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ORIGINAL ARTICLE

Effect of ENSO-driven precipitation on population irruptions of the Yangtze vole *Microtus fortis calamorum* in the Dongting Lake region of China

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Abstract

The Yangtze vole (*Microtus fortis* Buechner, 1889) is a small herbivore species that inhabits lake beaches in the Dongting Lake region along the Yangtze River in Southern China. Its population shows strong oscillations during the wet season due to summer precipitation-induced immigration away from the lake into adjacent rice fields. The effect of El Niño-Southern Oscillation-driven precipitation on population abundance and growth of the vole species is not fully understood. We undertook an analysis of the combined data of 4 time series covering 1981–2006 from 4 different sites and a separate analysis on a single time series (1981–2006) from one site. Our results demonstrate that a dual effect of El Niño-Southern Oscillation-driven precipitation on the population abundance of voles is time-dependent: precipitation in the current year has a positive effect, whereas precipitation in the previous year has a negative effect. The dual effect of precipitation on vole population is well explained by the unique interactions among vole population, precipitation water level and the lake beach habitat around Dongting Lake. We found that drier than average weather of the previous year benefited voles because their breeding habitats, lake beaches, were exposed for long stretches of time. Wet weather was found to increase the number of voles inhabiting rice fields because as the water level of the lake rose they were forced from beaches into surrounding rice fields. Summer precipitation in the Dongting Lake region was found to be positively associated with the sea surface temperature (SST) of the eastern tropical Pacific Ocean of the previous year and winter SST and spring SST of the current year. Annual rates of increase in the vole population of the reconstructed time series are negatively associated with the vole abundance and autumn precipitation of the previous year and winter precipitation of the current years. These results suggest that both extrinsic and density-dependent intrinsic factors may affect population dynamics of the Yangtze voles.

Key words: density-dependency, ENSO-driven precipitation, *Microtus fortis calamorum*, population outbreaks, Yangtze vole.

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INTRODUCTION

The Yangtze vole (*Microtus fortis* Buechner, 1889) is widely distributed in China. Among its 5 subspecies, the subspecies *Microtus fortis calamorum* has been identified as the primary rodent pest in the rice fields of the Yangtze River region (Chen *et al*. 1998). Since the 1970s, frequent population irruptions of the subspecies have been reported in the rice fields surrounding Dongting Lake, one of the largest lakes in the Yangtze River system. The area of lake beaches suitable for voles has increased rapidly since the 1970s due to cultivation of lake beaches, soil erosion and the establishment of hydropower stations in upper reaches (Zhou *et al*. 2002). The Yangtze voles migrate between lake beaches in the dry season and neighboring rice fields in the summer wet season. In the dry season from autumn to spring, the lake beaches serve as their breeding ground. Grasses on the lake beaches are favorite foods of the voles. In the wet season when the water level of the lake is high and flooding occurs, they retreat to the rice fields and cause huge damage to agricultural production. The damage is especially severe when the population density of the voles is high and when the lake water level rises rapidly, driven by heavy rain or water releases from upstream hydropower stations.

In June 2007, a large scale of population explosion suddenly occurred at Dongting Lake. The vole outbreak caused tremendous damage to agricultural crops and social panic among local farmers. For the first time, both central and provincial governments became actively involved in the control of these vole outbreaks. It was reported that a huge number of voles were captured within a few days of the population explosion.

Previous studies suggest several factors (e.g. precipitation, water-level and farming activities) that might contribute to population irruptions of the Yangtze vole in Dongting Lake. However, the results often contradict one another. For example, Wang *et al*. (2004) suggest that population abundances of voles are positively correlated to the duration of water levels below 27.5 m from autumn to the following spring, but negatively correlated to precipitation in March of the current year. Ye *et al*. (2006) report that the population abundance of the Yangtze vole is negatively correlated to lake water levels of previous flooding seasons, but positively correlated to the precipitation from December to March of the current year. Chen *et al*. (1998) and Guo *et al*. (2006) propose that cultivation of lake beaches since the early 1970s was probably an important reason for the worsening vole problem, whereas Li *et al*. (2007) believe that the recent government-driven programs to return cultivated farmlands to lake beaches might favor vole outbreaks. It is obvious that the present knowledge does not adequately explain the sharp spikes in vole populations. Furthermore, the present research does not allow for the prediction of outbreaks, which would lead to better management in the Dongting Lake region. There is an urgent need to clarify the links between vole population explosions and precipitation and the underlying mechanism between them. Because the size and distribution of vole populations are strongly influenced by the water level of the lake, the available site-specific studies are likely influenced by regional climatic factors, in particular by precipitation. Therefore, it is important to investigate the population dynamics of the voles at a regional scale.

