



Intensive grazing enhances grasshopper fitness and abundance in a meadow steppe



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ABSTRACT

Grazing management plays an important role in grassland conservation. Given that grasshoppers are key components in the grassland food web, various studies have been conducted to investigate the effects of grazing by large herbivores on grasshoppers at population and community levels. However, grazing effects on grasshopper fitness and abundance remain poorly understood. Here, using a field experiment in a meadow steppe, we examined the effects of sheep grazing, with different intensities, on grasshopper (*Euchorthippus unicolor*) fitness and abundance. Results showed that female grasshopper's survival rate, mean survival time, and egg production were positively associated with increasing grazing intensities. The positive relationships are likely due to changes in plant nitrogen content and microhabitat induced by large herbivore grazing activities for grasshoppers. Moreover, there were strong positive associations between the fitness and abundance of female grasshoppers, and between female and total grasshopper abundance, which are responsible for an increase in overall grasshopper abundance. These findings improve our understanding about the role of grasshopper fitness in explaining their abundance in response to grazing management. Our study also suggests that measuring grasshopper fitness should be considered for species conservation in management practices of moderate grazing.

1. Introduction

Grasslands provide essential ecosystem function and services, and support a rich biodiversity of both plants and animals (Kang et al., 2007). A large fraction of grassland ecosystems are influenced by anthropogenic activities, such as grazing by large herbivores (Chillo et al., 2017; Wang et al., 2019). Large herbivores, as key ecosystem drivers and ecological engineers, exert substantial influence on the composition and structure of plant communities (Liu et al., 2015; Herrero-Juregui and Oesterheld, 2018). Consequently, large herbivores are also central factors in affecting insects that make up major components of grassland ecosystems (Vandegehuchte et al., 2017; Zhu et al., 2019a). A large body of research has shown that grassland insects are threatened by grassland-use intensification, particularly grazing management (WallisDeVries et al., 2016; Tonelli et al., 2018). With significant declines in ecosystem function induced by excessive grassland management, the responses of insects are being increasingly appreciated (Ford

et al., 2013; van Klink et al., 2015; Berman et al., 2018; Zhu et al., 2019a).

Grasshoppers play an important role in structuring the grassland food web as they often contribute the largest amount of biomass and diversity among grassland invertebrates (Schmitz and Suttle, 2001; Buchkowschi et al., 2019). Mixed results have been found about the effects of large herbivore grazing on grasshopper abundance in grasslands, including positive, neutral, or negative effects (Gebeyehu and Samways, 2003; Jonas and Joern, 2007; Spalinger et al., 2012), implying that grasshopper abundance may depend on a variety of factors, such as grazing intensity, large herbivore assemblage, and habitat type (Marini et al., 2008; van der Plas and Olf, 2014v). In addition to direct consumptive effects by large herbivores (Gish et al., 2017), grazing can affect insect abundance indirectly by foraging and trampling (Laws and Joern, 2013). For example, large herbivores may modify microclimates, such as physical structure of vegetation and ground cover. This influences the thermal environment along with oviposition site availability,

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nymph development, and/or adult activity (O'Neill et al., 2003; Gardiner and Hassall, 2009), therefore altering insect abundance. Large herbivores could also change plant community composition (e.g. preferred food plants), and tissue quality (e.g. nitrogen content), which would then affect the availability of food resource for grasshoppers (Cease et al., 2012; van der Plas and Olff, 2014v; Zhu et al., 2019b). In fact, variation in grasshopper abundance is correlated with their fitness because insect survival and developmental time are important determinants of population size (Franzke and Reinhold, 2011).

Generally, insect fitness is strongly influenced by abiotic and biotic factors, including plant species richness (Specht et al., 2008; Unsicker et al., 2010), plant biomass (Branson, 2017), vegetation structure (Spalinger et al., 2012; Weiss et al., 2013), and physical characteristics (Clissold et al., 2009). Meanwhile, plant tissue carbon (C) and nitrogen (N) balance may be an important factor in mediating species' survival, reproduction, and fitness (Berner et al., 2005; Branson, 2017; Lebigier et al., 2018). In addition to the plant communities and nutrients, microclimate conditions could also affect insect mortality (Rebaudo et al., 2016). Large herbivores can modify the plant community composition, vegetation structure, and plant N content in a way that can directly impact insect diversity (Zhu et al., 2012, 2019b) and abundance (Zhu et al., 2015), including grasshoppers (Zhong et al., 2014; Zhu et al., 2017). However, little is still known about how grazing management affects grasshopper fitness and abundance. Here, we manipulated grazing intensity to test the effects of large herbivores on grasshopper fitness and abundance in a grazed grassland ecosystem with a widespread large herbivore, the domestic sheep (*Ovis aries* subsp.), and the dominant grasshopper species (*Euchorthippus unicolor*) in a meadow steppe. Specifically, we addressed the following questions: (1) how does grazing intensity affect grasshopper fitness through changing food resource and microhabitat, and (2) how does the grazing-induced change in grasshopper fitness associate with grasshopper abundance?

