Mathematical and Computer Modelling 57 (2013) 525–535

Contents lists available at SciVerse ScienceDirect

Mathematical and Computer Modelling

journal homepage: www.elsevier.com/locate/mcm

The effects of management on population dynamics of plateau pika

Hanwu Liu [a,b,c,*], Yuming Chen [c,1], Li Zhou [d], Zhen Jin [b]

[a] Electromechanical Engineering College, North University of China, Taiyuan, Shanxi 030051, PR China
[b] College of Science, North University of China, Taiyuan, Shanxi 030051, PR China
[c] Department of Applied Mathematics, Yuncheng University, Yuncheng, Shanxi 044000, PR China
[d] North-West Plateau Institute of Biology, the Chinese Academy of Sciences, Xining, Qinghai 810001, PR China

A R T I C L E I N F O

Article history:
Received 6 August 2011
Received in revised form 25 November 2011
Accepted 18 June 2012

Keywords:
Cellular automata model
Plateau pika (*Ochotona curzoniae*)
Contraceptive control
Lethal control
Vegetation restoration

A B S T R A C T

The plateau pika (*Ochotona curzoniae*) inhabits the Qinghai/Tibetan Plateau of China. Its role on the grassland ecosystem is not quite understood. Some researchers regard it as a keystone species while others treat it as a pest. At least, the overabundance of plateau pika population accelerates degrading of alpine meadows mainly through their burrowing activity. Therefore, it is necessary to manage pika population. The commonly employed management strategies are lethal control, contraceptive control, and vegetation restoration. To study the control effect, we develop a cellular automata model. In the simulation, we consider three time manners (single control, impulsive control at fixed times and state-dependent impulsive control) and two space manners (uniform control and mosaic control). Not surprisingly, a better control effect can be achieved with a larger killing rate in lethal control, or a larger contraception rate, or a larger degree in grassland restoration. On the other hand, uniform control has distinctly better results than mosaic control. Hence, in practice, uniform control is strongly recommended. With uniform control, some results are summarized as follows. In both lethal control and contraceptive control, the best strategy is to apply state-dependent impulsive control; if control is implemented in the non-growing season then the implementation time makes no difference. However, if control is implemented in the breeding season of pika, in lethal control, the later it is implemented the better is the control effect; while in contraceptive control, the earlier it is implemented the better is the control effect. Compared with lethal control, non-disseminating contraceptive control has a better control result if only one control is implemented; but if controls are implemented too often then lethal control has a better control effect.

1. Introduction

The plateau pika (*Ochotona curzoniae*) is a small, non-hibernating, diurnal lagomorph that inhabits alpine meadows on the Qinghai/Tibetan Plateau of China. The primary social unit is a family of adults and their young that inhabit interconnected burrows. The role of pika on the grassland ecosystem is not quite understood. Some researchers think that pika is a keystone species while others regard it as a pest.

A keystone species is one whose loss from an ecosystem would cause a greater than average change in other species' populations or ecosystem processes — one that has a disproportionately effect on other species in a community [1]. The

* Corresponding author at: Electromechanical Engineering College, North University of China, Taiyuan, Shanxi 030051, PR China. Tel.: +86 15035415283.
E-mail addresses: liuhanwu-china@163.com (H. Liu), ychen@wlu.ca (Y. Chen).
1 Permanent address: Department of Mathematics, Wilfrid Laurier University, Waterloo, ON N2L 3C5, Canada.

0895-7177/$ – see front matter © 2012 Elsevier Ltd. All rights reserved.
doi:10.1016/j.mcm.2012.06.032

plateau pika is regarded as a keystone species for biodiversity on the Tibetan Plateau because of several main reasons. First, the burrows made by the pikas are the primary nest to a wide variety of endemic birds (e.g. Hume's ground jay (*Pseudopodoces humilis*), snowfinch (*Montifringilla*)) and lizards (*Phrynocephalus vlangalii, Eremas multiocellata*). Second, pikas are the principal prey for nearly all of the Plateau's predator species, including golden eagles (*Aquila chrysaetos*), upland buzzards (*Buteo hemilasius*), saker falcons (*Falco cherrug*), goshawks (*Accipiter gentilis*), black kites (*Milvus migrans*), and little owls (*Athene noctua*). Third, the burrowing activity of plateau pika can enhance the ability of soil to absorb precipitation, accelerate available nutrient cycling, and create microhabitat that results in an increase in plant species richness [2–4].

