Agricultural irrigation mediates climatic effects and density dependence in population dynamics of Chinese striped hamster in North China Plain

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Summary

1. Several studies show that climatic (extrinsic) factors can interact with density-dependent (intrinsic) factors to alter long-term population dynamics, yet there is a surprising lack of investigations of how anthropogenic disturbance modifies such dynamics. Such interactions could be especially important in agricultural systems subject to climate change.

2. We investigated the effects of density dependence, climate, recurrent disturbance from flood irrigation and their interactions on the population dynamics of an important rodent pest, the Chinese striped hamster (*Cricetulus barabensis*), over 27 years in the croplands of the North China Plain.

3. Strong density-dependent feedbacks occurred at both annual and seasonal scales. While warmer weather increased population sizes in nonbreeding seasons, this effect was counteracted by the negative effect of flood irrigation in breeding seasons. Precipitation showed significant positive effects in nonbreeding seasons, but negative effects in breeding seasons.

4. There were important interactions between intrinsic dynamics, extrinsic dynamics and disturbance. Low temperature significantly increased the strength of density dependence in nonbreeding seasons, whereas intensification of flood irrigation area significantly increased the strength of density dependence but reduced the effect of summer precipitation in breeding seasons.

5. Overall climate change is expected to increase population levels, but anthropogenic disturbance from flood irrigation will help prevent long-term population increases. The interactions between anthropogenic disturbance and both intrinsic and extrinsic (weather-driven) population dynamics caution that we need to consider anthropogenic disturbance as an integral component of population responses to climate change.

Key-words: agricultural activity, global warming, human disturbance, small mammal

Introduction

Our earth has been experiencing intensified global warming during the past century, which may significantly influence the population dynamics of animals (Zhang 2012). Specially, winter temperature in Northern Hemisphere showed more obvious increase (Trenberth *et al.* 2007). Global warming often significantly changes precipitation patterns in many regions of the world (Trenberth *et al.* 2007), which may also affect population dynamic

processes of animals. Previous studies have demonstrated that temperature can affect populations of small rodents either directly through influencing survival and reproduction (Aars & Ims 2002; Zhong, Liu & Wan 2007) or indirectly through affecting their habitats (Kausrud *et al.* 2008; Jiang *et al.* 2011). Winter temperature was found to be very critical in affecting population dynamics of small mammals in Northern Hemisphere (Eriksson 1984; Lindström & Hörnfeldt 1994; Jon & Ims 2002; Korslund & Steen 2006). Precipitation is also well known to affect small rodent populations in arid and semi-arid environments either indirectly through its influence on plant

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growth and seed production (Previtali *et al.* 2009; Jiang *et al.* 2011) or directly by altering individual reproduction or survival (Brown & Ernest 2002). However, it is still unknown how current climate warming affects population dynamics of small mammals by interacting with the accelerated human disturbance and density dependence.

Our earth has also been experiencing intensified human disturbance because of rapid developments of agriculture, industry and population expansion during the past century. In human-disturbed agro-ecosystems, density dependence and precipitation were found to be important factors in affecting population dynamics of several rodent species (Leirs *et al.* 1997; Singleton *et al.* 2001; Stenseth *et al.* 2003a; Andreo *et al.* 2009; Lima *et al.* 2009). However, human impacts on small rodents have not been quantitatively assessed in the previous studies. In agro-ecosystems, human activities may interact with natural population dynamics and produce outcomes that are hard to predict. In fact, small rodents can thrive very well in agro-ecosystems (de la Pena *et al.* 2003), although their population can be influenced by farming practices (Jacob & Hempel 2003). Compared with natural ecosystems, food supply in croplands is more secure and stable than in natural conditions because of regular crop planting. The small mammal population is likely to fluctuate according to harvesting practice and shows spatial pattern with crop structure (Williams *et al.* 1994; Ellis *et al.* 1997). The human disturbance of agricultural activities (e.g. ploughing, irrigation) may also negatively impact small rodents by destroying their burrow systems or through drowning (Marsh 1994; Lloveras 2001; Jacob 2003). Thus, agricultural activities may have important impacts on the small mammals in agro-ecosystem, but studies on how agricultural activities interact with intrinsic process and climate warming are still lacking.

The effects of interactions between intrinsic and extrinsic factors on population dynamics have drawn much attention to ecologists in recent years (Previtali *et al.* 2009; Wang *et al.* 2009). A few studies found that density dependence was influenced by conditions of weather, resources and predation (Forchhammer *et al.* 1998; Barbraud & Weimerskirch 2003; Jacobson *et al.* 2004; Wang *et al.* 2006; Previtali *et al.* 2009; Wang *et al.* 2009). It was suggested that alteration of environmental carrying capacity might be an explanation (Lima, Previtali & Meserve 2006; Wang *et al.* 2006). Human disturbances may interact with effects of density dependence and climate in affecting population dynamics; unfortunately, such studies have not been conducted. Interactions such as these could have important implications for predicting the effects of climate change in human-disturbed systems.

The Chinese striped hamster (*Cricetulus barabensis*, Pallas 1773) is a dominant pest rodent species of the North China Plain, an area that contains most of the arable land and almost one-third of crop production in China (Zhang 2011). This species is solitary and breeds throughout the year, but the pregnancy rates are very low in winter because of cool temperature. Population densities of *C. barabensis* generally peak in spring and exhibit irregular multi-annual fluctuations. During the past three decades, populations were impacted by enhanced irrigation, fertilization, ploughing and so on because of rapid agricultural modernization in China, but they might have benefited from continued climate warming that may increase survival and reproduction in winter. In this study, we investigated the effects of density dependence, climate, irrigation and their interactions on the population dynamics of *C. barabensis* at annual and seasonal scales, based on long-term data collected from 1984 to 2010. We tested three hypotheses: (i) climate warming will enhance population growth of *C. barabensis* in the nonbreeding season; (ii) intensified flood irrigation will negatively affect populations in the breeding season; (iii) climate and irrigation will alter the strength of density dependence, and the effects of irrigation and climate on density dependence will interact. Tests of these hypotheses would add to our understanding of the effects of climate change on population dynamics of pest species in agro-ecosystems.

