

Differential responses to warming and increased precipitation among three contrasting grasshopper species

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Abstract

We conducted a field manipulation experiment to investigate developmental and demographic responses to warming and increased precipitation in three Inner Mongolian grasshopper species that differ in phenology (an early-season species *Dasyhippus barbipes*, a mid-season species *Oedaleus asiaticus*, and a late-season species *Chorthippus fallax*). Infrared heaters were used for warming the ground surface by 1–2 °C above the ambient condition and periodic irrigations were applied to simulate a 50% increase in annual precipitation. We found that warming advanced the timing for egg hatching and grasshopper eclosion in each of the three species. However, grasshopper diapause and increased precipitation appeared to offset the effect of warming on egg development. Hatching and development were more strongly affected by warming in the mid-season *O. asiaticus* and the late-season *C. fallax* relative to the early-season *D. barbipes*. Warming by ~1.5 °C advanced the occurrence of the mid-season *O. asiaticus* by an average of 4.96 days; while warming and increased precipitation interactively affected the occurrence of the late-season *C. fallax*, which advanced by 5.53 days. Our data and those of others suggest that most grasshopper species in the Inner Mongolian grassland are likely to extend their distribution northward with climate change. However, because of the differential response to warming we demonstrate for these species, the different grasshopper species are predicted to aggregate toward the middle period of the growing season, potentially increasing interspecific competition and grazing pressure on grasslands.

Keywords: climate change, diapause, grasshoppers, grassland, Inner Mongolia, phenology

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Introduction

Global warming has been a worldwide concern, particularly for its impact on ecosystem structure and function. The latest International Panel on Climate Change (IPCC) assessment on climate change indicates that global average temperature has risen by about 0.74 °C since 1850 and may continue to increase by 1.1–6.4 °C more by the end of this century (IPCC, 2007). The warming has brought profound effects on terrestrial ecosystems across a wide range of processes ranging from the behavior of individual organisms to community-level biodiversity and the function of entire eco-

systems (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003; Parmesan, 2006).

For individual organisms, increased temperature directly affects processes such as photosynthesis, respiration and growth in plants, and metabolic and developmental rates in many animals (Hughes, 2000; Kiritani, 2006; Musolin, 2007). Studies covering a diverse range of taxonomic groups and biological events have also demonstrated strong relationships between phenological events and climate. For example, analyses of long-term meteorological data and biological observations have shown that warming causes advancement in the occurrence of first leaf (Menzel, 2000; Menzel *et al.*, 2001) and flower (Fitter *et al.*, 1995; Luo *et al.*, 2007) in plants, earlier calling and breeding of amphibians (Beebe, 1995; Gibbs & Breisch, 2001), and

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laying and migration of birds (Both *et al.*, 2004; Gaston *et al.*, 2005). Global warming is also likely to cause shifts of species distribution to higher latitude (Smith, 1994; Thomas & Lennon, 1999; White *et al.*, 1999) or altitude (Grabherr *et al.*, 1994; Pounds *et al.*, 1999; Luckman & Kavanagh, 2000) as well as extensions of the growing season (Menzel & Fabian, 1999; White *et al.*, 1999; Menzel, 2000). Other known biological effects of warming include changes in population dynamics (Sillett *et al.*, 2000; Cullen *et al.*, 2001), biodiversity and community composition (Harte & Shaw, 1995; Sagarin *et al.*, 1999; Barbraud & Weimerskirch, 2001; Bradshaw & Holzapfel, 2001; Gross, 2005), and carbon cycling in ecosystems (Cox *et al.*, 2000; Luo, 2007).