On the other hand, pikas cause a lot of damage to the grass vegetation, mainly by feeding, gnawing grass roots and burrowing. They also compete with livestock for available vegetation (e.g. yaks (*Bos grunniens*) and Tibetan sheep (*Ovis aries*)) [5]. This contributes to soil erosion [6], plant losses and consequent grassland degradation. The damage level to the grassland is closely related to the population density of pikas. Pikas prefer open habitats and avoid dense shrub or higher vegetation [7]. Degradation of alpine meadows leads to the increase of their population density and vice versa.

As a result, for an appropriate spatio-temporal distribution of pikas, it is necessary to monitor and manage the pika population. The purpose of this paper is to investigate the effects of three commonly applied management strategies on the plateau pika population. These strategies are lethal control, contraceptive control, and vegetation restoration in degraded grasslands through sowing with grass.

In areas where plateau pikas have reached high densities, rodenticides are used to reduce the pika population. However, poisoning programs only transiently reduce the abundance of plateau pika. The remnant population recovers rapidly [8]. Because of the important ecological role played by plateau pika, abrupt decreasing of its population could result in turbulence of biomass flow, energy flow and information flow in the alpine meadow ecosystem. When managing plateau pika, both economic and ecological benefits should be taken into account. The use of rodenticides may affect non-target animals, pollute the environment and is considered inhumane by animal rights and welfare organizations. But such problems will not be encountered in contraceptive control. Therefore, controlling plateau pika by making them sterile is proposed by ecologists and local governments.

Contraceptive control is defined as, through certain measure, inducing the females or (and) males to be sterile, blocking implantation of embryos or interdicting development of juvenile individuals. Thus, contraceptive control can reduce the birth rate of a population and consequently reduce the population size. The competitive reproductive interference from sterile individuals reduces the actual percentage of reproductive females, so it further reduces the birth rate of a population. Sterile individuals not only have no contribution to reproduction in the population but also occupy territories and consume food. This keeps the population under high stress and thus reproductive compensation declines. Thereby, in principle, a population would recover much slowly after contraceptive control. A contraceptive control can be non-disseminating or self-disseminating. For the non-disseminating mode, contraception can be achieved through surgery or ingesting bait that contains contraceptives. In this mode, the sterile individuals can not cause other individuals to lose their fertile ability, whereas, for the self-disseminating mode, contraception can be achieved through infecting individuals with a certain virus which is genetically modified to carry a gene encoding the reproductive protein of a target species. This activates production of antibodies against gametes, thereby blocks fertilization [9]. The sterile individuals can transmit virus to fertile individuals through sufficient contacts and thus cause the fertile individuals to be sterile. The self-disseminating contraceptive control is usually referred to as virus-vectored immunocontraception.

As mentioned earlier, the degradation of the alpine grassland will dramatically increase the plateau pika density. Therefore, increasing the vegetation cover may be a good way to control the plateau pika population. This has been supported by field experiments, which have demonstrated that vegetation restoration can decrease damage caused by plateau pika and the plateau pika population can reach a proper level naturally after vegetation restoration [10].

In this paper, we use a cellular automata (CA) model to study the effects of the above control measures. This CA model is the materialization of the one described by Liu and Zhou [11], that is, most of the important parameters used in our CA model are from field data. Moreover, our model is based on ecological characteristics of plateau pika and alpine meadows.

The fundamental work of a CA model was developed by von Neumann and Burks [12]. Since then, CA models have been used in areas such as sociology, economics, military science and scientific research. Behavior of such simple models is qualitatively and quantitatively similar to that of much more complex models [13]. In ecology, CA models have been used to simulate ecological processes [14,15], animal group behavior [16,17], and dispersal of community [18–21].