Materials and methods

STUDY SITE

The study area is located close to Wugong Town (38°05′–38°09′ N, 115°34′–115°44′E), Raoyang County, Hebei Province, North China (Fig. 1a). It lies in the warm temperate zone with four distinct seasons: spring (March–May), summer (June–August), autumn (September–November) and winter (December–February). This study area is characterized by a warm temperate monsoon climate with warm summer and cold winter. The average annual precipitation is approximately 553 mm and falls mostly in summer. The average annual temperature is about 12·7 °C. Vegetation consists mainly of crops such as wheat, corn, peanuts and cotton. Irrigation and ploughing are the most important agricultural disturbances to *C. barabensis* populations; they mainly occurred during the breeding season (from spring to autumn) of hamsters in the study region. During the past three decades, flood irrigation area has increased steadily in this region. Although flood irrigation significantly increased crop yield, which may benefit the hamster species, it could also help reduce population density of the hamster species by destroying their burrow systems in the farmland.

RODENT ABUNDANCES AND DEMOGRAPHIC DATA

The abundance of rodents was surveyed monthly in croplands from January 1984 to December 2010 (Fig. 1b), using wooden snare traps (14 × 5·5 × 1 cm). There were up to 21 sampling sites (Fig. 1a), and about four sites of the 21 sites were selected for sampling per month. Within each site, there were four to eight plots covering main habitat types (approximately 50 m apart). Within each plot, there were two trapping lines (parallel 25–30 m apart). Along each trapping line, 25 traps were set with an interval of about 5 m. Wooden snare traps baited with peanuts were set after sunset and collected the next morning. The trapping was conducted for 3 successive days in each plot. To
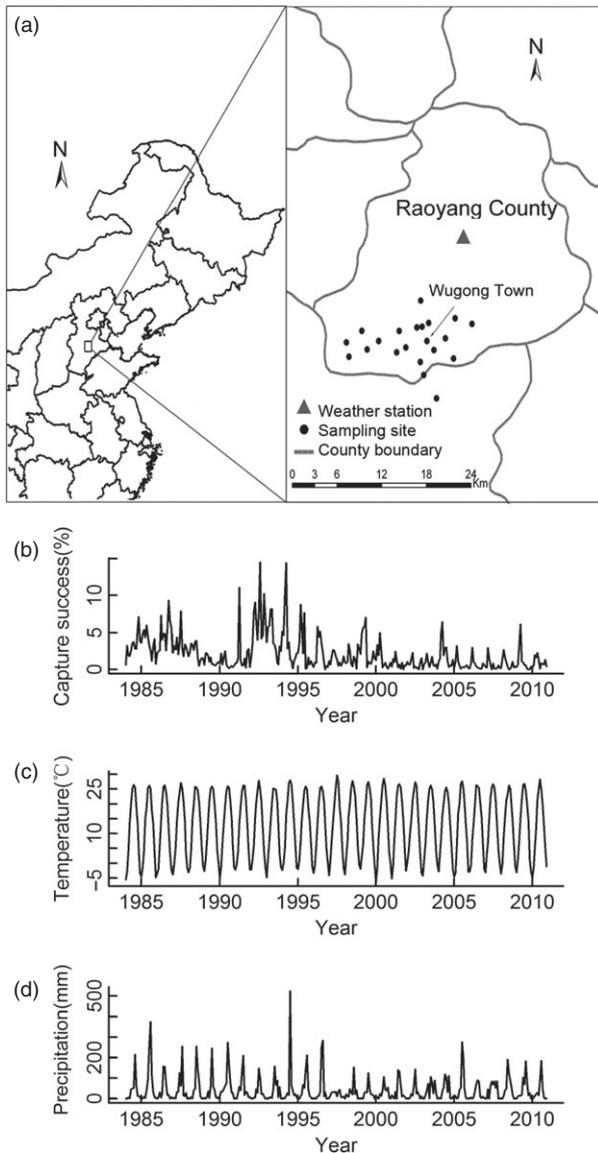
Fig. 1. The study site, *C. barabensis* population and climate data. Study area and sampling sites nearby Wugong Town, Raoyang County, Hebei Province, China (a); monthly variations of population density (capture success,%) of *C. barabensis* (b), temperature (c) and precipitation (d) in the study site.

minimize the negative effect of successive trapping on population dynamics, each site was surveyed with an interval of at least 3 months. Because the dispersal rate of the hamsters is very high under frequent agricultural disturbances (Zhang, Zhu & Yang 1993), and the area of sampling plots was small relative to the size of the study area, losses because of trapping would have had only minor impacts on population dynamics. The captured rodents were identified, weighed and dissected to ascertain pregnancy and body mass. The relative monthly population abundance was represented by the capture success (%), defined as (total number of captured animals/total number of snare traps) × 100. Annual and seasonal abundances were calculated by averaging the monthly data of the durations. In the study area, there are four other sympatric rodent species, including Greater long-tailed hamster (*Tscherskia triton*), Striped field mouse (*Apodemus agrarius*), House mouse (*Mus musculus*) and

Brown rat (*Rattus norvegicus*). These species are potential competitors because they have similar diets or habitat demands in field conditions. Population density of all four species was pooled to be the population density of competitors of *C. barabensis*. The age of *C. barabensis* was defined using body masses, with juveniles $\leq$ 15 g, 15 g < subadults $\leq$ 20 g, adults >20 g (Chang 1985).

CLIMATE AND AGRICULTURAL DATA

Local monthly temperature (°C) and precipitation (mm) data were obtained from the China Meteorological Data Sharing Service System (http://cdc.cma.gov.cn; Fig. 1c,d). Annual and seasonal climate data were calculated from the monthly data. Annual irrigation area (ha) and crop yield in the study area during 1984–2008 were obtained from local Bureau of Agriculture of the Raoyang County (data were not available for 2009 and 2010). However, because crop yield was highly correlated with irrigation area (Pearson's correlation = 0·86, $P < 0·001$), and likely was determined by irrigation area, we used only irrigation area in our analyses to avoid problems of multicollinearity.