2. Materials and methods

2.1. Study site and organism

Our experiment was performed at the Grassland Ecological Research Station of Northeast Normal University, Jilin Province, P.R. China (44°45'N, 123°45'E). The site is predominated by perennial grass, *Leymus chinensis*, located in a meadow steppe region with a semi-arid, continental and monsoon climate (see Wang et al., 2017; Zhu et al., 2019a for detailed site description).

We used *Euchorthippus unicolor*, the most common grasshopper species found in the studied meadow steppe, to examine the effects of large herbivores on grasshopper fitness and abundance. *E. unicolor* feeds preferably on grass species such as *L. chinensis* (Zhong et al., 2014; Zhu et al., 2017), and is usually in frequent contact with sheep that are common livestock species in our grazed experimental site (Zhong et al., 2017; Zhu et al., 2019a).

2.2. Experimental design and grazing treatments

A randomized block design was employed in this study. Four 60 m × 100 m blocks that were spaced ~40 m apart with similar soil and vegetation conditions were established in 2010, and three 40 m × 30 m plots (~15 m apart) were installed in each block (Fig. S1). During the growing seasons of 2010–2013, one of three intensity treatments, including (i) ungrazed (NG); (ii) a moderate grazing intensity (MG, 4 sheep); and (iii) a high grazing intensity (HG, 8 sheep), were randomly assigned to each plot within a block. Sheep body weight was 33 ± 1.6 kg (mean ± SE). Grazing occurred from early May to late July each year of the study period.

2.3. Grasshopper caging experiment

To estimate the survival of *E. unicolor* under different sheep grazing intensities, microcosm experiments were conducted following grazing treatments. Four cylindrical cages were installed in each of the 12 plots, resulting in a total of 48 cages. These cages were 1.0 m in height and 0.6 m in diameter and wrapped with aluminum mesh at the top (3 mm × 3 mm mesh size). To prevent grasshoppers from escaping, the bottom of the cage was buried ~10 cm into the ground. Within each plot, two 3 m × 4 m subplots were randomly selected to place these cages (per subplot, Fig. S1). In each subplot, one cage was randomly selected to contain *E. unicolor* grasshoppers, and one served as control (no grasshoppers) for observing natural emergence of eggs from the soil to correct survival number of grasshoppers in the cage with grasshoppers. During the experiment, no emergence of grasshoppers in control cage was observed, and so data from a cage with grasshoppers was used to further analyze.

All cages were cleared of any terrestrial invertebrates with a vacuum cleaner (John W. Hock Company, Florida, USA). Between the 6th and 10th of July 2013, 1200 fifth-instar *E. unicolor* nymphs (based on their cross vein) were sampled using sweep nets from the surrounding area. Each treatment cage received 42 nymphs (female:male = 2:1) in two consecutive days (21 nymphs each day). Initial body mass of nymphs was determined using an analytical balance by weighting five individuals together for each sex in a jar. Initial female and male nymph body mass did not statistically differ among all plots (female: $F_{2,21} = 3.415$, $p = 0.202$; male: $F_{2,21} = 2.841$, $p = 0.394$).

2.4. Performance measurement

2.4.1. Survival and body mass

Survival measurements were conducted between July 15 and August 27 in 2013, the number of grasshoppers was counted every other day. Survival rate was calculated by comparing survival number of grasshoppers of the end with total number of the beginning. We used the Kaplan-Meier survivorship curve to estimate median survival time of grasshoppers for each cage.

We weighted the body mass of adult grasshoppers by randomly selecting five female and five male adults in each cage on each sampling date. The average of three measurements (dates) for body mass was considered as adult mass on the 5th day after putting them into cages (once in late July and twice in August). Log-transformed body mass gain was calculated: Weight gain = $\ln(\text{adult mass}) - \ln(\text{initial mass})$.

2.4.2. Fecundity

For oviposition measurements, one 25 cm in diameter and 50 cm in height cage was installed per subplot between the two larger survival cages (Specht et al., 2008; Fig. S1). Oviposition cages were placed between the survival cages, because extracting the top soil layer could result in vegetation damage within the larger grasshopper cages. These small cylindrical cages were made from 3 mm mesh size aluminum fixed on a plastic frame of the same diameter. Seven females and three males were transferred from the survival cage to the oviposition cages after the maturity molt (a total of 240 individuals were transferred). In each oviposition cage, a plastic cup (10 cm in diameter) filled with a mixture of sand and soil (1:1) was provided. The substrate inside each cup was sieved to extract the oothecae at the end of the experiment. In addition, soil cores (30 cm in diameter and 10 cm in depth) were taken underneath each oviposition and oothecae were extracted from the soil cores and root balls. We calculated the number of oothecae as the sum of oothecae number of seven female grasshoppers from the oviposition cup and the soil and roots in the oviposition cage per subplot. And furthermore, the number of eggs per oothecae was counted for a total of 15 oothecae being recorded in the oviposition cage per subplot, and was calculated as the sum of total number of eggs from 15 oothecae.