A CA model is a dynamic system where space, time and state are discrete and interactions are local. The states of the cells are updated simultaneously at discrete time steps, based on states of themselves and their neighborhoods at the preceding time step. The algorithm used to compute the cell states at the next time step is referred to as the CA local rule. Usually the same local rule applies to all cells of the CA model. We refer the readers to [19,21] for more details.

The remaining part of this paper is organized as follows. We build the CA model in Section 2, followed by the description of simulation in Section 3. Section 4 is devoted to the main results. We mainly simulate the population size under different management strategies and compare the effects of these controls. The paper concludes with a short discussion.

2. The model

Factors affecting plateau pika's habitat selection are habitat position, soil texture, distance to water, shrub coverage, height of broad leaf vegetation [7], distribution of natural enemies [22], and human activities [23]. Environment transition,

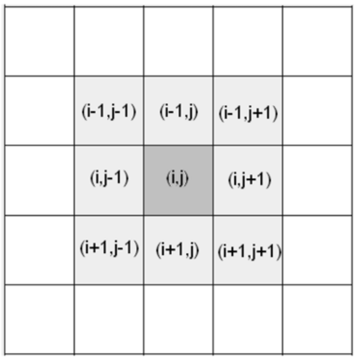

Fig. 1. The 9 neighborhoods (shaded in grey) of the cell (i, j).

predation pressure [22] and nidifugity drive plateau pika to disperse. The natality and mortality of plateau pika are regulated according to food availability and the ratio of population density to carrying capacity. All aforementioned factors are not mutually independent. For simplicity, we only consider the height of vegetation and the ratio of plateau pika density to carrying capacity. The growing season of alpine meadows in the Qinghai/Tibetan Plateau is from April to September, and the herbivorous plateau pika breeds during the period from April to August.

To build the CA model. We consider a homogenous alpine meadow of the size 870 m $\times$ 870 m and divide it into 50 $\times$ 50 equal squares with side-length 17.4 m, the dispersal distance of plateau pika in a month [24]. These squares are regarded as cells [24] and all 2500 cells constitute the cellular space. For a cell (i, j), let $N(i, j)$ be the set of all neighboring cells of (i, j). In simulation, we employ 9 neighborhoods (Fig. 1), 1-month time step and a periodic boundary condition.

The cell (i, j) has two associated dynamical variables $h(t)$ and $m^t_{(i,j)}$, $h(t)$ represents the height of vegetation at time t and $m^t_{(i,j)}$ represents the volume of active burrows at time t. Suppose that the possible maximum height of vegetation is H and the possible maximum volume of active burrows in one cell is M. Hence, the state space of height of vegetation is the interval $[0, H]$ and the state space of active burrows is the interval $[0, M]$. In the present CA model, $h(t)$ and $m^t_{(i,j)}$ are not discrete, they may take any value in their state spaces.

The $h(t)$ follows the same rule in all cells and height of vegetation in cell (i, j) is independent of height of vegetation in other cells. From April to September, the vegetation height, h (cm), satisfies the logistic model,

$$h = \frac{6.4}{1 + 204.1e^{-0.93t}};$$

and $t = 4.5, 5.5, 6.5, 7.5, 8.5, 9.5$ for April, May, June, July, August, September respectively. From October to the next March, h satisfies the Malthusian model,

$$h(t) = 39.13e^{-0.21t}$$

and $t = 10.5, 11.5, 12.5, 13.5, 14.515.5$ for October, November, December, January, February, March respectively. The vegetation height h is assumed to be proportional to the dry biomass x (g) in a quadrat of size 25 cm $\times$ 25 cm. In this paper, $h = 0.42x$ (see [24]).