Dongting Lake is located in the lower reaches of the Yangtze River. El Niño-Southern Oscillation (ENSO) has been shown to affect the precipitation of the Yangtze River (Zhang & Xue 1994). In El Niño years, the lower reaches of the Yangtze River typically receive less rain than normal years, but in the year following an El Niño, this region often gets more precipitation than average (Zhang & Xue 1994). Therefore, Dongting Lake is a very suitable site for studying the impact of ENSO–driven precipitation on vole outbreaks, and understanding the ecological consequences of global climate variations.

The Yangtze vole is one of the few vole species that is affected by large population fluctuations in the subtropical region. Periodic population oscillations of voles often occur in temperate and tundra zones, and many hypotheses have been suggested to explain the population cycles of voles (Batzli 1992, 1996; Krebs 1999). Understanding how external and intrinsic factors affect the population dynamics of Yangtze voles in the subtropical zone would benefit studies of population cycles of voles in temperate and tundra zones.

This study aims to study the effect of ENSO-driven precipitation on abundance and the annual rates of increase of the Yangtze vole populations in Dongting Lake through re-analysis of the available historical data. We also examine the association between the vole population and El Niño or sea surface temperature (SST) of the Eastern Tropical Pacific Ocean through precipitation in this region. Because in the year following an El Niño the lower Yangtze receives above average rainfall during the wet season (Zhang & Xue 1994), Dongting Lake experiences an increase in water level. The hypothesis we tested was that the rapid increase in water level during the wet season drives voles to migrate from lake beaches to the surrounding rice fields, which results in damage to rice fields. Based on this hypothesis, we made 2 predictions. First, summer precipitation in the Dongting Lake should be positively associated with the SST of the previous year. Second, the population abundance of voles should be positively associated with the summer rainfall of current years.

MATERIALS AND METHODS

Population data

Prior to 1980, there is no available population data for Yangtze voles in the Dongting Lake. Since 1980, there have been 4 sites around Dongting Lake where the vole population has been surveyed and investigated (Fig. 1). Chen *et al*. (1998) summarize data on the number of voles captured by several local farms during the wet season in Ruanjiang County (lower Dongting Lake) from 1981–1988. Local farmers captured swarming voles using trapping barrier systems along the lake dyke where huge jars were buried as pitfall traps. Ye *et al*. (2006) present a ranking system of vole abundance based on both population density and crop damages in Yiyang County (lower mid-Dongting Lake) from 1982–2005. The highest rank is defined as population densities > 2 vole burrows per 1 m^2 or crop damage > 20%. Li *et al* (2007) present data on vole abundance based on trap success (%) in the farmlands of Yueyang County (north Dongting Lake) in the wet seasons from 1992–2006 (excluding 1997, 1998, 1999 and 2001). Wang *et al*. (2004) provide data ranking vole abundance in Yueyang County between 1982 and 1993. The 5 ranks they designate are defined by trap success (%) using snare wooden traps: rank 1, < 7%; rank 2, 7.1–14%; rank 3, 14.1–21%; rank 4, 21.1–31%; rank 5, > 31%. The trap success (%) was calculated as: total number of captured voles/total number of traps.

In the present study, we reconstructed a regional time series of vole abundance from 1981–2006 based on the 4 available time series of Yangtze voles around Dongting Lake. There are 2 reasons for following this method. First, previous studies suggest that vole abundance in the wet season is mostly driven by the water level of the Dongting Lake. Therefore, regional precipitation should play a more important role in population outbreaks of voles than local precipitation. Furthermore, we were also interested in the ENSO-driven precipitation effect on the vole populations. Thus, we needed to analyze data relating to the regional-scale response of vole populations. Analysis at a regional scale requires correlation analysis between the pooled data of vole abundance and precipitation. Second, except for the time series by Ye *et al*. (2006), the 3 other time series are insufficiently long, but they are overlapped in time. This makes the reconstruction of a longer time series possible. All 4 time series mentioned above were standardized (zero mean and stand deviation = 1) for time-series analysis. This standardization made the 4 time series comparable despite the fact that they were compiled using different methods. However, to compare the differences between pooled data and site data, we also analyzed the relationship between vole population abundance and climate data of the 4 sites separately.