POPULATION DYNAMIC MODELS

We used the *R*-function (Berryman & Turchin 2001), $R_t = \ln(N_t) - \ln(N_{t-1})$, to represent the realized per capita population change rate of *C. barabensis*. We used per capita population change rates (*R* values) as dependent variables, natural logarithm (ln) transformed population density (*X*), ln-transformed population density of all competitors (described above; *Z*), temperature, precipitation and irrigation area (hereafter 'irrigation') as independent variables. We modified the variables and constructed separate models for annual and seasonal timescales. Because of small sample sizes, we only considered additive effects in models, and separately investigated interactions afterwards.

In the following equations, the smoothed functions (f_i, h_i and g_i) were all implemented using natural cubic spline functions, with a maximum of four knots. A natural cubic spline is constructed from sections of a cubic polynomial, which is widely used to detect nonlinearity (Wood 2006). We also defined the parameters α as an intercept and ε as a normally distributed stochastic perturbation. We modified α and ε with subscripts to represent annual and seasonal models.

Annual model

We constructed a model of annual population change rates to investigate the effects of density, competition, temperature, precipitation and irrigation. The subscript *y* refers to annual (yearly) timescale. The subscript *d* refers to time lag ($d = 0$ or 1 year). Ln-transformed annual density of the Chinese striped hamster and its all competitors in year $t-1$ are $X_{y,t-1}$ and $Z_{y,t-1}$, respectively. Average annual temperature in year $t-d$ is temperature$_{y,t-d}$, annual precipitation in year $t-d$ is precipitation$_{y,t-d}$ and annual irrigation area in year $t-d$ is irrigation$_{y,t-d}$. By conducting analysis of partial autocorrelation function (PACF) of the striped hamster population (see Fig. S1, Supporting information), we found the hamster species showed only first-order feedback structure. Thus, we only consider the time lag of one year in our models.

$$R_{y,t} = \alpha_{y,t} + f_1(X_{y,t-1}) + f_2(Z_{y,t-1}) + h_1(\text{temperature}_{y,t-d})$$
$$+ h_2(\text{precipitation}_{y,t-d}) + g_1(\text{irrigation}_{y,t-d}) + \epsilon_{y,t} \qquad \text{eqn 1}$$

Seasonal models

We defined the population change rate in breeding season ($R_{b,t}$) as the population change from spring to autumn and the population change rate in nonbreeding season ($R_{n,t}$) as the population change from last autumn to current spring. In the nonbreeding season, especially in winter, there is a small amount of reproduction. Nonbreeding season model (eqn 2) and breeding season model (eqn 3) were constructed to investigate seasonal population dynamics. Variables used in the following two models were all seasonal. Ln-transformed densities of *C. barabensis* in the spring and autumn of year t are $X_{s,t}$ and $X_{a,t}$, respectively. The competitor density in the autumn of year $t-1$ is $Z_{a,t-1}$, and the competitor density in the spring of year t is $Z_{s,t}$. The temperature and precipitation variables used in the following models are seasonal variables covering the respective seasons (autumn$_{t-1}$, winter$_{t-1}$ or spring$_{t-1}$ for nonbreeding season model; spring$_t$, summer$_t$ or autumn$_t$ for breeding season model). Because irrigation was only conducted during the breeding season, the effect of irrigation was only considered in the breeding season model (eqn 3), and the values of irrigation$_{b,t}$ were the same as irrigation$_{y,t}$.

$$R_{n,t} = X_{s,t} - X_{a,t-1} = \alpha_{n,t} + f_3(X_{a,t-1}) + f_4(Z_{a,t-1}) \\ + h_3(\text{temperature}_n) + h_4(\text{precipitation}_n) + \epsilon_{n,t} \quad \text{eqn 2}$$

$$R_{b,t} = X_{a,t} - X_{s,t} = \alpha_{b,t} + f_5(X_{s,t}) + f_6(Z_{s,t}) \\ + h_5(\text{temperature}_b) + h_6(\text{precipitation}_b) \\ + g_2(\text{irrigation}_{b,t}) + \epsilon_{b,t} \quad \text{eqn 3}$$

We used generalized additive models (GAM; Hastie & Tibshirani 1990) to fit the above models (eqns 1–3) to the data. All analyses were carried out in R version 2.12.1 using the MGCV package version 1.7–2 (Wood 2006; R Development Core Team 2010). The optimal roughness of the smoothing terms was determined by minimizing the generalized cross-validation value (GCV; Stige *et al.* 2006). The GCV of a model is an index for the model's out-of-sample predictive mean squared error (Cox *et al.* 1981) and is also used to compare alternative model formulations. The best-fitting models were selected from candidate models (annual: 107; nonbreeding season: 87; breeding season: 127) by following the rule of minimization of GCV on the condition that all variables must be statistically significant ($P < 0.05$), and then were used for inferences (see Tables S1 and S2, Supporting information). Residuals from GAMs were approximately normally distributed across all the models and showed no significant autocorrelation (see Figs S2 and S3, Supporting information). For model validation, we also used data of the first 20 years (1984–2003) for fitting seasonal GAMs and made the prediction for the rest years.

PARAMETRIC MODELLING ANALYSES

As an alternative analysis to GAMs, we also constructed parametric linear regression models (LMs). The LMs structure were the same as eqns 1–3 in GAMs except that the functions (f_i, h_i and g_i) were replaced by linear regressions. We also considered the pairwise interactive terms. LMs model selections were conducted by following the above same rules of GAMs (Tables S1, S3 and S4, Supporting information).

ANALYSES OF INTERACTIONS IN GAMS

In addition to the interactive analyses in LMs, to test the possible interactive effects between density dependence and climate or irrigation area, we used another two methods: a moving-window method (which is a new method proposed in this study) and the tensor product smoothing method (TE, implemented in MGCV package). For moving-window analysis (see details in Fig. S4, Supporting information), we selected a time window (from 7 to 12 years) to estimate the density dependence coefficient b using linear regression models (e.g. in breeding seasons, $R_{n,t} = a + b \times X_{a,t-1}$), and the average temperature or precipitation or irrigation area. Then, we tested the significance of correlation coefficients between b and the average temperature, precipitation or irrigation area for a given time window. In the same way, the interaction between precipitation and irrigation area in breeding seasons was also tested. TE is also appropriate for studying interactions of quantities measured using different units and helps illustrate the interactive relationship between two variables (Wood 2006). Different combinations of exploratory variables described in the above models were smoothed by TE for annual and seasonal time-scales, and statistically significant terms (at $P < 0.05$) were used to make inferences.