Because the plateau pika density is proportional to active burrow density, we only consider the latter. As mentioned in the introduction, pikas avoid dense shrub or thick vegetation. One reason is that very high vegetation prevents pikas from seeing predators. Therefore, along with the increasing vegetation height, the carrying capacity $K^t_{i,j}$ (number of active burrows) of cell (i, j) at time t first increases and then decreases to 0. According to Liu et al. [24], we take

$$K^t_{i,j} = \begin{cases} 4.71h(t) + 13.04, & 0 < h(t) < 4.87, \\ 35.99, & h(t) = 4.87, \\ -3.08h(t) + 50.98, & 4.87 < h(t) < 16.5, \\ 0, & h(t) \geq 16.5. \end{cases}$$

The dynamic characteristic of active burrows originates from the birth and death within each cell and from dispersal among cells. Let $m^t_{i,j}$ be the number of active burrows in cell (i, j) at time t. From April to August, the new active burrows born at $t + 1$ are $0.749m^t_{i,j}\left(1 - \frac{m^t_{i,j}}{K^t_{i,j}}\right)$; and, from September to the next March, the disappeared active burrows are $r_4 m^t_{i,j}$. Here we make a convention that $m^t_{i,j} = 0$ when $K^t_{i,j} = 0$. In the above, 0.749 is the growth rate of the plateau pika population during the growing season [25] and r_4 is the mortality of it during the non-growing season.

Define $C^t_{i,j} = m^t_{i,j}/K^t_{i,j}$, according to the difference of value C between a cell (i, j) and its neighborhoods, at the next time step, there would be active burrows dispersal or not between cell (i, j) and its neighborhoods. Let $(p, q) \in N(i, j)$. If $C^t_{i,j} - C^t_{p,q} > \alpha$, then at the next time step $t + 1$ cell (i, j) will transfer active burrows to cell (p, q); if $C^t_{i,j} - C^t_{p,q} < -\alpha$, then at the next time step $t+1$ cell (i,j) will accept active burrows from cell (p,q); and if $-\alpha \le C_{i,j}^t - C_{p,q}^t \le \alpha$, then at the next time step $t+1$ there is no migration of active burrows between cell (i,j) and cell (p,q). Here, α is a parameter representing the reluctance of plateau pika to leave the occupied habitat. Larger α implies more reluctance. Plateau pika is a gregarious animal, so in the same natural environment living with a family would ensure more advantage than living alone.

Through solving the system of linear algebraic equations, we can get the number of active burrows that possibly migrate from cell (i,j) to its 9 neighborhoods. We formulate the system of linear algebraic equations based on that after migration the C of cells that accepted active burrows from cell (i,j) is smaller than C of cell (i,j) by α. We denote the number of active burrows transferred between cell (i,j) and its neighborhoods cell (p,q) by $d_{(i,j)\to(p,q)}$, $(p,q) \in N(i,j) \setminus (i,j)$. For $(p,q) \in N(i,j) \setminus (i,j)$, define

$$\delta_{(i,j)\to(p,q)} = \begin{cases} 1, & C_{i,j}^t - C_{p,q}^t > \alpha, \\ -1, & C_{i,j}^t - C_{p,q}^t < -\alpha, \\ 0, & -\alpha < C_{i,j}^t - C_{p,q}^t < \alpha. \end{cases}$$

When $\delta_{(i,j)\to(p,q)} = 0$, then the corresponding $d_{(i,j)\to(p,q)} = 0$. If there are some $\delta_{(i,j)\to(p,q)} \neq 0$, then the set $\Omega = \{(p,q) \in N(i,j) \mid \delta_{(i,j)\to(p,q)} \neq 0\}$ is not empty. For every $(p,q) \in \Omega$ we can formulate

$$\frac{m_{i,j}^t - \sum_{(u,v)\in\Omega} \delta_{(i,j)\to(u,v)} d_{(i,j)\to(u,v)}}{K_{i,j}^t} = \frac{m_{p,q}^t + \delta_{(i,j)\to(p,q)} d_{(i,j)\to(p,q)}}{K_{p,q}^t} + \delta_{(i,j)\to(p,q)}\alpha.$$

After solving the above equations, we can obtain all $d_{(i,j)\to(p,q)}$. Hence,

$$m_{i,j}^{t+1} = m_{i,j}^t - \sum_{(p,q)\in N(i,j)} \delta_{(i,j)\to(p,q)} d_{(i,j)\to(p,q)},$$

$$m_{p,q}^{t+1} = m_{p,q}^t + \delta_{(i,j)\to(p,q)} d_{(i,j)\to(p,q)}, \quad (p,q) \in N(i,j).$$