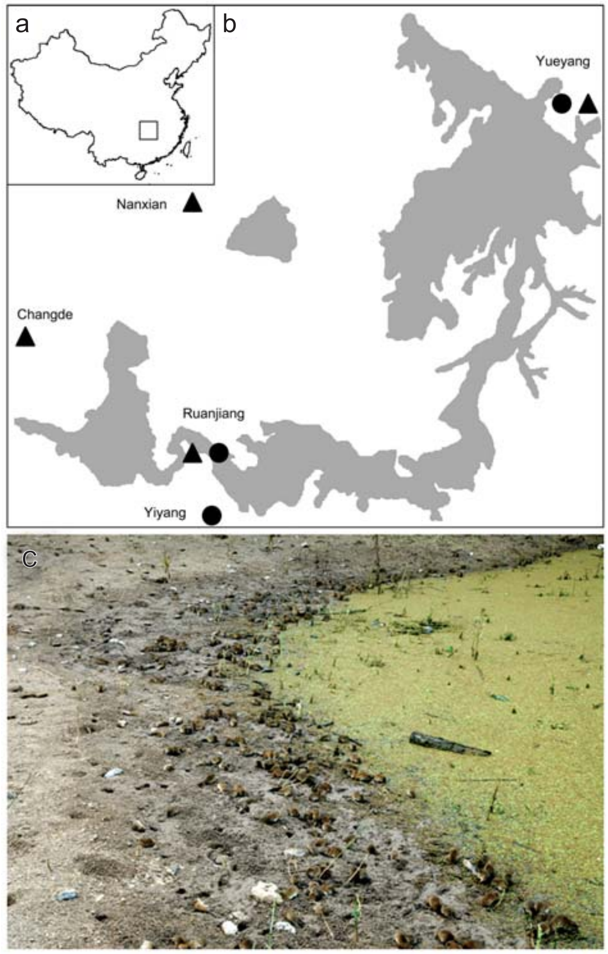

Figure 1 Study sites of the 4 vole-abundance time series (● Ruanjiang, Yiyang, Yueyang) and relevant climate stations (▲ Changde, Ruanjiang, Yueyang, Nanxian) in the Dongting Lake, Hunan province, China. (a) map of China (b) Dongting Lake (c) Bodies of expired Yangtze voles on Dongting Lake beaches in 2007 (photo by Li Bo).

We obtained the reconstructed time series of population abundance by averaging the 4 standardized time series during 1981–2006. The 4 original time series were given equal weight in constructing the pooled time series. The annual rate of increase of voles at year t was calculated as $r = \ln(N_{t+1}) - \ln(N_t)$, following Zhang *et al*. (2003). N_t is the standardized value of vole abundances. We use the corrected equation to calculate the annual increase rate: $r = \ln(N_{t+1}+2) - \ln(N_t+2)$ because many values of N_t are