Insects are the largest group of terrestrial animals comprising more than one million species. As poikilothermal animals, insects are sensitive to climate change (Roy & Sparks, 2000). Past studies have indicated that warming can increase overwintering survival (Kiritani, 2006), accelerate growth, and enhance fecundity (Miles *et al.*, 1997) of insects. As in other plants and animals, many insect species, especially those in the temperate zone, have been found to shift their distribution to higher latitudes in concert with recent climate warming (Paulson, 2001; Battisti *et al.*, 2005; Hassall *et al.*, 2007). For example, among the butterfly species investigated in Europe, 63% expanded their distribution northward (Parmesan *et al.*, 1999) while the northern boundary of Bush Hopper, *Ampittia dioscorides*, in America extended 420 km further north in the past four decades (Crozier, 2003, 2004). Various species have also shifted their distribution to higher altitudes (Battisti *et al.*, 2005). Many insects have shown advanced phenophases with climate warming. For example, in England, warmer springs have advanced the appearance and flight of butterflies and dragonflies (Roy & Sparks, 2000; Forister & Shapiro, 2003); higher winter temperature caused by heating pipes advanced the phenophase in species of Auchenorrhyncha (Masters *et al.*, 1998). For species that are unable to shift their distributions, climate change can contribute to habitat loss or alteration. For example, it has been found that in just 30 years, a 1.3 °C rise in temperature has reduced habitat area by one-third for 16 butterfly species in central Spain (Wilson *et al.*, 2005). Overall, studies to date show that, while global warming has different effects on different species, in total these may result in major changes in ecosystem trophic structure (Roth & Masters, 2000; Andrew & Hughes, 2005), potentially leading to mismatches of insects with their host plants.

Grasslands are an important terrestrial ecosystem in the biosphere, in which grasshoppers occur not only as insect pests but also as important primary consumers in mediating transfer of plant production to higher trophic

levels. Therefore, studying the responses of grasshoppers to climate change is important in assessing the possible effects of climate change on grassland ecosystems. There are about 10 000 grasshopper species worldwide (Yin *et al.*, 1996), with 172 being found in Inner Mongolian grasslands (Li *et al.*, 2007) and displaying significant niche differentiation in temporal, spatial and food dimensions (Kang & Chen, 1994). Among the Inner Mongolian grasshoppers, all species have only one generation per annum, occur in different seasons, and form sequential developmental cohorts (Kang *et al.*, 2007). According to the timing of occurrence, grasshopper species in Inner Mongolia can be categorized into three groups: early-, mid- and late-season (Kang & Chen, 1994). All of these species overwinter as eggs in soil. To cope with seasonal fluctuations in climate, complex life histories have evolved; these permit maximum exploitation of warmer seasons while cooler seasons are survived by production of more resistant forms, such as diapause stage (Butterfield & Coulson, 1997). Inner Mongolian grasshoppers lay both diapause and nondiapause eggs, most of which can safely survive during the winter season. In most cases, the diapause eggs enter diapause in embryo stage 19 (Hao & Kang, 2004a, b, c; Zhao *et al.*, 2005).

With regard to the specificity of grasshopper traits and the response of other insects to climate change, we hypothesized that each species would respond differentially to warming and increased precipitation due to their distinctive phenologies. Early-season species occur in late spring, when temperature is lower than that of the occurrence time of mid- and late-season species, and could be more susceptible to increase in temperature. Moreover, as temperature and precipitation often covary, increased precipitation could partially offset the amplitude of temperature increase. Finally, because there is only one generation for grasshoppers of Inner Mongolia, diapause could counteract the effects of warming on egg development. To test those hypotheses, we conducted a field manipulation experiment in Inner Mongolian grassland during 2006–2007 using three species differing in phenological strategy. For each grasshopper species, (1) development, diapause and hatching of eggs, (2) survival and development of nymphs, (3) longevity and fecundity of adults, and (4) sex ratio and survival of their offspring were studied to assess the effects of artificially increased temperature and precipitation.

Materials and methods

Study site and grasshopper species

The experiment was conducted in Duolun County of Inner Mongolia Autonomous Region (latitude

41°46'–42°39'N, longitude 115°50'–116°55'E, elevation 1150–1800 m a.s.l.), China. The site is in a semiarid steppe region where mean annual temperature, precipitation and potential evaporation are 1.6 °C, 386 and 1748 mm, respectively. Mean temperature for the most recent 10 years rose by 1.89 °C compared with the 10-year period in the 1950's, while annual precipitation has varied somewhat erratically. *Stipa krylovii*, *Artemisia frigida* and *Potentilla acaulis* are dominant plant species on the study site.

Three dominant grasshopper species of contrasting occurrence time were chosen to investigate the effect of warming and increased precipitation. The three species are: *Dasyhippus barbipes*, which is an early-season species, whose adult population peak in mid-June; *Oedaleus asiaticus*, which is a mid-season species, whose adults mainly occur in mid-July; and *Chorthippus fallax*, which is a late-season species, whose peak of adult population appears in mid-August (Kang & Chen, 1994).