During the growing season, after being grazed by plateau pika, vegetation would produce more biomass, this is the "compensatory growth". So, plateau pika consume less vegetation during the vegetation growing season. On average, from April to September each plateau pika consumes 2.4 g dry biomass in a day and from October to the next March 23.5238 g per day [5]. There is an economic threshold. When the number of plateau pika is larger than this threshold, alpine meadows would be destroyed; otherwise, there is no destruction. Liu et al. [26] suggested that this threshold is 9.05 individuals per hectare, meanwhile, they allude that there are 0.4 head of plateau pika living in each active burrow. So, the economic threshold is 0.69 active burrows per cell. It follows that each active burrow consumes 0.96 g dry biomass per day from April to September and 9.41 g dry biomass per day from October to the next March.

3. Simulation

The aim of this section is to describe the simulation method. The CA model was performed with MATLAB (The MathWorks, Inc.). We perform the CA model 59 times continuously for each scenario. That is, the model is run for a total of 5 years. At the beginning of simulation (April), there are 5 active burrows in every cell and there is no population control during the initial 12 months. We choose $\alpha = 0.1$ empirically as there is no existing study on it. Through careful calculation, we select $r_4 = -0.26$, so that when each cell contains five live holes at April, the number of live holes would recur year on year. Thus, in simulation, the difference between population dynamics of plateau pika must originate from different management strategies rather than from the CA model itself.

Controls are applied at April, June, September or December. Because plateau pika breeds from April to August, at these 4 points of time the plateau pika population size is at its lowest, is increasing, is at its highest, and is decreasing, respectively.

We simulate four managements with various time manners and space manners. The four managements are lethal control, non-disseminating contraceptive control, self-disseminating contraceptive control, and vegetation restoration. The time manners considered are as follows.

(i) Single control: as a whole, implement a control only once;
(ii) Impulsive control at fixed times: implement the same control at some fixed times during every year;
(iii) State-dependent impulsive control: implement the same control whenever the plateau pika density reaches the harmful level (0.69 active burrows per cell).

We also take into account the following two space manners.

(i) Uniform control: in every cell, successfully implement a certain control measure on the same proportion of plateau pika individuals.
(ii) Mosaic control: in each cell, the proportion of plateau pika individuals that are successfully acted on by a certain control measure may be different.

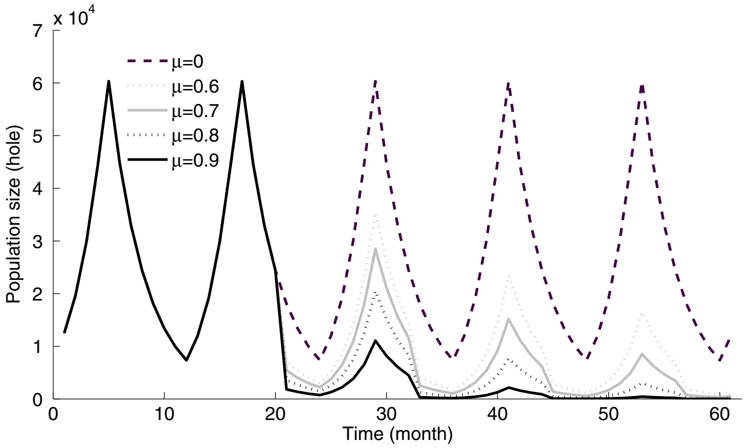

Fig. 2. The effect of killing rate (μ) on the plateau pika population size on the experimental area (the total active burrows), where the lethal control is implemented in every December starting from the second year.

In general, during the breeding season, the growth rate of the plateau pika population equals the difference between the actual natality and the actual mortality. In simulation, the actual mortality is 0.1185 [27] and the actual natality is $0.749 + 0.1185 = 0.8675$.