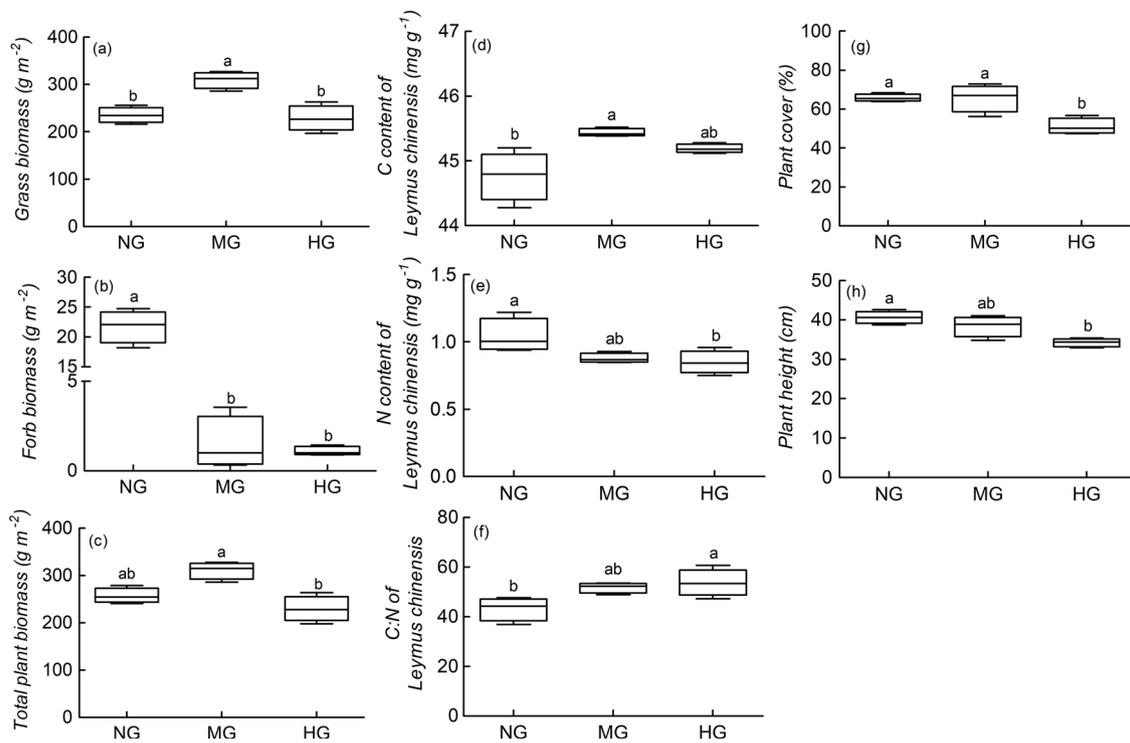


Fig. 1. Effects of different herbivore grazing intensities (NG: Ungrazed, MG: moderate grazing intensity, and HG: high grazing intensity) on grass biomass (a), forb biomass (b), plant biomass (c), N content of *Leymus chinensis* (d), C content of *Leymus chinensis* (e), C/N of *Leymus chinensis* (f), plant cover (g), and plant height (h). Different lowercase letters indicate significant effects of grazing by large herbivores on measured variables ($n = 4$, the *post-hoc* test, $p < 0.05$).

2.5. Grasshopper sampling

To determine the effects of sheep grazing on grasshopper abundance, we sampled grasshoppers using standardized sweep netting along four 25 m transects spaced 6 m apart in each plot (Zhu et al., 2012, 2017). Each net was swept vigorously by two persons at each 5 m interval while walking steadily along the transect. Each sampling consisted of 20 sweeps and two samplings were conducted in each plot. Contents of the sweep nets were preserved in ethyl acetate bottles. Between mid-July and late August, grasshoppers were sampled in each plot on four sunny days between 09:30 and 15:30 with light or no winds. All plots were visited on the same day and the order of plots were sampled in was assigned randomly.

2.6. Vegetation and microclimate measurements

Vegetation and microclimate in cages were sampled during peak biomass in August of 2013. Plant height and cover of each species within the cage was recorded. Plant height was measured to the nearest centimeter using a ruled rod, and plant cover was estimated visually as the percentage of surface area covered by each species (with a maximum of 100% total cover). Aboveground plant biomass was measured by clipping standing plant material from one randomly located $0.5 \text{ m} \times 0.5 \text{ m}$ quadrats per cage. Plants samples were divided into grasses and forbs, and dried with an air-forced oven for 48 h at 80°C , and weighed. Total biomass was calculated as the sum of grass and forb biomass. *L. chinensis* is the main food plant species for grasshoppers, therefore N and C contents of *L. chinensis* in the biomass quadrats were measured by oven-dried milled material with an element analyzer (vario EL cube, ELEMENTAR).

Characteristics of microclimates were measured between 15 July and 27 August in 2013 at four-day interval for a total of ten samples. Each measurement was conducted with eight points per cage at the times of 9:00, 11:00, 13:00, 15:00, and 17:00. Solar radiation was measured using light illuminometer (TES-1339, TaiShi Instrument, Ltd.,

TaiWan), and air temperature and humidity were measured using a Thermo-Hydro recorder (TES-1360A, TaiShi Instrument, Ltd., TaiWan) at the height of 5 cm and 30 cm above the ground (i.e. the point where most insects were present). Microclimate variables for each cage were calculated as the average of measurements from eight points at five sampling times on ten sampling dates prior to analysis.