Experimental design and treatments

Experimental design was a split-plot with two levels of warming (i.e. with or without warming treatment) as the main factor and two levels of water input (i.e. natural precipitation or supplemented water input by irrigation to produce a 50% increase in annual precipitation) as the subfactor, with five replications. There were five pairs of 3 m × 4 m plots. In each pair, one plot received the warming treatment while the other was kept under the natural temperature. The warming treatment was achieved by suspending a 165 cm × 15 cm MSR-2420 infrared radiator (Kalglo Electronics, Bethlehem, PA, USA) 1.85 m above each plot. For plots being kept under the natural temperature, 'dummy' heaters of the same shape, size and installation were used for mimicking the shading effect artificially introduced into the experiment by the warming facilities.

Each 3 m × 4 m plot was equally divided into four subplots. Two diagonal subplots in each plot, which were assigned randomly, were sprinkle-irrigated with 20 mm water twice a month from May through September in 2006 and 2007, while the other two subplots were left untreated. Polyvinyl chloride barriers, 25 cm in height (with 20 cm being inserted into the soil), were used to separate the irrigated and nonirrigated subplots. In total, there were four treatments in the experiments: natural condition (W_0P_0), warming (W_1P_0), increased precipitation (W_0P_1), and warming + increased precipitation (W_1P_1).

In each subplot, three 60 cm × 60 cm × 45 cm cages, which were made of 40-mesh white nylon screen, were installed for containing the grasshoppers, one for each species arranged in random order. The bottom edge of

the cages was inserted into the soil to prevent escape. The screening reduced solar radiation by 30%, but only altered temperature slightly.

Soil temperature and water content were measured at 5 cm depth in subplot center with a Hobo H8 weather station (Onset Computer, Bourne, MA, USA) in three subplots for each treatment. Data were recorded at a 10 min interval and averaged hourly from July through November in 2006 and from April through June in 2007.

Grasshopper and egg collection

During the occurrence time of each species, adults of *D. barbipes*, *O. asiaticus*, and *C. fallax* were collected near the experimental site. Several thousand adults were collected for each grasshopper species and used in the experiments.

Eggs were collected in two ways. The adults of each species were divided into two groups. One group of adults was transferred into cages of the plot and directly laid eggs into the soil ('natural eggs'). Another group were caged in rearing boxes maintained at 30 ± 1 °C during the day and 25 ± 1 °C at night in the laboratory with a photoperiod of 14/10 h day/night, which matches with the natural conditions of the grasshopper occurrence period. Sand was placed on the bottom of boxes as oviposition substrate. Eggs were collected and reserved in the refrigerator at 5 °C until we obtained sufficient quantity. All eggs were relatively uniform in embryonic stage; in the following these are referred to as 'initially synchronized eggs.' For *D. barbipes* and *C. fallax*, 10 sets of initially synchronized eggs were embedded into soil at 5 cm depth in each subplot, with a minimum of 100 eggs in each set. For *O. asiaticus*, five sets of initially synchronized eggs were embedded into soil at 5 cm depth in each subplot, with 80 eggs in each set. Natural eggs of each species were dug out and allotted in the subplots with the same sample size as initially synchronized eggs.

Development, hatching and diapause of eggs

A sample of the embedded eggs was retrieved every month until winter and the live eggs were dissected to examine their embryonic stages. In the following year, the eggs were sampled and dissected from April onward. When eggs with the most advanced stage were about to hatch (or reached embryonic stage 25 or 26), all eggs were transferred into an incubator at 26 °C. The hatchlings were counted and recorded daily. The initially synchronized eggs and natural eggs were sampled separately, but the data were merged in statistical analysis as the two types of eggs did not differ significantly in treatment responses.

By the end of September of 2006, the embedded eggs were sampled and transferred into an incubator at 30 °C. Egg hatching was monitored daily for up to 90 days. The hatchlings were recorded and removed daily. If eggs turned flaccid, brown or moldy, they were classified as dead (Hao & Kang, 2004a,b,c). The cream-colored and robust eggs were considered alive even after 90 days, and were dissected at the end of the experiment to determine their embryonic development stage (Hao & Kang, 2004a,b,c). Those at embryonic stage 19 after 90 days of incubation were considered as diapause eggs (Hao & Kang, 2004a,b,c), and included in the calculation of diapause rate.