We assume that the contraceptive control causes no accidental death of plateau pika. For self-disseminating contraceptive control, new sterile individuals come into the world continuously. For simplicity, assume that there is a constant proportion of plateau pika being sterile and this constant proportion is referred to as the contraception rate.

There are many different measures to restore degraded alpine grassland. In our study, we only concern ourselves with the consequence of vegetation restoration. Thus, in our simulation, we just respectively add 0 (cm), 10 (cm), and 20 (cm) to the vegetation height at the first April. We change the carrying capacity accordingly and keep the other parameters unchanged.

4. Results and comparison of control effects

In this section, we report the simulations for different controls and compare the control effects.

4.1. The lethal control

Not surprisingly, a higher killing rate has a better control effect, which shortens the damaged time of the alpine grassland. Fig. 2 shows how the killing rate (μ) affects the plateau pika population (the total active burrows in the experimental area). In Fig. 2, the lethal control is implemented in every December starting from the second year.

To study the effect of time manners and space manners, we take the killing rate μ to be 0.9.

First, we consider the space manners. We observe that uniform control is distinctly better than mosaic control. This is because, in mosaic control, the killing rate is less than 0.9 in some cells. It follows that the plateau pika population is not being suppressed ideally or is severely damaged. Hence more cubs can be reproduced and discrepancies among $C_{i,j}^t$'s occur, which may result in dispersal among cells. Through dispersal, plateau pika could damage more cells and could find more suitable habitat and reproduce rapidly. Fig. 3 illustrates the effects of uniform control and mosaic control on population size, population dispersal among cells, newborns, and damage. In Fig. 3, the lethal control is implemented in every April starting from the second year.

In the practice of lethal control, the space manner of uniform control is strongly recommended. Thus in the following, we assume that the space manner of lethal control is uniform control.

Obviously, a single lethal control could not root up the damage caused by plateau pika. After a single lethal control, relying on high growth rate, the remnant population would reach the damage level again rapidly (sometimes, the remnant population is still large enough to damage the alpine grassland). The best strategy is to apply the state-dependent impulsive control. Fig. 4 shows the effects of the three time manners on the population size. In Fig. 4, we consider three time manners: A single lethal control is done at the seventeenth month; one impulsive control is done at the seventeenth, twenty ninth, forty first, and fifty third months in order; another impulsive control is done at the seventeenth, eighteenth, and fortieth months when damage happens. After the meaningless fifty-third month lethal control, the effect of the impulsive control at fixed time is still not ideal. Relying on a consolidating control being implemented at the eighteenth month, the effect of the state-dependent impulsive control is the best with the fewest controls implemented.

To conclude this subsection, we study the effect of the implementing time of lethal control on the population size. First, assume that lethal control is only implemented in the non-growing season. In a non-growing season, the dynamics of population satisfies the Malthus equation, hence the population size decreases proportionally by month. Let this

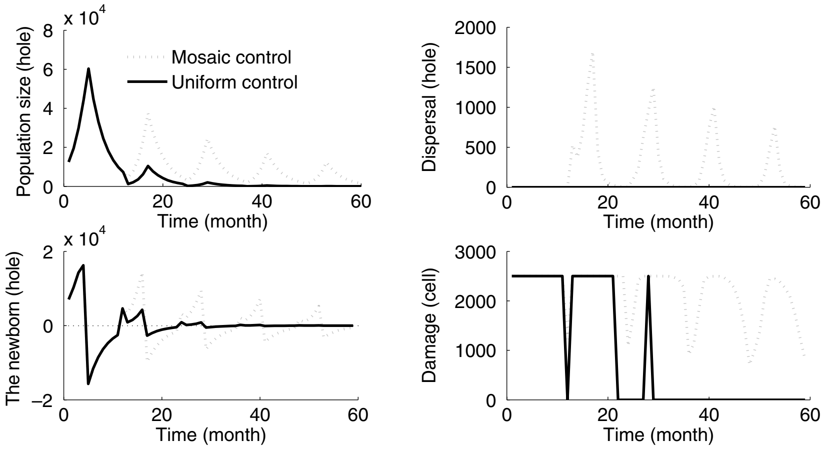

Fig. 3. Comparison of effects of mosaic and uniform lethal controls on population size, population dispersal among cells, newborns, and the damage, where lethal control is implemented in every April starting from the second year.