WINTER REPRODUCTION AND SEASONALITY

The monthly population data were standardized to illustrate the seasonal fluctuation by (monthly density – yearly mean)/yearly standard deviation. We also analysed the pregnancy rate and proportion of juveniles to identify the effects of climate warming on reproduction of the hamster species. The 27-year data were divided into five periods, and the data for each period were pooled to calculate pregnancy rate in winter and proportion of juveniles in spring. The effects of climate and population density on pregnancy rate in winter, and the proportion of juveniles in spring were also analysed using GAMs and LMs (see Table S5, Supporting information).
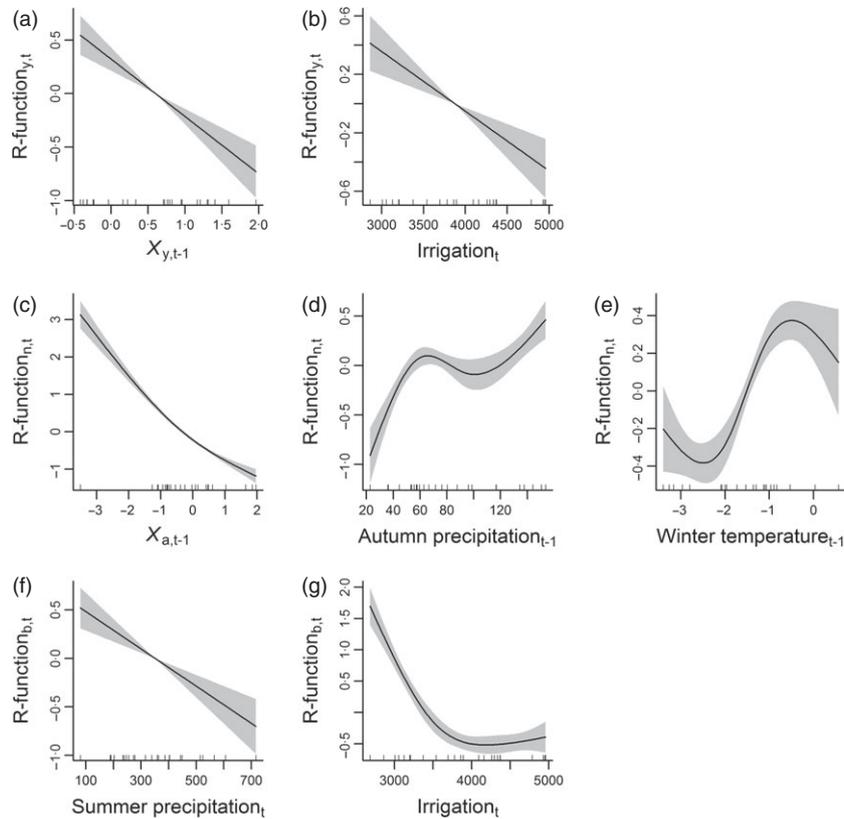
Results

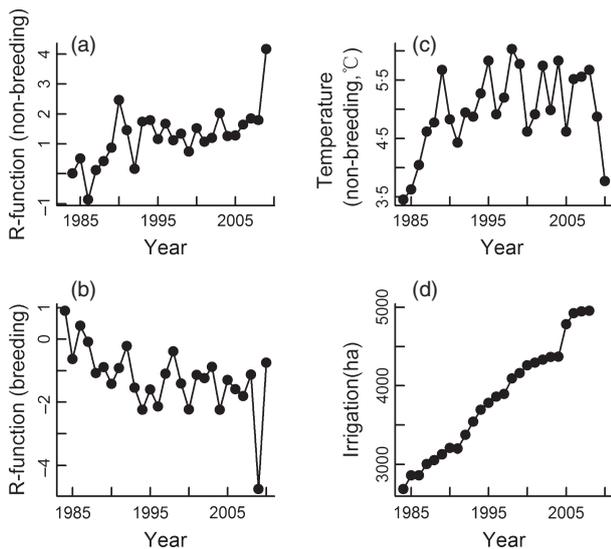### ANNUAL POPULATION CHANGE RATE

The best-fitting annual model from GAMs revealed a linear negative first-order feedback effect of density ($F_{1, 21} = 8.85$; $P < 0.01$; Fig. 2a) and a linear negative effect of irrigation ($F_{1, 21} = 4.82$; $P < 0.05$; Fig. 2b) and explained 30.1% of the total deviance. The best-fitting model results from main-effect LMs showed negative effects of density ($X_{y,t-1}$) and irrigation (Irrigation$_{y,t}$) on annual change rate ($R_{y,t}$): $R_{y,t} = 1.837045 - 0.535818 X_{y,t-1} - 0.000408$ Irrigation$_{y,t}$ (deviance explained, 30.1%, Table S1, Supporting information). The results of LMs were the same as those of GAMs.

POPULATION CHANGE RATE IN NONBREEDING SEASONS

The population change rate in nonbreeding seasons and temperature showed increasing temporal trends (Fig. 3a,c).

Fig. 2. The results of annual and seasonal generalized additive models for *C. barabensis*. Partial effects of annual density (a) and irrigation area (b) on the annual population change (R-function$_{y,t}$); partial effects of the last autumn density (c), the last autumn precipitation (d) and the last winter temperature (e) on the nonbreeding season population change (R-function$_{n,t}$); partial effects of summer precipitation (f) and irrigation area (g) on the breeding season population change (R-function$_{b,t}$). Shaded areas: 95% confidence bands.


Fig. 3. The seasonal population change rates (R-functions) for *C. barabensis* (a,b); temperature covering the nonbreeding season (c) and yearly irrigation area (d).