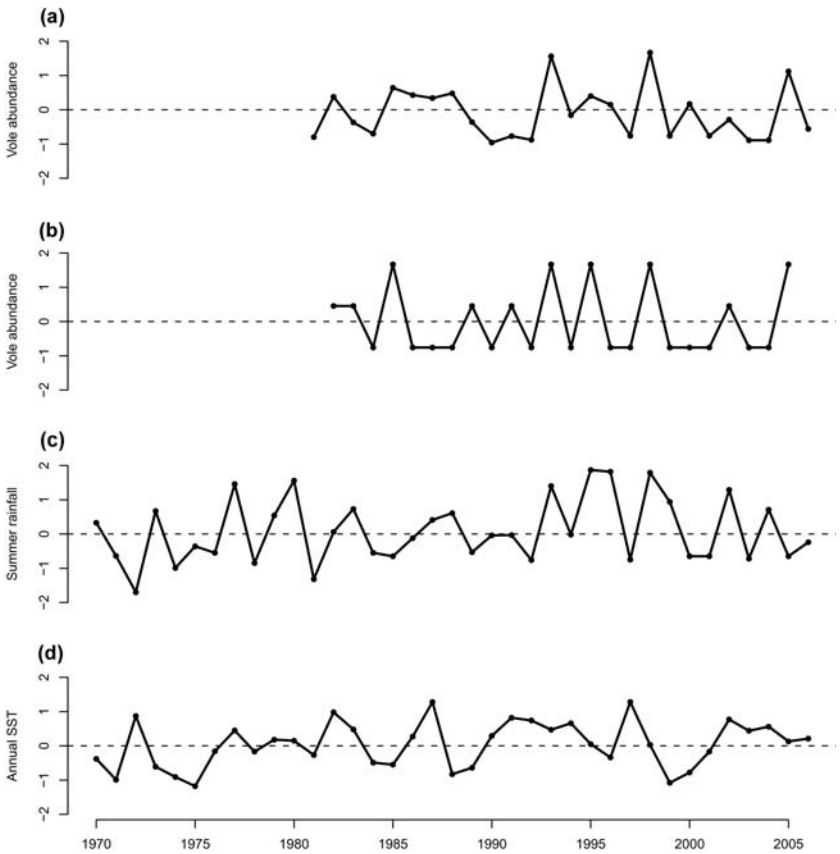

Figure 2 (a) Standardized values of vole abundance reconstructed based on 4 time series 1981–2006, (b) vole abundances of Yiyang site, (c) summer rainfall in the Dongting Lake region, and (d) annual SST.

negative (with the maximum approaching –1). We believe the constructed time series is a good reflection of population abundances of the Yangtze voles in the rice fields around Dongting Lake at regional scale.

Climate data

Monthly climate data were provided by the Chinese National Climate Center. There are 4 climate stations near Dongting Lake: in Changde, Ruanjiang, Yueyang and Nanxian counties (Fig. 1). The monthly average precipitation of the Dongting Lake region was calculated as the average of the 4 stations, and they were standardized for time-series analysis. Based on monthly averages of precipitation, we calculated the seasonal averages for spring (March, April and May), summer (June, July and August), autumn (September, October and November) and winter (previous December, current January, current February).

Monthly SST data were obtained from the National Oceanic Atmospheric Administration website. Based on monthly averages of SST in the El Niño 3.4 region (5°N–5°S, 120°W–170°W), we calculated seasonal averages of SST for spring (March, April and May), summer (June, July and August), autumn (September, October and November) and winter (previous December, current January, current February) and standardized for time-series analysis. The annual SST was calculated as the average of SST for all 12 years. The seasonal and annual SSTs were used for statistical analysis. The annual vole abundances (reconstructed), annual precipitations and annual SST are shown in Fig. 2.

Statistical analysis

Cross-correlation function (ccf) analysis was used to identify significant time-lagged associations among vole abundance, seasonal or annual precipitation and SST. Multiple stepwise regression analysis was used to identify the time-lagged effect of vole abundance (log-transformed) and precipitation on the annual increase rate of vole abundance. Preliminary analysis indicates that the

Table 1 The cross-correlation function (ccf) coefficients between vole abundance and precipitation ($P < 0.05$)

	Time lag (years)	ccf coefficient	*n*
Annual precipitation	1	–0.405	25
Summer precipitation	0	0.445	26
Winter precipitation	1	–0.474	25
Winter precipitation	0	0.376	26

dominant significant associations fall within a 1-year time lag, thus analysis was confined to the current and previous years. SPSS software was used for conducting cross-correlation and multiple stepwise regression analysis. The significance level was set at $P < 0.05$.

RESULTS

Using the pooled data of 4 sites, cross-correlation analysis demonstrated that during 1981–2006, the vole abundances were positively associated with the summer and autumn precipitation of the current year, but negatively associated with the annual precipitation and winter precipitation of the previous years (Table 1). Summer rainfall was positively associated with the annual SST, spring SST, autumn SST and summer SST of previous years, and also positively associated with the spring SST and winter SST of the current years (Table 2). The annual increase rates of voles were negatively associated with the annual precipitation, summer precipitation and winter precipitation of the current years (Table 3). Annual increase rates of voles were also negatively associated with the vole abundance (log-transformed) of the current years (Table 3), showing a strong negative density-dependency effect. The 3 major significant associations among vole abundance, precipitation and SST are shown in Fig. 3a–c.