2.7. Statistical analysis

We pooled grasshopper performance data (survival rate, median survival time, the number of oothecae, and the number of eggs) and vegetation data (plant height, plant cover, biomass of grasses, forbs, and plant community, and C content, N content, and C/N of *L. chinensis*) from two survival or oviposition cages with grasshoppers in each plot (resulting in four replicates per grazing treatment) for further analysis. The cumulative abundance of grasshoppers (both nymphs and adults) using sweep-netting in plots was calculated throughout sampling periods.

Before the application of our statistical analysis, we tested the normality and heteroscedasticity of our data. All data were analyzed using R version 3.2.4 (R Development Core Team, 2016). One-way ANOVA was used to determine the difference in all plant and grasshopper variables among the different grazing intensities by the aov-function. Tukey's multiple comparison was used for post hoc analysis of significant differences among grazing intensity treatments. We tested for relationships between grasshopper performance and environmental variables using Pearson's correlation coefficients with the cor-function. A correlation was considered significant if its 95% confidence interval excluded zero. We applied linear regressions to examine the relationships between performance and abundance of female grasshoppers, and between total grasshopper abundance and female abundance with lm-function.

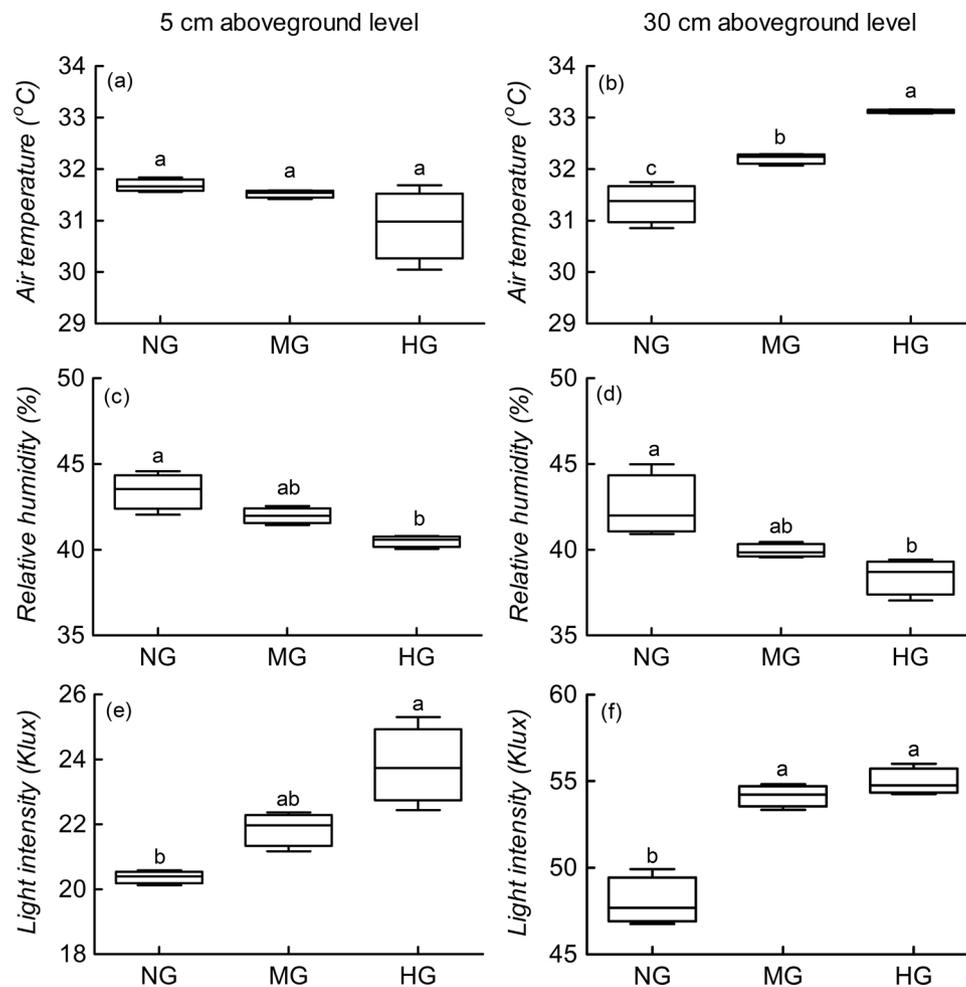


Fig. 2. Effects of different herbivore grazing intensities (NG: Ungrazed, MG: moderate grazing intensity, and HG: high grazing intensity) on microclimate, including air temperature (a, b), relative humidity (c, d), and light intensity (e, f) at 5 cm and 30 cm above ground level. Different lowercase letters indicate significant effects of grazing by large herbivores on measured variables ($n = 4$, the *post-hoc* test, $p < 0.05$).

3. Results

3.1. Effects of grazing on characteristics of vegetation and microclimate

We found significant effects of grazing by large herbivores on grassland vegetation and microclimate (Figs. 1 and 2). For vegetation, grass biomass in grazed plots with moderate intensity were higher by 31.6% and 35.7% than that of ungrazed and high grazing intensity plots, respectively (Fig. 1a). Forb biomass significantly decreased by 93.2% and 98.1% in both moderate and high grazing intensities (Fig. 1b). Total plant biomass in grazed plots with moderate intensity was higher by 35.5% than that of plots with high grazing intensity (Fig. 1c). N content of *Leymus chinensis* was higher in ungrazed plots than in grazed plots (Fig. 1d), but the opposite was found for C content, and C/N ratio (Fig. 1f and e). Plant cover and height were 22.4% and 15.7% higher in ungrazed plots than high-intensity grazed plots (Fig. 1g and h).