The best-fitting nonbreeding season model from GAMs showed a nonlinear negative feedback of density ($F_{2, 17.4} = 55.95$; $P < 0.001$; Fig. 2c), nonlinear positive

effects of autumn precipitation ($F_{3, 17.4} = 4.34$; $P < 0.05$; Fig. 2d) and winter temperature ($F_{3, 17.4} = 5.00$; $P < 0.05$; Fig. 2e). In total, the nonbreeding season model explained 91% of deviance.

Moving-window analyses showed that the strength of density dependence in nonbreeding season decreased with increase of winter temperature (Fig. 4a; results of other time windows are similar, see Fig. S5, Supporting information). The tensor product smoothing method (TE) showed similar results (Fig. 4d).

As compared with GAMs, the best-fitting model from main-effect LMs showed negative effect of autumn density ($X_{a,t-1}$) and positive effect of autumn precipitation (Pre. au$_{t-1}$): $R_{n, t} = 0.656672 - 0.664917X_{a, t-1} + 0.006044$ Pre. au$_{t-1}$ (deviance explained, 80%, Table S1, Supporting information). Significant positive interaction between winter temperature (Temp. wi$_{t-1}$) and autumn density was also found in the interactive LMs: $R_{n,t} = 0.958365 + 0.007349$Pre.au$_{t-1} + 0.223652$Temp.wi$_{t-1} + 0.268709$ Temp. wi$_{t-1} \times X_{a,t-1}$ (deviance explained, 84%, Table S4, Supporting information). The negative effects of autumn density and positive effects of autumn precipitation and winter temperature observed in GAMs were also seen either in the main-effect or interactive LMs. Positive interaction between autumn density and winter temperature was observed in both GAMs and LMs.
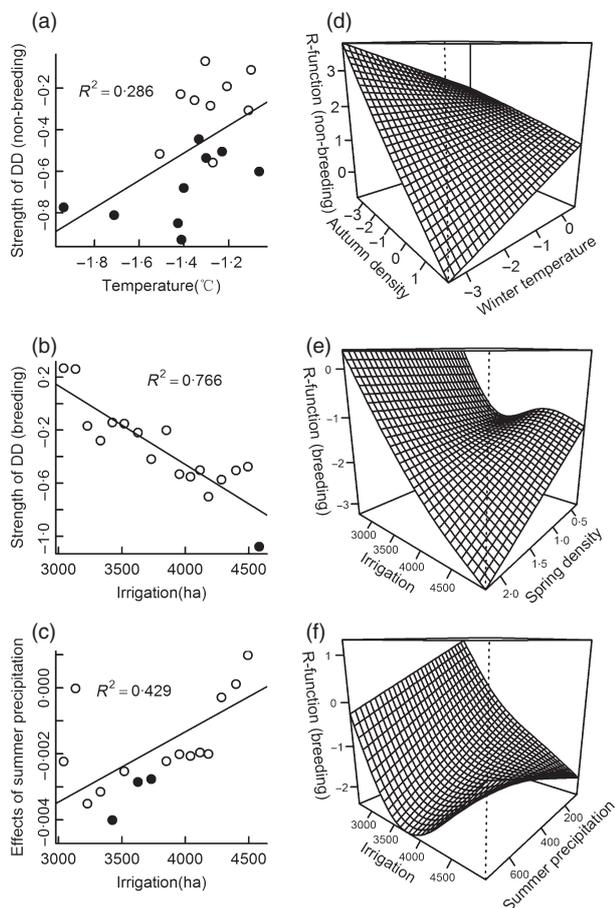
Fig. 4. Interactions among density dependence (DD), climate and irrigation. Relationships between strength of DD for non-breeding season and winter temperature (a), strength of DD for breeding season and irrigation (b), the effects of summer precipitation on breeding season *R*-function and irrigation (c). The regressions were based on 9-year moving-window analyses (described in Methods; solid dots, $P < 0.05$; hollow dots, $P \geq 0.05$). The interactive effects of density and winter temperature on *R*-function for nonbreeding season (d), of density and irrigation on *R*-function for breeding season (e) and of summer precipitation and irrigation on *R*-function for breeding season (f), predicted from tensor product smooths respectively.

POPULATION CHANGE RATE IN BREEDING SEASONS

The population change rate in breeding seasons showed decreasing trend but irrigation area showed increasing trend (Fig. 3b,d). The best-fitting breeding season model from GAMs showed a linear negative effect of summer precipitation ($F_{1, 20.6} = 6.16$; $P < 0.05$; Fig. 2f) and a non-linear negative effect of irrigation ($F_{2.8, 20.6} = 7.07$; $P < 0.05$; Fig. 2g). In total, 65% of deviance was explained for breeding season population change.

Moving-window analyses showed the strength of density dependence in breeding seasons increased with increase of irrigation area (Fig. 4b; for other moving windows, see Fig. S6, Supporting information). Tensor product smoothing showed similar results (Fig. 4e). Additionally, the moving-window method showed that the

strength of the effect of summer precipitation on population change was decreased with increases in irrigation area (Fig. 4c; for other moving windows, see Fig. S7, Supporting information). The tensor product smoothing method showed similar results but with some nonlinearity for irrigation when precipitation was high (Fig. 4f).

As compared with GAMs, the best-fitting model from main-effect LMs showed negative effects of spring density ($X_{s,t}$) and irrigation (Irrigation$_{b,t}$): $R_{b,t} = 2.577092 - 0.510549X_{s,t} - 0.000818$ Irrigation$_{b,t}$ (deviance explained, 45%, Table S1, Supporting information). The results from the interactive LMs showed a significant negative interaction between spring density and irrigation, as well as a negative interaction between density and summer precipitation (Pre.su$_t$): $R_{b,t} = -0.681352 + 4.247129X_{s,t} - 0.001113$ Irrigation$_{b,t} \times X_{s,t} - 0.001485$ Pre.su$_t \times X_{s,t}$ (deviance explained, 66.6%, Table S4, Supporting information). The results from GAMs and LMs are similar: the negative effects of spring density, irrigation and summer precipitation were all observed either in the main-effect models or in the interactive models. The different findings are as follows: LMs revealed the interaction between density and summer precipitation, while GAMs revealed the negative interaction between summer precipitation and irrigation; besides, LMs showed positive effect of spring density when irrigation and precipitation were low.