Using the vole abundance data of Yiyang County and precipitation data of the nearest meteorological site located in Ruanjiang County, we obtained similar results on the relationship between vole population and precipitation. We found that vole abundance was positively associated with the annual precipitation of the current year (ccf = 0.485, $n = 26$, $P < 0.05$), but negatively associated with the annual precipitation of previous years (ccf = –0.544, $n = 25$, $P < 0.05$). We also found that vole abundance was positively associated with the winter precipitation of the current year (ccf = 0.672, $n = 26$, $P < 0.05$), but negatively associated with the winter precipitation of previous years (ccf = –0.467, $n = 25$, $P < 0.05$). Data from the other 3 time series did not yield any significant findings on the relationship between vole population and precipitation in the Yueyang County and Nanxian County. This is probably due to the fact that these 3 time series are short and/or incomplete.

For the pooled data, multiple stepwise regression analysis revealed that winter precipitation of the previous years (PW_{t-1}) had a negative effect on vole abundance (N_t), whereas summer precipitation of the current years (PS_t) had a positive effect. There was no significant effect of N_{t-1}. The regression model is:

$$N_t = 0.072 - 0.343PW_{t-1} + 0.377PS_t \; (R^2 = 0.419). \quad (1)$$

Summer precipitation (PS_t) was positively related to autumn SST ($SSTA_{t-1}$) of the previous years. The regression model is:

$$PS_t = 0.076 + 0.626SSTA_{t-1} \; (R^2 = 0.195). \quad (2)$$

Vole abundance (log-transformed) had a negative effect on the annual increase rate (r_t), whereas autumn precipitation (PA_{t-1}) of the previous year and winter precipitation (previous December, current January and February) (PW_t) of the current years had negative effects on the annual increase rate of vole population. The regression model is:

$$r_t = 0.724 - 1.444N_t - 0.195PA_{t-1} - 0.137PW_t \quad (3)$$
$$(R^2 = 0.797).$$

The negative correlation between the increase rate and vole abundance is shown in Fig. 3d.

DISCUSSION

Our study demonstrates that precipitation of the current year has a significant positive effect on vole abundance of the current year, whereas precipitation of the previous year has a negative effect on vole abundance of the current year (Table 1, Eqn 1). Eqn 1 indicates the independent positive and negative effects of precipitation. Precipitation of the current year and the previous autumn and vole abundance of the current year have a negative effect on the annual increase rate of the current year (Table 3, Eqn 3). Summer precipitation was positively related to the SST of the previous year and spring and before SST of the current years (Table 2, Eqn 2).

The results of this study support our second prediction that population abundance of voles is positively related to summer rainfall of the current years. This finding gives clear evidence in support of the hypothesis that an increase of the water level under heavy rain is an impor-

Table 2 The cross-correlation function (ccf) coefficients between summer precipitation and sea surface temperature (SST) during 1970–2006 ($P < 0.05$)

	Time lag (years)	ccf coefficient	*n*
Annual SST	1	0.437	36
Spring SST	1	0.346	36
Spring SST	0	0.344	37
Summer SST	1	0.396	36
Autumn SST	1	0.396	36
Winter SST	0	0.415	37

tant factor in population outbreaks of voles in rice fields surrounding Dongting Lake. It is speculated that as water levels rise, voles are forced to migrate from lake beaches to rice fields. The finding of positive effect of winter precipitation (previous December, current January and current February) on vole abundance is similar to that of Ye *et al*. (2006). An abundance of winter precipitation might benefit vole breeding (Ye *et al*. 2006).

Our finding regarding the negative effect of precipitation of the previous year on vole abundance supports the previous observations by both Wang *et al*. (2004) and Ye *et al*. (2006). Wang *et al*. (2004) report that population abundances of voles were positively correlated to the duration of water levels below 27.5m from fall to the next spring. Ye *et al*. (2006) reported that vole abundance was negatively related to water levels of Dongting Lake. Our finding provides a reasonable explanation for the observed relations between vole abundance and the water level of the Dongting Lake. Low precipitation of the previous year will reduce water levels and then increase favorable habitats or extend the duration or breeding on lake beaches.