The microclimate, temperature at 30 cm above the ground, significantly increased with the gradient of grazing intensities (Fig. 2b). Relative humidity at 5 cm and 30 cm above the ground in ungrazed plots were higher by 6.7% and 9.4% than in high intensity grazed plots (Fig. 2c and d). Light intensity at 5 cm above the ground in ungrazed plots was 16.8% lower than in high intensity grazed plots, but was 12.8% and 14.4% lower than both grazing intensities at 30 cm above the ground (Fig. 2e and f).

3.2. Effects of grazing on grasshopper fitness and abundance

Grazing by sheep significantly affected *E. unicolor* fitness and abundance. The survival rate of females in ungrazed plots was lower by 50% than in both moderate and high intensities grazed plots. The survival rate of total grasshoppers was lower by 47.7% than moderate intensity and by 51.7% than high intensity (Fig. 3a and c). Median survival times of female and total grasshoppers in ungrazed plots were lower by 28.6% and 29.2% than in grazed plots with high grazing intensity (Fig. 3d and f). The number of oothecae did not change among the three grazing treatments (Fig. 4a). Total number of eggs in ungrazed plots was lower by 17.7% and 32.6% than in grazed plots with moderate and high grazing intensities respectively (Fig. 4b), and the number of eggs per oothecae in ungrazed plots was lower by 17.4% than in high intensity grazed plots (Fig. 4c).

There was no grazing effect on the weight gain of females or males approximately 5–7 days after caging when grasshoppers went through their maturity molt (females: $F_{2,21} = 3.415$, $P = 0.020$; males: $F_{2,21} = 2.841$, $P = 0.394$; 432 females and 432 males).

Grasshopper abundance was increased with increasing intensity of sheep grazing. The abundance of female grasshoppers in ungrazed plots were lower by 68.6% than in grazed plots with high grazing intensity, but lower by 53.8% for total grasshopper abundance (Fig. 4d and f). There was no difference in abundance of male grasshoppers between ungrazed and the two grazed plots (Fig. 4e).

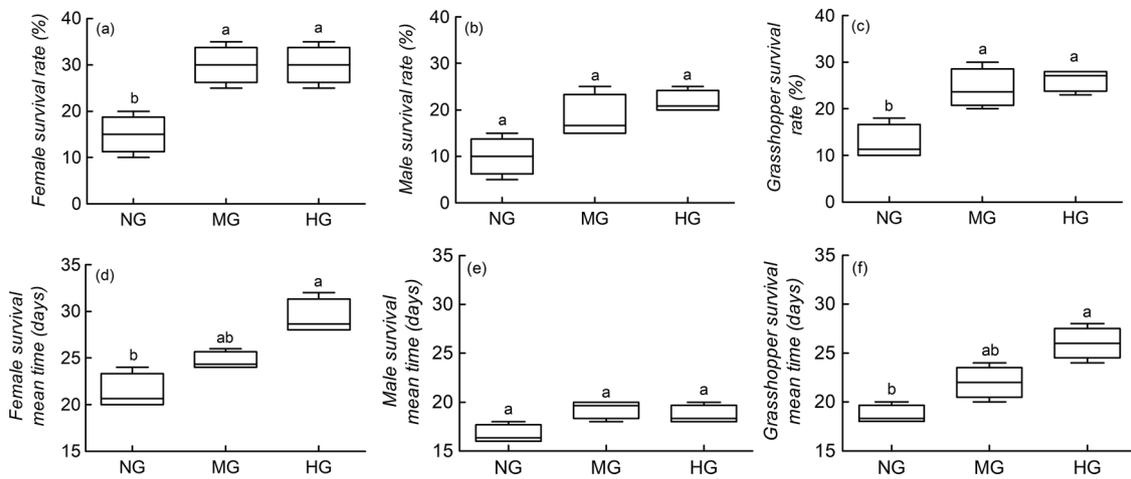


Fig. 3. Effects of different herbivore grazing intensities (NG: Ungrazed, MG: moderate grazing intensity, and HG: high grazing intensity) on survival rate (a, b, and c) and median survival time (d- f) of female, male and total grasshoppers, and on number of oothecae from 14 female grasshoppers (g), number of eggs from 30 oothecae (h), and number eggs per oothecae (i). Different lowercase letters indicate significant effects of grazing by large herbivores on measured variables ($n = 4$, the *post-hoc* test, $p < 0.05$).