Survival and eclosion of the nymphs

The eggs that remained after sampling and dissection were preserved in plots over winter. In spring and summer of 2007, they were transferred into incubators at 30 °C before their natural hatching time. First instar nymphs were collected and transferred into cages installed in each subplot within 2 days. Nymphs of *D. barbipes* and *C. fallax* were transferred into 40 cages with 90 individuals in each and *O. asiaticus* into 20 cages with 50 individuals in each. Sufficient grass seedlings were provided daily. The quantity and stage of nymphs were determined every 4 or 5 days until they reached the fifth instar, after which they were inspected daily. The newly molted adults were removed, sexed and recorded, and the survival and eclosion time of the nymphs were then determined.

Longevity and fecundity of adults

During eclosion, adults were transferred into new cages in the same subplots. Sixty individuals for each of *D. barbipes* and *C. fallax* (sex ratio of 1:1), and 40 individuals for *O. asiaticus* (sex ratio of 1:1) were transferred into each cage for each species. The number of adults was recorded every 2 or 3 days. After one and a half months, cages were removed and the soil was sieved to obtain egg pods, and the longevity and fecundity were then determined before eggs were refrigerated at 5 °C. In the following year, the eggs were cultured in an incubator at 26 °C. The sex ratio of hatchlings and survival rate of those eggs were determined.

Statistical analyses

Analysis of variance (ANOVA) for split-plot design was used to evaluate the effects of warming, increased precipitation and their respective interactions. To correct for heterogeneity of variances, frequency data were transformed by arcsine-square root for statistical ana-

lyses. Data for embryonic stage were analyzed using repeated-measures ANOVA to accommodate the multiple measurements of eggs across sampling dates. Multiple comparisons were performed to detect the difference among three species using Tukey's test ($P < 0.05$). All analyses were performed with SPSS software (SPSS 13.0).

Results

Treatment effects of warming and irrigation on microclimate

The microclimate data showed that in the natural precipitation and irrigated subplots, warming resulted in an average increase by 1.50 and 1.34 °C in soil temperature and decrease by 0.24% and 1.27% in soil water content respectively, while irrigation reduced the soil temperature by 0.32 and 0.48 °C and increased soil water content by 2.11% and 1.08%, respectively, in the natural temperature and warming subplots (Fig. 1).

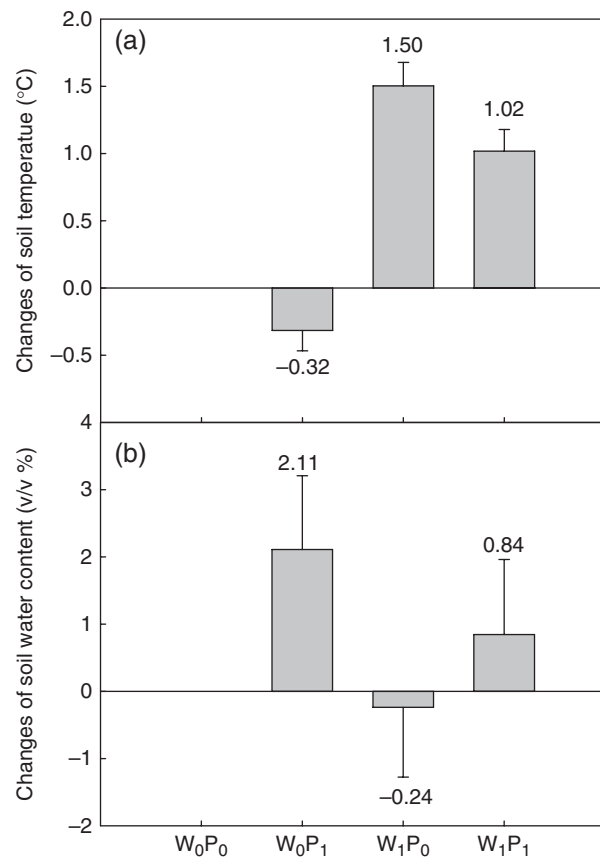


Fig. 1 Changes of mean soil temperature and water content at 5-cm depth induced by warming and increase in precipitation. W₀P₀, natural condition; W₀P₁, increased precipitation; W₁P₀, warming; W₁P₁, warming + increased precipitation. Data are mean values ± SE.