WINTER REPRODUCTION AND SEASONALITY

From 1991 onwards, the spring peaks of *C. barabensis* population became higher than between 1984 and 1990 (Fig. 5a). The pregnancy rate in winter (December, January and February) became higher after 1990 (Fig. 5b) and the proportion of juveniles also became higher in February, March, April and May (Fig. 5c; chi-square test, all $P < 0.01$).

The GAM model analysis of winter pregnancy rate revealed a nonlinear negative effect of density in winter ($F_{2, 22} = 60.89$; $P < 0.001$; Fig. 5d) and a positive effect of temperature in winter ($F_{1.4, 22} = 13.96$; $P < 0.001$; Fig. 5e). In addition, there was a negative effect of density in spring ($F_{1.2, 22.9} = 29.00$; $P < 0.001$; Fig. 5f) and a positive effect of temperature in winter ($F_{1, 22.9} = 21.52$; $P < 0.001$; Fig. 5g) on the proportion of juveniles of *C. barabensis* in spring.

The results from LMs were rather similar to those above (Table S5, Supporting information). The LMs analysis of winter pregnancy rate (P.wi$_t$) revealed a negative effect of density in winter (N$_{w,t}$) and a positive effect of temperature in winter (Temp.wi$_t$): Logit(P. wi$_t$) = $1.48714 - 0.46398$ N$_{w,t} + 0.25573$ Temp.wi$_t$. There was a negative effect of density in spring (N$_{s,t}$) and a positive effect of temperature in winter (Temp. wi$_{t-1}$) on the proportion of juveniles of *C. barabensis* in spring (J.sp$_t$): Logit(J.sp$_t$) = $-1.24714 - 0.12466$N$_{s,t} + 0.18371$ Temp. wi$_{t-1}$.
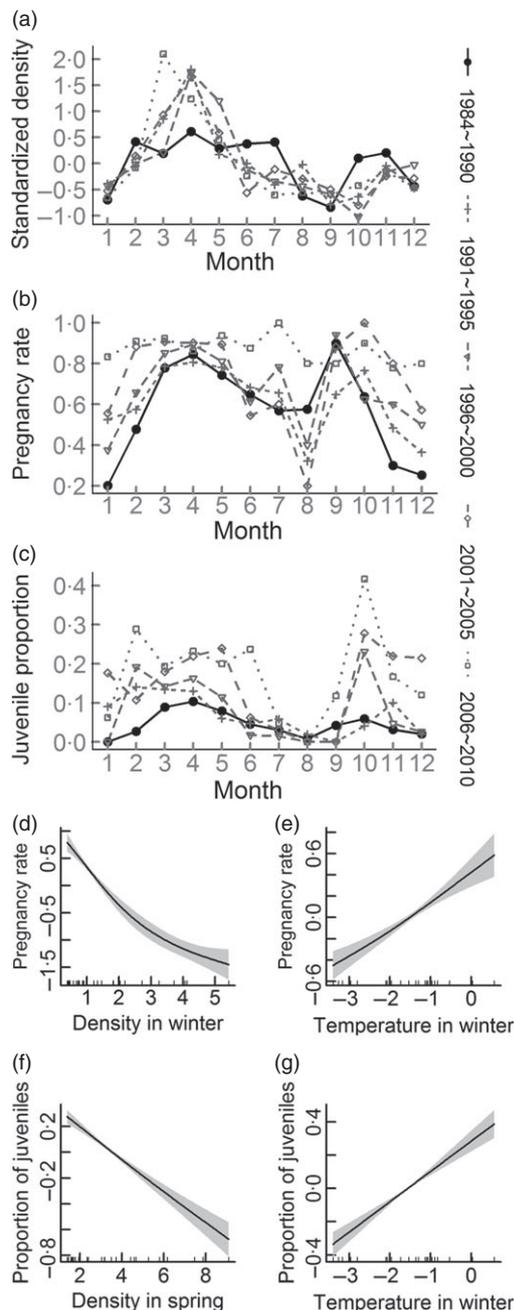
Fig. 5. Analyses of seasonality and winter production. Seasonal population pattern and winter reproduction of *C. barabensis* represented by population density (a), pregnancy rate (b) and proportion of juveniles, respectively (c). Partial effects of winter population density and winter temperature on the pregnancy rate in winter (d,e); partial effects of spring population density and winter temperature on the proportion of juveniles in spring (f,g).

MODEL PREDICTION

To validate our GAM models, we conducted analysis by splitting the data into two periods (1984–2003; 2004–2008, because the irrigation data was extended to 2008). For sake of simplification, we focused on re-analysis of seasonal GAMs because they had high explanatory power. The best-fitting nonbreeding season model showed a lin-

ear negative feedback of density ($F_{1,\ 13.2} = 27.1$; $P < 0.001$; Fig. 6a), a nonlinear positive effect of autumn precipitation ($F_{3,\ 13.2} = 5.68$, $P < 0.05$; Fig. 6b) and a linear positive effect of winter temperature ($F_{1,\ 13.2} = 6.95$, $P < 0.05$; Fig. 6c). In total, 83% of deviance was explained for nonbreeding season population change. The best-fitting breeding season model showed a linear negative effect of summer precipitation ($F_{1,\ 15.8} = 10.34$; $P < 0.01$; Fig. 6d) and a nonlinear effect of irrigation ($F_{2.6,\ 15.8} = 10.34$; $P < 0.001$; Fig. 6e). In total, 73% of deviance was explained for breeding season population change. No significant autocorrelation was found in residuals. The model results using data of 1984–2003 were very similar to those of models using the full data, and the prediction for period of 2004–2008 was quite good (Fig. 6f), suggesting the GAM models were robust.