The observation that summer rainfall is positively related to SST of the previous year supports our first prediction, and also confirms the findings of the previous study by Zhang and Xue (1994) analyzing El Niño and precipitation time series in China from 1500–1990 and 1950–1990, respectively. Analysis of both time series demonstrated in El Niño years that there was less rain in the lower reaches of the Yangtze River, but in the year following an El Niño year or years, there was more rain in the region (Zhang & Xue 1994). Because ENSO signals can be accurately predicted several months or even seasons in advance (Latif *et al*. 1998), the findings of close associations between summer rainfall and SST of the previous year in the present study will be very useful in early warning or forecasting of vole outbreaks in the Dongting Lake region. When an El Niño event occurs, it is very likely that vole outbreaks will occur in the next year's summer. Indeed, the large-scale population explosion of voles in the summer of 2007 followed the El Niño year of 2006. However, because the relation between precipitation and SST is relatively weak, it is necessary to correct predictions of vole outbreaks based on precipitation.

Several studies have shown that ENSO-driven precipitation has significant and positive impacts on population dynamics of small rodents (Zhang 1995; Jaksic *et al*. 1997; Zhang & Wang 1998; Lima *et al*. 1999, 2003; Zhang *et al*. 2003, 2007b; Mike & Christopher 2006). It is true, however, that some studies reveal little association (Krebs *et al*. 2004). The possible underlying mechanism is abundant rainfall after El Niño years increases food resources for rodents resulting in increased rates of reproduction. In the present study, we find a time-dependent dual effect of precipitation on vole abundance: a positive effect of summer precipitation in the current year, but a negative effect of precipitation from the previous year. It is obvious that the positive effect of summer precipitation influences vole populations directly through flooding because the vole population is forced to migrate as a result of pressure from rising water levels. The mechanism of the negative effect of precipitation on vole the population is likely that drought increases the available breeding habitat (lake beaches), which might lead to increases in vole populations. In fact, El Niño not only leads to population outbreaks of Yangtze voles in the following year, but might also contribute to the population growth of voles during El Niño years as the lower reaches of the Yangtze River receive less rain and lake beaches are exposed. Our results suggest that the effect of the same climate factor (e. g. El Niño or precipitation) on rodents might be time-dependent. A recent study demonstrates that the effect of temperature on migratory locusts in China is frequency-dependent: positive for a small time-scale but negative for

Table 3 The cross-correlation function (ccf) coefficients between annual increase rate of voles and vole abundance (log-transformed) or precipitation ($P < 0.05$)

	Time lag (years)	ccf coefficient	*n*
Vole abundance	0	–0.770	26
Annual precipitation	0	–0.437	26
Summer precipitation	0	–0.432	26
Winter precipitation	0	–0.535	26

