conclusions

Our results provide important insights into the ecological interactions and complex nutritional relationships among swollen galls, gall inducer groups, and their parasitoids. Additionally, the importance of exploring the gall formation, species composition of gall inhabitants, abundance of natural enemies, and morphometric relationships for *N. sibirica* is highlighted. However, the process of gall formation is complicated and remains to be fully understood, especially for the swollen galls on *N. sibirica* with multiple chambers. Future studies should demonstrate which hypothesis was directly supported by the formation of the swollen galls. Nevertheless, this study improves our understanding of the biology and ecology of *Contarinia* sp. on *N. sibirica* and its parasitoids and may pave the way for the future development of management strategies for gall inducers.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0007485323000342

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