Development, hatching and diapause of eggs

Warming significantly advanced egg development in all three grasshopper species (*D. barbipes*: $P = 0.007$; *O. asiaticus*: $P < 0.001$; *C. fallax*: $P < 0.001$) (Fig. 2, Table 1). However, the magnitude of this effect differed for the three species. In *D. barbipes*, warming advanced the egg development by less than one stage overall (Fig. 2a). In *O. asiaticus*, warming advanced egg development by 1.34 stages in September and by as much as 5.55 stages in May of the following year (Fig. 2b). In *C. fallax*, warming advanced egg development by 2.91 stages in October and by up to 3.65 stages the following May. The test of the following June showed a markedly decreased effect of warming on egg development (Fig. 2c). Increased precipitation decelerated egg development in *O. asiaticus* ($P = 0.015$), while showing no significant effect in *D. barbipes* and *C. fallax* (Fig. 2, Table 1).

Warming significantly advanced the hatching of eggs in all three grasshopper species (*D. barbipes*: $P < 0.001$; *O. asiaticus*: $P < 0.001$; *C. fallax*: $P = 0.019$) (Fig. 3, Table 1), with advancement of 0.55 days in *D. barbipes*, 3.23 days in *O. asiaticus*, and 0.50 days in *C. fallax*. Increased precipitation delayed egg hatching by 1.38 days in *O. asiaticus* ($P = 0.003$) while showing no significant in

D. barbipes. In *C. fallax*, egg hatching was advanced by 1.10 days (Fig. 3, Table 1).

Warming and increased precipitation interactively advanced egg hatching in *C. fallax* by 4.55 days ($P = 0.044$) compared with the natural environment control. However, it had no apparent effect in other two species.

The egg diapause rate differed significantly ($P < 0.001$) among the three grasshopper species, and was not affected by warming or increased precipitation (Table 1). Almost all eggs in *D. barbipes* ($99.7 \pm 0.2\%$) and a significantly high proportion ($86.8 \pm 1.1\%$) in *O. asiaticus* entered diapause before the late autumn, whereas the eggs of *C. fallax* had the lowest diapause rate ($1.6 \pm 0.3\%$).

Survival and eclosion of nymphs

Warming significantly advanced the eclosion in *O. asiaticus* (female: $P = 0.020$; male: $P = 0.005$) and *C. fallax* (female: $P = 0.025$; male: $P = 0.032$) (Fig. 4, Table 1). Increased precipitation significantly delayed eclosion in *D. barbipes* (female: $P = 0.002$; male: $P < 0.001$) and *O. asiaticus* (female: $P = 0.005$; male: $P = 0.020$). Warming advanced eclosion by 0.75 days in *D. barbipes*, 1.73 days in *O. asiaticus*, and 1.58 days in *C. fallax*; whereas increased precipitation delayed eclosion by 1.05 days in *D. barbipes* and 2.63 days in *O. asiaticus*, but had no significant effect in *C. fallax*. Warming and increased precipitation had no significant effects on nymph survival of *D. barbipes* and *O. asiaticus*, but increased precipitation significantly ($P = 0.018$) improved the nymph survival in *C. fallax* (Table 1).

Longevity and fecundity of adults

Warming had no significant effect on the longevity and fecundity of the three grasshopper species (Table 1) although increased precipitation significantly ($P = 0.002$) reduced the Lt50 (the time for 50% survival rate of individuals) of males by 10% and the fecundity ($P = 0.048$) by 17% in *O. asiaticus* (Table 1). Warming, increased precipitation and their interaction did not have significant effect on the sex ratio and survival of offspring (Table 1).

Discussion

The grasshoppers of Inner Mongolia form seasonally sequential cohorts because of differences in development thresholds, accumulative growth temperatures, and diapause traits (Hao & Kang, 2004a,b; Zhao *et al.*, 2005). Here we selected three grasshopper species of different occurrence time to test their responses to artificial warming, and found that warming by 1.5°C advanced the phenology of each of the three