3.3. Relationship between plants and grasshoppers, and female and grasshopper abundance

Significant associations between grasshopper fitness and environmental variables were found (Fig. 5). The survival rate of grasshoppers,

including female, and total grasshoppers were positively correlated with C/N of *L. chinensis*, light intensity at 5 cm and 30 cm aboveground level, and air temperature at 30 cm above the ground, but were negatively related to forb biomass, N content of *L. chinensis*, plant height, and humidity. Survival mean time of female and total grasshoppers

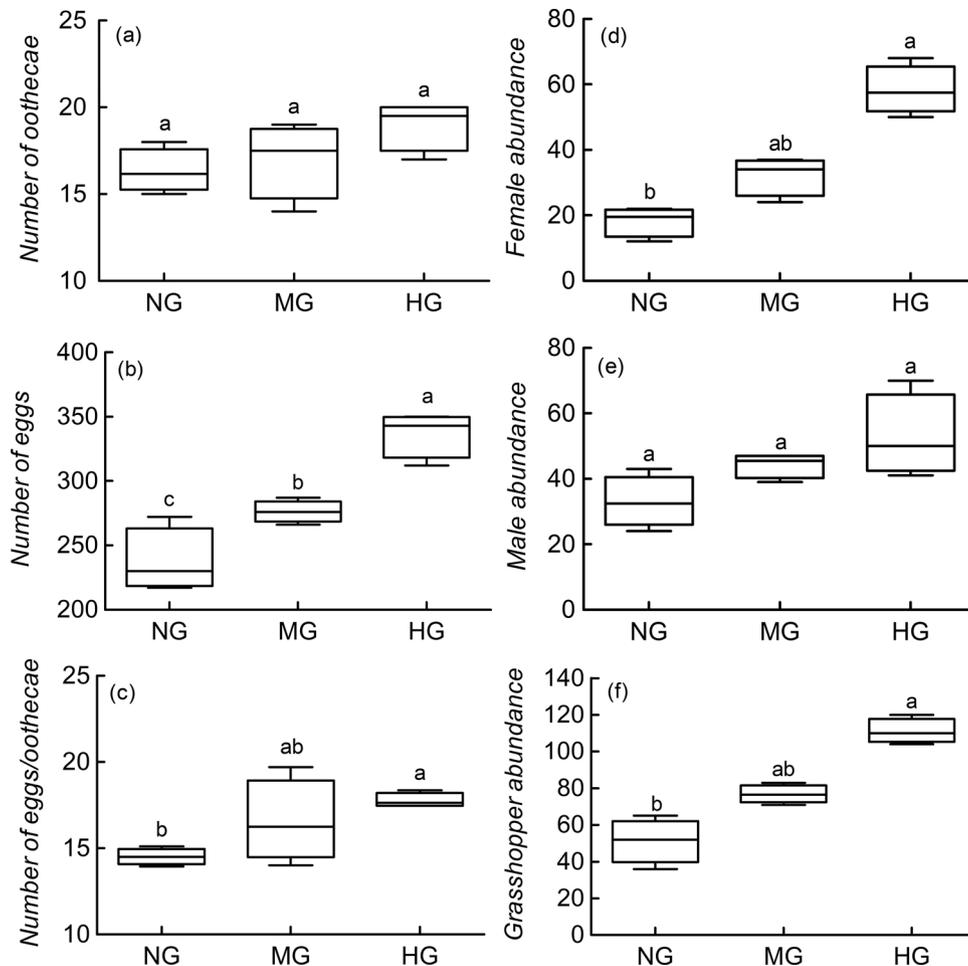


Fig. 4. Effects of different herbivore grazing intensities (NG: Ungrazed, MG: moderate grazing intensity, and HG: high grazing intensity) on abundance of female, male and total grasshoppers. Different lowercase letters indicate significant effects of grazing by large herbivores on measured variables ($n = 4$, the *post-hoc* test, $p < 0.05$).

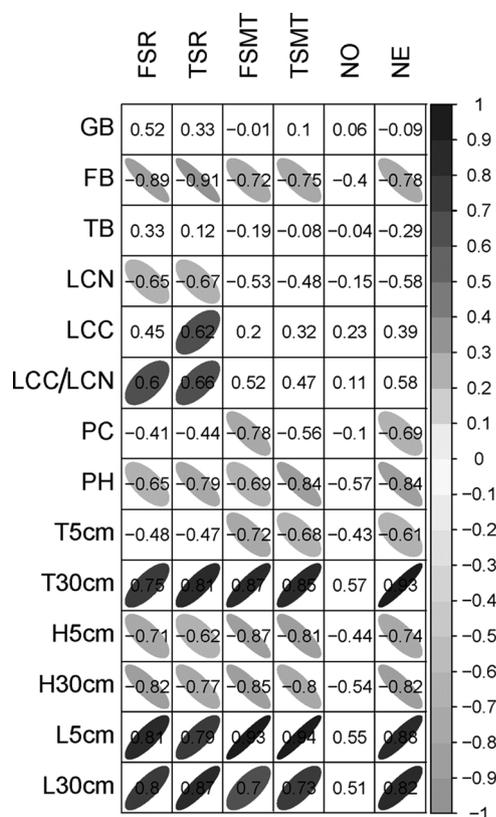


Fig. 5. Correlations between grasshopper fitness and environmental variables (including vegetation and microclimate) under grazing intensities. Significant correlation coefficients ($n = 12$, $p < 0.05$) are highlighted in different grey colors. Color intensity and size of ellipse are proportional to correlation coefficients. Vegetation and microclimate variables include grass biomass (GB), forb biomass (FB), total plant biomass (TB), N content of *L. chinensis* (LCN), C content of *Leymus chinensis* (LCC), C/N of *L. chinensis* (LCC/LCN), plant cover (PC), plant height (PH), air temperature of 5 cm and 30 cm above the ground (T5cm, and T30 cm), air humidity of 5 cm and 30 cm above the ground (H5cm, and H30 cm), light intensity of 5 cm and 30 cm above the ground (L5cm, and L30 cm). Grasshopper performance includes survival rate of females (FSR), and total grasshoppers (TSR), survival mean time of females (FSMT), and total grasshoppers (TSMT), number of oothecae (NO), and number of eggs (NE).