Discussion

DENSITY-DEPENDENT EFFECTS

Previous studies have shown how density-dependent effects are altered by weather variables (Forchhammer *et al.* 1998; Barbraud & Weimerskirch 2003; Forcada *et al.* 2006; Wang *et al.* 2006). However, previous studies have not looked at how human disturbance interacts with such dynamics. There was an increase in negative feedback for penguins coupled with temperature decrease (Forcada *et al.* 2006). Variation in winter temperature was positively correlated with strength of density dependence in large herbivores because extremes of weather condition are likely to reduce carrying capacity of habitats (Wang *et al.* 2006). In this study, we also found that in the nonbreeding season, low temperature increased the strength of density dependence in *C. barabensis*, supporting the above observations in birds. In cold winters, hamsters need more foods for countering the low temperature in winter, which then may enhance intraspecific competition for food in caches or on the ground. In this study, we found for the first time that agricultural activity altered density dependence in breeding seasons. Specifically, we found that high flood irrigation area increased the strength of density dependence of the hamster species. This is probably because increase of flood irrigation area will reduce the suitable habitats in farmlands, likely increasing crowding and within-species competition. Our previous study indicated that flood irrigation would destroy burrows of hamsters in lower lands and forced them to assemble in higher lands or banks (Zhang *et al.* 1997), which may have enhanced intraspecific competition for space during breeding seasons. Interestingly, LMs revealed that high summer precipitation also increased strength of density dependence; the mechanism of summer precipitation might be similar to flood irrigation in affecting the habitats and burrows of hamsters.

As the main endogenous factor, density dependence has been widely recognized in many studies (Hansen, Stenseth &
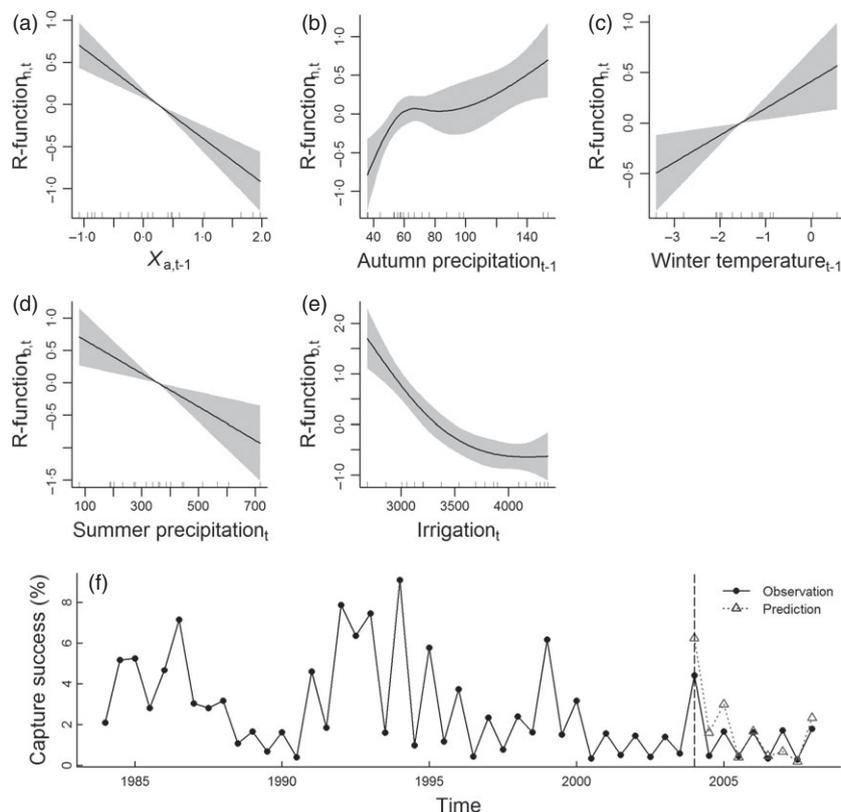
Fig. 6. The results of seasonal models fitting to the time series 1984–2003 and predictions for 2004–2008. Partial effects of the last autumn density (a), the last autumn precipitation (b) and the last winter temperature (c) on the nonbreeding season population change (R-function$_{n,t}$); partial effects of summer precipitation (d) and irrigation area (e) on the breeding season population change (R-function$_{b,t}$). The observed and predicted population of *C. barabensis* (f).

Henttonen 1999; Lima, A. Berryman & Chr. Stenseth 2006). Our results captured density dependence at annual and seasonal scales, indicating strong intraspecific competition also affect the population dynamics of rodents in the agro-ecosystem we studied. Based on previous both laboratory and field observations, *C. barabensis* is solitary and very aggressive. The intraspecific competition may result from food or space limitation (Rosenzweig & Abramsky 1985; Yoccoz *et al.* 2001).

It has been reported that density dependence may be different among seasons (Mallorie & Flowerdew 1994; Hansen, Stenseth & Henttonen 1999; Ratikainen *et al.* 2008). Some studies stressed the crucial role of density dependence in nonbreeding season for the rodent population dynamics in Northern Hemisphere (Hansen, Stenseth & Henttonen 1999; Saitoh *et al.* 2003; Stenseth *et al.* 2003b; Zhang *et al.* 2003), while others found that some rodents (e.g. leaf-eared mouse) showed density dependence only in the breeding season in a semi-arid region of Chile (Lima, Stenseth & Jaksic 2002b). Our seasonal analyses of GAMs show that significant seasonal density dependence is detected in the nonbreeding season as a main effect, while in breeding season as an interactive effect. Both main-effect and interactive LMs showed density dependence in both breeding season and nonbreeding seasons (Tables S1 and S4, Supporting information). It is

notable that interactive LMs revealed the positive effect of spring density on population change rate in breeding season when irrigation and precipitation were low, which is hard to explain. This was likely be caused by artificial effect of linear model fitting by considering interactions.

EFFECTS OF TEMPERATURE

Global warming is an increasing concern around the world. Temperature rise may affect rodent population growth. Pucek *et al.* (1993) reported that the warm June–July climate of the preceding year (bud formation year) triggered heavy seed crops and then outbreaks of forest rodents in the following year (Pucek *et al.* 1993). Increased temperature may benefit plant growth in early spring (Chmielewski & Rotzer 2001) and then may trigger earlier reproduction for hibernating rodents (Negus & Pinter 1966). However, winter temperature, linked to snow condition in some areas, may be negatively correlated with survival of rodents (Aars & Ims 2002; Korslund & Steen 2006). We found a nonlinear positive effect of winter temperature on the rate of population change of *C. barabensis* (Table S6, Supporting information). Increased temperature may benefit overwinter survival of rodents in areas without prolonged snow cover. Furthermore, we found that winter temperature increased

the hamster pregnancy rate in winter and the proportion of juveniles in spring (Fig. 5e,g).