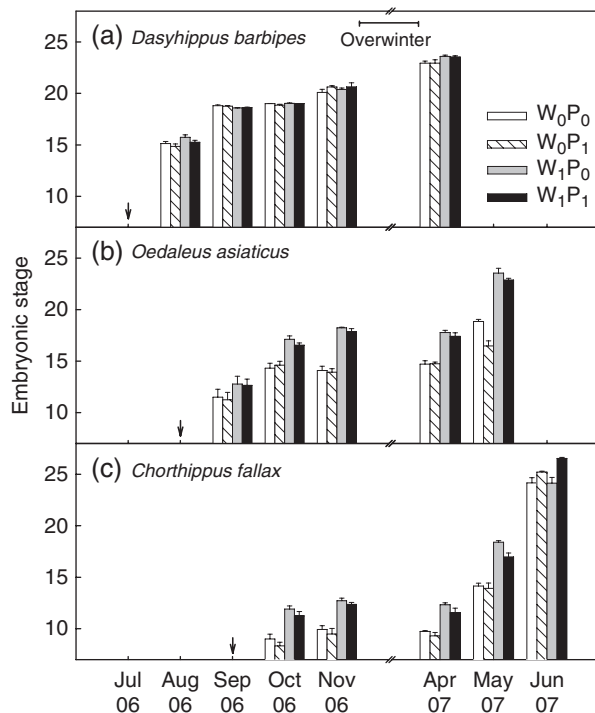


Fig. 2 Embryonic stage of eggs of (a) *Dasyhippus barbipes*, (b) *Oedaleus asiaticus* and (c) *Chorthippus fallax*. W_0P_0 , natural condition; W_0P_1 , increased precipitation; W_1P_0 , warming; W_1P_1 , warming + increased precipitation. The arrow indicates egg embedding into the soil. Data are mean values \pm SE. $n = 5$.

Table 1 Results (*P* values) of split-plot ANOVA on the effect of primary factor: warming (W) and secondary factor: increase in precipitation (P) on egg, nymph, adult and offspring of three grasshopper species

Developmental stage	Index	Source of variance	Species					
			<i>Dasyhippus barbipes</i>		<i>Oedaleus asiaticus</i>		<i>Chorthippus fallax</i>	
			♀	♂	♀	♂	♀	♂
Egg	Embryonic development	W	0.007		<0.001		<0.001	
		P	0.761		0.015		0.437	
		W × P	0.691		0.822		0.960	
	Diapause rate	W	0.142		0.479		0.937	
		P	0.937		0.786		0.853	
		W × P	0.937		0.498		0.110	
	50% hatching time	W	<0.001		<0.001		0.019	
		P	0.347		0.003		0.005	
		W × P	0.347		0.605		0.044	
Nymph	50% eclosion time	W	0.093	0.074	0.020	0.005	0.025	0.032
		P	0.002	<0.001	0.005	0.020	0.367	0.250
		W × P	0.141	0.050	0.473	0.578	0.645	0.416
	Survival	W	0.842		0.740		0.787	
		P	0.412		0.816		0.018	
		W × P	0.924		0.753		0.810	
Adult	50% survival time	W	0.958	0.615	0.636	0.609	0.679	0.494
		P	0.963	0.214	0.246	0.002	0.661	1.000
		W × P	0.309	0.896	0.884	0.537	0.422	0.195
	Fecundity	W	0.239		0.185		0.983	
		P	0.124		0.048		0.059	
		W × P	0.866		0.487		0.929	
Offspring	Sex ratio	W	0.352		0.080		0.806	
		P	0.438		0.646		0.318	
		W × P	0.901		0.806		0.546	
	Survival	W	0.947		0.202		0.453	
		P	0.799		0.864		0.364	
		W × P	0.571		0.618		0.176	

grasshopper species, mainly by accelerating the development of eggs and nymphs. Mean hatching and eclosion time advanced by 0.55 and 0.75 days in early-season *D. barbipes*, 3.23 and 1.73 days in mid-season *O. asiaticus*, and 0.50 and 1.58 days in late-season *C. fallax* in natural precipitation. Warming more strongly affected the phenology of mid- and late-season grasshopper species, while having a decreased effect upon early-season species. Therefore, various responses of different grasshoppers to climate warming likely depend on their diapause and eco-physiological traits, other than simply thermal accumulation.

Most grasshopper species in temperate regions have one generation per year and lay eggs that overwinter in soil. In Inner Mongolia, early-season species predominantly lay diapause eggs, late-season species lay nondiapause eggs, and mid-season species lay both diapause and nondiapause eggs. This specificity in diapause appears to be a common phenomenon in

grasshoppers of the region (Hao & Kang, 2004a,b). Egg diapause normally occurs in embryonic stage 19, and terminates during winter or in next spring (Fisher *et al.*, 1996; Hao & Kang, 2004a,b). Therefore, warming accelerates the development of diapause eggs until they reach embryonic stage 19. The nondiapause eggs develop before winter and continue development until hatching if environmental conditions are appropriate (Fig. 5). In our study, early-season *D. barbipes* produced diapause eggs, and the eggs were therefore least responsive to warming, which obviously accelerated the development of nymph stage. However, the late-season *C. fallax* produced predominantly nondiapause eggs, and thus warming advanced the phenology of egg development. The mid-season *O. asiaticus* produces both diapause and nondiapause eggs, but most eggs enter diapause in autumn. Warming advanced the development of nondiapause eggs and the timing of diapause of diapause eggs of *O. asiaticus*.