were positively linked to air temperature at 30 cm above the ground, and light intensity at both 5 cm and 30 cm above the ground, but were negatively related to forb biomass, plant height, air temperature at 5 cm above the ground, and humidity. The number of eggs was positively linked to light intensity, and air temperature at 30 cm above the ground, and negatively related with forb biomass, plant cover and height, and air humidity.

Results of regression analyses between grasshopper abundance and grasshopper fitness are shown in Fig. 6. Female abundance significantly increased with female survival rate, female survival mean time, and the number of eggs, but not with the number of oothecae (Fig. 6a-d). The abundance of grasshoppers significantly increased with female abundance (Fig. 6e).

4. Discussion

Grazing management with large herbivores is one of the critical human impacts on grasslands, having far-reaching effects on plant community composition (Liu et al., 2015; van der Plas et al., 2016v; Herrero-Juregui and Oesterheld, 2018), and insects (Cease et al., 2012; Vandegehuchte et al., 2017; Zhu et al., 2019a). To our knowledge, this study provides new evidence that grasshopper fitness is mediating the relationships between large herbivores and insect abundance. Our

findings suggest that grassland grazing intensification may be an important factor that can increase population size of grasshoppers by affecting their fitness.

4.1. Grazing effects on grasshopper fitness

In this study, large herbivore grazing significantly increased grasshopper fitness, with enhancement in survival rate and time, and female egg production (Fig. 3). Generally, insect fitness is associated with the availability of food and habitat (Ritchie and Tilman, 1992). The grasshopper species, *Euchorthippus unicolor*, feed mainly on grasses in our experimental site (Zhong et al., 2014). A small increase in grass biomass yield in plots with moderate grazing intensity was found (Fig. 1b), likely because of sheep's preference for forbs improved grass competition, and further stimulated the growth of grasses (Gao et al., 2008; Zhu et al., 2017), but excessive sheep foraging is not beneficial for grasses. Furthermore, previous studies found a positive impact of grass presence on grasshopper fitness (Hudewenz et al., 2012; Specht et al., 2008). However, this was not observed in this study (Fig. 5), possibly because food availability may not be an important factor, considering the small intake of grasshoppers (White, 2008; Branson, 2017).

Herbivorous insects fitness has long been linked to food quality, especially plant nitrogen, because higher plant nitrogen content could enhance plant protein needed by herbivores (Awmack and Leather, 2002; Rode et al., 2017). Contradicting these findings, our results showed that sheep grazing decreased N content of *L. chinensis* (Fig. 1d), but improved grasshopper fitness (Fig. 5), which is consistent with other cases (Cease et al., 2012). Other studies also showed that N-fertilization can negatively affect grasshopper survival (Ebeling et al., 2013; Zhu et al., 2019b). Several potential mechanisms may explain this negative relationship. First, nitrogen enrichment often causes a stoichiometric mismatch between plants and their herbivores, which can prevent a grasshopper from reaching the intake target due to a surplus or a deficit of particular elements in the nutrient content of its food (Ibanez et al., 2017). Second, changes in N content can affect a plant's physical and chemical traits (Zhu et al., 2019b), which may in turn alter *E. unicolor* food selection. These two mechanisms may be responsible for the negative relationships between N content of *L. chinensis* and survival of *E. unicolor*. Although our results indicated that plant nitrogen is likely an important driver of grasshopper fitness, further experiments are needed to elucidate the mechanism for how changes in plant nitrogen content influence grasshopper fitness.

Microclimates of habitat for insects is another important factor for their fitness (Buckley and Nufio, 2014; Branson, 2017). In our study, grazing by large herbivores reduced plant cover and height (Fig. 1g and h), which may alter microclimate for *E. unicolor*, with an increase in light intensity and air temperature and a decrease in air humidity (Fig. 2). The change in microclimate caused by grazing may be responsible for enhancement in fitness of *E. unicolor*. Grasshopper activity and growth are temperature-dependent, so habitat with more favorable air temperatures can help them to achieve their preferred body temperature (Ahnesjö and Forsman, 2006), and improves metabolic efficiency (Willott and Hassall, 1998). Sunlight may be necessary for grasshopper survival and oviposition in the study area, which explains why there were more grasshoppers in sites receiving more sunlight (H. Zhu et al., observation). However, large scale (i.e. four-day interval) recording of microclimatic variables in this study may not adequately capture the exact favorable microclimate for grasshoppers. Although grasshoppers are adept at behavioral thermoregulation, the detailed mechanism of solar radiation and thermal radiation effects on grasshopper fitness needs further exploration.