Several studies suggest that temperature rise in spring or winter may alter species' phenology (Walther *et al.* 2002; Parmesan 2006). In this study, we found global warming since 1984 significantly changed the seasonal pattern of *C. barabensis*. During the study period, the nonbreeding season temperature showed obvious increase since 1984 (Fig. 3c). The seasonality of *C. barabensis* changed to a higher peak in spring, which happened around 1990. There was an obvious increase of pregnancy rate in winter and proportion of juveniles in early springs after 1990. Winter temperature showed positive effect on the pregnancy rate in winter and proportion of juveniles in spring; thus, rise of winter temperature may result in advanced and high breeding in nonbreeding seasons.

In our study, we found the effects of temperature on rodent population occurred at the seasonal scale but not at the annual scale. This is probably because the positive effects of temperature in the nonbreeding season were counteracted by the negative effects of irrigation area in the breeding season, resulting in nonsignificant effects of temperature on the annual scale. In addition, we found climate warming in winter also benefited hamsters by reducing the density-dependent effect (see above). Because the winter temperature is facing continuous increase in the study region, we should caution the potential population increase in nonbreeding seasons of the hamster species which often cause damages in agricultural production in early spring.

EFFECTS OF IRRIGATION

Croplands in the North China Plain are highly disturbed by many agricultural activities, an important one of which is flood irrigation. As far as we know, no study has been carried out to conduct quantitative analysis on the effect of agricultural activity on rodent population growth, and its effects on density dependence is also unclear. At annual and seasonal scales, we found consistent negative effects of irrigation on population change rate in breeding seasons (see Table S6, Supporting information). During the past three decades, the irrigated area has increased in size because of large governmental investment (Fig. 3d), which also increased per capita production of crops. Because *C. barabensis* prefers dry habitats and heavily relies on deep burrows in the field, frequent flood irrigation imposes catastrophic effect on their burrow systems (Zhang *et al.* 1997). Additionally, peanuts and soybean are favourable food of *C. barabensis* (Wang *et al.* 1992), and they are commonly planted in nonirrigated areas, while wheat and corn are planted in irrigation areas. Increase of irrigation also significantly reduced the plantation area of peanuts and soybeans, which might have imposed negative effect on *C. barabensis*. Owing to agricultural modernization in China, not only irrigation area increased

rapidly, but also harvesting efficiency was also improved, which made it more difficult for hamsters to store sufficient food for winter. It is notable that the strong negative effect of irrigation in the breeding seasons significantly outweighs the positive effect of warmer temperature in nonbreeding seasons. The overall result was a continued decline of hamster population density in the last 17 years. In addition, we found flood irrigation area interacted with the strength of density dependence in breeding seasons. Larger irrigation areas led to stronger density dependence in rates of population change during breeding seasons. Because flood irrigation can greatly reduce the suitable habitats (Zhang *et al.* 1997), we hypothesized that the increased strength of density dependence under increase of irrigation area might be caused by alteration of space resources, not by limitation of food resources.

It should be pointed out that traditional flood irrigation is not a high efficient way of using water resources. In the coming future, spraying irrigation is likely adopted in the agricultural regions, which would significantly reduce or remove the negative effect of flood irrigation on population growth of the hamster species.

EFFECTS OF PRECIPITATION

The positive effects of precipitation on population growth of rodents are well documented in arid and semi-arid areas (Dickman *et al.* 1999; Lima, Stenseth & Jaksic 2002a). A nonlinear relationship was also reported between rodent populations and precipitation in the flood plain of Australia because rodents cannot breed in very wet or dry conditions (Madsen *et al.* 2006). Precipitation may impose direct and indirect impacts on small rodents because moderate precipitation may benefit plant growth and then rodents, whereas heavy precipitation may kill rodents by flooding their burrows and nests (Brown & Ernest 2002). Our results indicate that precipitation exhibits different effects on population change of *C. barabensis* between nonbreeding season and breeding season. Autumn precipitation produced nonlinear positive effects on nonbreeding season population change, probably because of extending the crop harvest time, which may increase food storage for hamsters. Conversely, heavy summer precipitation may reduce hamster populations by destroying hamster burrows and drowning the infants. We found a novel interaction between climate and agricultural activities, whereby the negative effect of summer precipitation was reduced with the increase of irrigation area in breeding seasons. It seems reasonable that heavy rain and flood irrigation show similar negative effects in destroying the burrows of hamsters in breeding seasons. The weather became much drier recently in the study region than before, and such trend shows no sign of changing. Thus, flood irrigation will be still important in reducing population growth of the hamster species in breeding seasons.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. The partial autocorrelation of annual population density.

Fig. S2. Residual diagnostics for annual model.

Fig. S3. Residual diagnostics for non-breeding season model (a,b) and breeding season model (c,d).

Fig. S4. Illustration for moving window method.

Fig. S5. Moving-window analyses for the relationship between strength of density dependence (DD) and temperature in non-breeding seasons.

Fig. S6. Moving-window analyses for the relationship between strength of density dependence (DD) and irrigation in breeding seasons.

Fig. S7. Moving-window analyses for the relationship between effects of summer precipitation and irrigation in breeding seasons.

Table S1. Best-fitting main-effect population dynamic models (GAM and LM) fitted for *C. barabensis*.

Table S2. The annual, non-breeding season and breeding season candidate GAMs (only showing the ones including all significant terms, the same as below).

Table S3. Main-effect linear candidate models.

Table S4. Non-breeding and breeding season candidate models with interactions (only models with lower GCV than respect season main-effect linear models).

Table S5. Best-fitting models (GAM and LM) fitted to study the climatic effects on the reproduction of *C. barabensis* in winter.

Table S6. Summary of population dynamics GAM model results at the annual and seasonal scales for *C. barabensis*, with time lag in brackets.

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