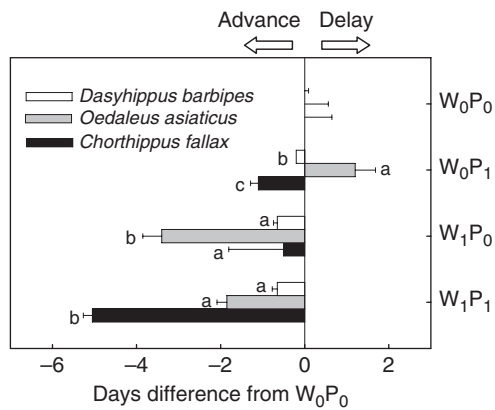


Fig. 3 Changes in the 50% hatching time of eggs compared with W_0P_0 of *Dasyhippus barbipes* (white bar), *Oedaleus asiaticus* (grey bar) and *Chorthippus fallax* (black bar). W_0P_0 : natural condition; W_0P_1 : increased precipitation; W_1P_0 : warming; W_1P_1 : warming + increased precipitation. Data are mean values \pm SE. $n = 5$. Different letters indicate significantly different values between treatments ($P < 0.05$).

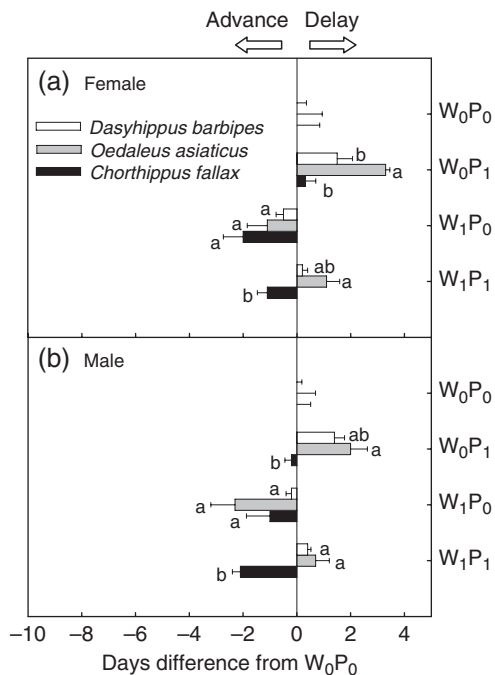


Fig. 4 Changes in the 50% eclosion time compared with W_0P_0 of *Dasyhippus barbipes* (white bar), *Oedaleus asiaticus* (grey bar) and *Chorthippus fallax* (black bar). (a) Female; (b) Male. W_0P_0 : natural condition; W_0P_1 : increased precipitation; W_1P_0 : warming; W_1P_1 : warming + increased precipitation. Data are mean values \pm SE. $n = 5$. Different letters indicate significantly different values between treatments ($P < 0.05$).

When all developmental stages were considered, we estimated that warming by $\sim 1.5^\circ\text{C}$ could advance the occurrence of the mid-season *O. asiaticus* by 4.96 days

and the late-season *C. fallax* by 2.08 days; combination of warming and increased precipitation advanced the occurrence of the late-season *C. fallax* by 5.53 days. However, the early-season *D. barbipes* displayed relatively little response (1.30 days), largely because it produces diapause eggs. Thus, our results indicate that diapause partially counteracts the impact of warming in a given year. Our study agrees with the result of Hassall *et al.* (2007) on the relationship between phenology and temperature in British Odonata: there was a tendency in Odonate species with display egg nondiapause to advance their phenology. So, diapause is not only a primary factor in achieving seasonal synchronization but also buffers the effect of changing temperature (Cherrill & Begon, 1989; Bale *et al.*, 2002).