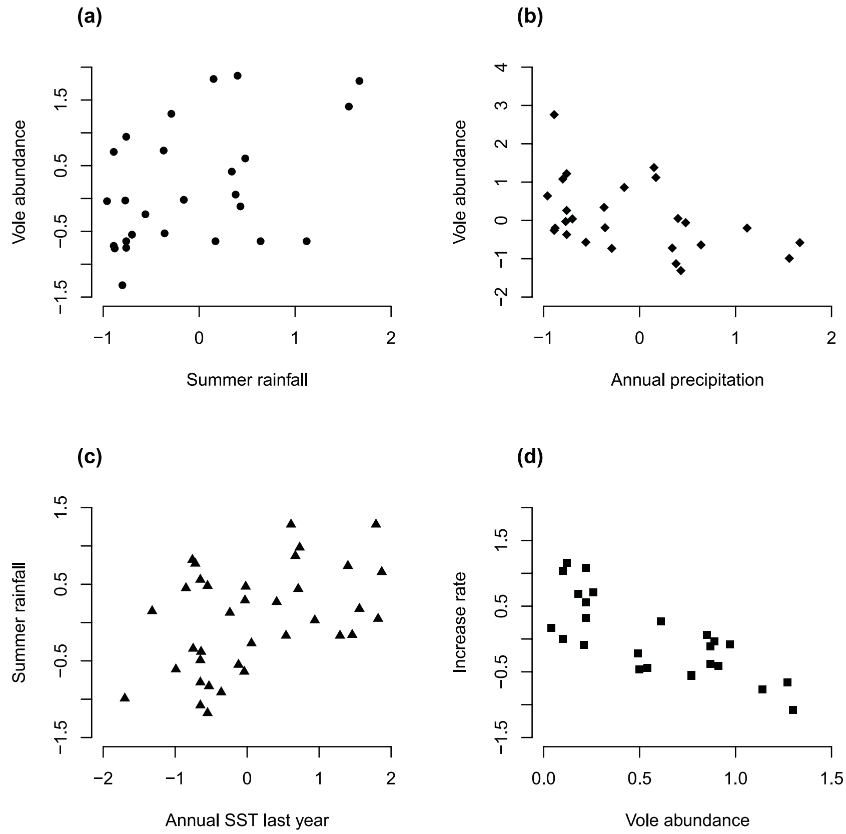

Figure 3 Relationship between (a) vole abundance and summer precipitation of the current year, (b) vole abundance and annual precipitation of the previous year, (c) summer precipitation and annual SST of the previous year, and (d) annual increase rate and vole abundance in the Dongting Lake region.

a large time-scale (Stige *et al*. 2007). This phenomenon needs further investigation so that a better understanding of the complex mechanism of ecological consequences of climate factors can be attained.

The observation that the annual increase rate in vole populations around Dongting Lake is negatively related to vole abundance suggests that there is a strong negative density-dependent regulation in the vole populations. Dead bodies are commonly seen after voles are driven into rice fields by the rising water levels of the lake in the wet season. Most voles die as a result of flooding or hunger within about 2 weeks. A few survive the wet season in the rice fields and return to lake beaches in autumn. To ensure positive values of the increase rate, we added 2 to the standardized population abundances before data log-transformation. Because this arbitrary correction value might dampen or inflate the estimated values of the increase rate, it might affect the correlation strength or slope, but it does not change the positive or negative relation. In this study, the correction for log-transformation has no obvious inflating effect on annual increase rates, considering the obtained clear and negative relations between the increase rate and population abundances of voles.

The role of intrinsic and extrinsic factors has been fervently debated within the field of ecology for almost a century, and it is now generally agreed that both intrinsic density-dependent factors and extrinsic density-independent factors the determine population dynamics of animals (Stenseth 2007). Many recent studies have demonstrated that both density dependency and precipitation affect population dynamics of small rodents in Australia (Singleton & Redhead 1990; Pech *et al*. 1999), Africa (Leirs *et al*. 1997, 1999), North America (Jaksic *et al*. 1997; Lima *et al*. 1999, 2003; Zhang *et al*. 2007a) and Asia (Stenseth *et al*. 2003; Zhang *et al*. 2003). The present study provides another example of how both intrinsic and extrinsic factors are important in the population fluctuation of voles. We have demonstrated that the effect of precipitation on the Yangtze voles is time-dependent in the Dongting Lake region wet seasons.

Human activities, especially cultivation of lake beaches and construction of flood control projects in the Three Gorges River Dam in the upper stream of the Yangtze River, might affect the population dynamics of Yangtze voles in

Dongting Lake (Chen *et al*. 1998; Zhou *et al*. 2002; Guo *et al*. 2006). To reduce human disturbance in Dongting Lake, previously cultivated lake beaches are being restored as lake beaches under the direction of the central government. This might significantly increase vole habitats in the region. The flood control measures might also accelerate the effects of precipitation. For safety and for transportation reasons, there is less water released from the Three Gorges River Dam during the dry seasons of drought years, whereas in the wet years there is more released. Based on the results of this study, both measures are likely to accelerate vole population outbreaks in Dongting Lake. In future research, the effect of human disturbance should be investigated further.

There are several limitations of the present study. First, 3 of the 4 time series we used are incomplete, and all time series were obtained using different methods. In this study, we constructed the time series of the Yangtze vole by averaging the standardized values of the 4 time series. Although they were compiled using different methods, the 4 time series were given equal weight when constructing our time series. This pooled data obviously ignored differences of reliabilities among different methods. Second, based on the available data and analysis of this study, we were not able to discern the role of human population growth and immigration on the observed population outbreaks of voles in the rice fields. However, we hope that the preliminary observation on the relationship between vole abundance and precipitation of the current year and the previous year of this study will stimulate future investigations into population dynamics driven by both population growth and immigration under climate change.

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