4.2. Grazing effects on grasshopper abundance

A growing body of research has found that higher grazing intensity

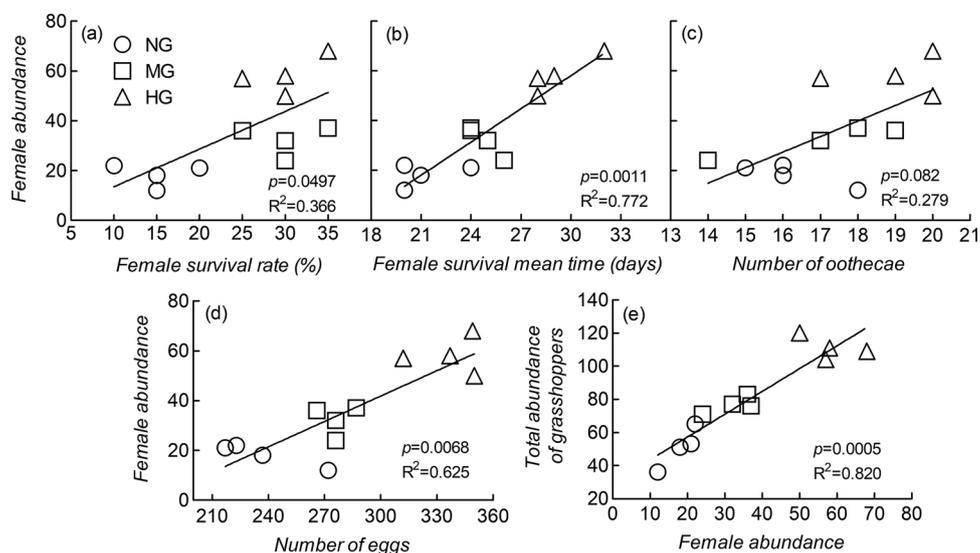


Fig. 6. Relationships between female abundance and female survival rate (a), and female survival mean time (b), and female survival mean time (b), and number of oothecae (c), and number of eggs (d), and between total abundance of grasshoppers and female abundance (e) under different grazing intensities (NG: ungrazed; MG: moderate grazing intensity; HG: heavy grazing intensity) ($n = 12$, regression analysis, $p < 0.05$).

tends to increase grasshopper abundance (Cease et al., 2012; Joubert et al., 2016; Zhu et al., 2017). Our results reinforce this finding (Fig. 4). Change in *E. unicolor* abundance induced by grazing is likely attributed to two possible reasons. The increase in *E. unicolor* abundance could be partially due to immigration. It is well-known that insects migrate towards favorable habitat that benefits their survival and reproduction, contributing to overall population growth (Doak, 2000; Hu et al., 2014). Our study suggests that large herbivore grazing may induce more grasshoppers to migrate into habitat where there is a favorable microclimate for them. This immigration of grasshoppers leads to higher grasshopper abundance in grazed plots. Additionally, our results showed that higher survival and egg production of *E. unicolor* females in grazed plots were positively linked to female abundance (Fig. 6). The finding indicates that insect fitness may be closely linked to their abundance, which is consistent with other cases (Vannette and Hunter, 2009; Xi et al., 2018). Such higher intrinsic rate of fitness could in turn enhance *E. unicolor* abundance.

4.3. Implication for grazing management

Recommendations for insect-oriented grazing practices depend on the targeted species and their associated habitats. A higher grazing intensity (9.2 sheep ha⁻¹ in this study) is often recommended in a meadow steppe (Hao et al., 2015; Zhu et al., 2017), whereas a low intensity is often suggested in tall grasslands (van Klink et al., 2015; WallisDeVries et al., 2016). These results are inconsistent with the intermediate disturbance hypothesis that suggests some insect species may perform the best under moderate grazing intensity (Jerrentrup et al., 2014; Lázaro et al., 2016), but the abundance of some species could negatively respond to increasing grazing intensity (Johansson et al., 2019; Perrin et al., 2020). In our studied system, grazing management with higher intensity benefits grasshopper abundance (Zhong et al., 2014; Zhu et al., 2017), which is similar with other cases (Kruess and Tschamtko, 2002; Jauregui et al., 2008). Therefore, to increase grasshopper population or other species with similar traits in meadow steppe, extensive grazing intensity comparable to the level in our study is suggested. However, caution is needed when increasing grazing intensity as we need to consider the interplay of a suite of sustainable conservation issues and agro-economic targets. Multiple factors, such as grassland type (WallisDeVries et al., 2016), large herbivore species (Zhu et al., 2015), and insect guild or species identity (Vandegheuchte et al., 2017; Zhu et al., 2019a) should be paid attention to. Additional experiments are also needed in the future to quantify complex relationships between these factors, and their effects on grassland

grasshoppers.

5. Conclusion

In this study, we demonstrated that extensive grazing intensity can significantly enhance grasshopper fitness, thereby favoring their abundance. Therefore, grasshopper fitness should be integrated into grassland management when considering the conservation and monitoring of grasshoppers (Gardiner, 2018). However, as grasshoppers are only one of the components of the insect community in grassland ecosystems and the responses of insect species in various grassland types may differ, we advocate flexible and adaptive management practices to balance the optimization of insect populations and communities and other management objectives for grassland conservation.

Declaration of Competing Interest

None of the authors on this manuscript have competing interests on this work.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2020.107012>.

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