The impact of climate change on organisms mostly results from altered thermal and precipitation dynamics, which are two auto-correlated factors. The responses of grasshopper to climate change are not only determined by individual effects of temperature and precipitation, but also their interactions. In this study, warming and increased precipitation interactively affected hatching of eggs in *C. fallax*. For the other two grasshopper species, warming and increased precipitation had no significant interactive effect. This is because increased precipitation partially counteracted the effect of warming in *D. barbipes* and *O. asiaticus*, and decelerated the egg development and reduced the population survival rate in *O. asiaticus*, leading to lack of response to a combination of warming and increased precipitation. Both *D. barbipes* and *O. asiaticus* are xerophytous species (Kang & Chen, 1994), adapted to the arid environment of the Inner Mongolian grassland region. Therefore, increased precipitation could have adverse effects on these two xerophytous species. Under natural precipitation, warming led to the greatest phenological advancement in *O. asiaticus*. In contrast, *C. fallax* is a mesophytous species with high requirements for moisture; both warming and increased precipitation are in favor of the hatching and egg development of *C. fallax*. In other grasshopper species, drought has been found to reduce hatching and nymph development (Mukerji & Gage, 1978). Consistent with this, *C. fallax* had the largest advancement induced by both warming and increased precipitation.

Overall, because of their strong cold tolerance, the grasshopper species in this study are anticipated to expand their distributions northward in response to global warming (Hao & Kang, 2004a,b,c; Zhao *et al.*, 2005) as growing season warming would be beneficial to adult migration and dispersal. However, continued warming could increase the extinction risk of more southerly populations of the late-season species, whose eggs could hatch before the winter due to lack of

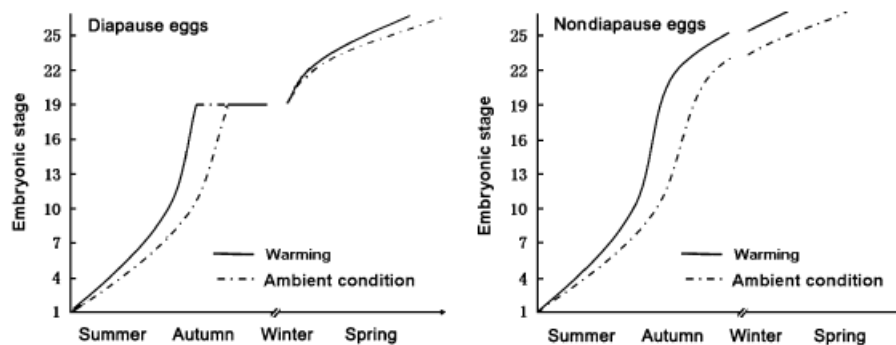


Fig. 5 Developmental divergence of non- and diapause eggs in warming and ambient conditions.

diapause and therefore suffer from chilling stress. This would result in major changes in the structure and diversity of the local grasshopper communities.

Climate change may also alter the probability of grasshopper outbreaks. In particular, the different sensitivities of different grasshopper species to changes in temperature regimes may affect their population outbreaks and their damage to grasslands. Although increased temperature had the smallest effects on early period species, warming may prolong the occurrence period of mid-season species and advance the initial occurrence of late-season species. As a result of these differential responses to warming, the three species are predicted to increase temporal overlap during the middle period of growing seasons, thereby increasing interspecific competition and intensifying grazing pressure on the grasslands. Such effects would be consistent with previous proposals that continued climate warming would cause a disruption of interspecies relationships (Voigt *et al.*, 2007) and enhance survival of overwintering eggs (Chladny & Whitman, 1998).

Like other herbivores, insects interact with other organisms through bottom-up and top-down mechanisms (Walker & Hones, 2001; van Asch *et al.*, 2007). Different trophic levels show different sensitivities to climate and these sensitivities increase with trophic rank: carnivore > herbivore > producer (Gordo & Sanz, 2005; Parmesan, 2007; Voigt *et al.*, 2007). A meta-analysis of phenology change in 203 species of different trophic rank from the northern hemisphere showed that the mean phenological advance of butterfly species is significantly larger than that for herb and grass taxa (Parmesan, 2007). Other studies also indicate that insects are more sensitive to changing temperature regimes than their host plants (Parmesan & Yohe, 2003; Root *et al.*, 2003). However, it is yet to be determined whether the observed phenological changes we document for different Inner Mongolian grasshopper species in response to warming and precipitation would match their host plants.

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