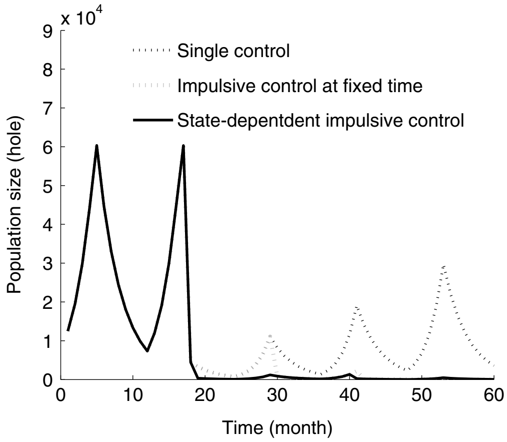

Fig. 4. Under lethal control with uniform control space manner, the state-dependent impulsive control has the best control effect on the population size among the three time manners. Here, the single control is implemented at the seventeenth month; the impulsive control is implemented at the seventeenth, twenty ninth, forty first, and fifty third months in order; the state-dependent impulsive control is implemented at the seventeenth, eighteenth, fortieth months when damage happens.

Table 1
The evolution of the plateau pika population with lethal control being respectively implemented in September and December during the non-growing season.

Time	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	
September-control	bA	abA	a^2bA	a^3bA	a^4bA	a^5bA	Growing season
December-control	A	aA	a^2A	a^3bA	a^4bA	a^5bA	

proportional constant be $a \in (0, 1)$. Suppose that the plateau pika population size at August is A and the killing rate is b. Table 1 summarizes the evolution of the population sizes with one lethal control being implemented in September and another in December. It turns out there is no big difference between the two processes. Second, we consider the situation that lethal control is implemented in the breeding season of plateau pika. Roughly speaking, in each cell, during the breeding season, the dynamics of the plateau pika population satisfies the logistic equation $dx/dt = rx(1 - x/K)$. Assume that lethal control is implemented at times t_0 and t_1 respectively with $t_0 < t_1$. Let the plateau pika population size be x_0 at time t_0 and after the lethal control it will be $p(0 < p < 1)$ times of the quondam one. Table 2 summarizes the population sizes of the two cases and compares the corresponding sizes. It turns out that a later implementing time implies a better effect on suppressing the population. After t_1, the population size is larger if lethal control is implemented earlier. This phenomenon roots in the compensatory growth of population. Predating lethal control results in a smaller population and remained longer in the breeding season, which implies that the plateau pika population can grow with a larger growth rate and take a longer time.

Table 2
The plateau pika population size after lethal control being implemented at two different times during the breeding season.

	Controlled at t_0		Controlled at t_1
$t = t_0$	px_0	$<$	x_0
$t_0 < t < t_1$	$\frac{1}{\frac{1}{K}+\left(\frac{1}{px_0}-\frac{1}{K}\right)e^{-r(t-t_0)}}$	$<$	$\frac{1}{\frac{1}{K}+\left(\frac{1}{x_0}-\frac{1}{K}\right)e^{-r(t-t_0)}}$
$t = t_1$	$\frac{1}{\frac{1}{K}+\left(\frac{1}{px_0}-\frac{1}{K}\right)e^{-r(t_1-t_0)}}$	$>$	$\frac{p}{\frac{1}{K}+\left(\frac{1}{x_0}-\frac{1}{K}\right)e^{-r(t_1-t_0)}}$
$t > t_1$	$\frac{1}{\frac{1}{K}+\left(\frac{1}{px_0}-\frac{1}{K}\right)e^{-r(t-t_0)}}$	$>$	$\frac{1}{\frac{1}{K}+\left(\frac{1}{px_0}-\frac{1}{K}\right)e^{-r(t-t_0)}+\left(\frac{1}{pK}-\frac{1}{K}\right)(1-e^{-r(t_1-t_0)})e^{-r(t-t_1)}}$

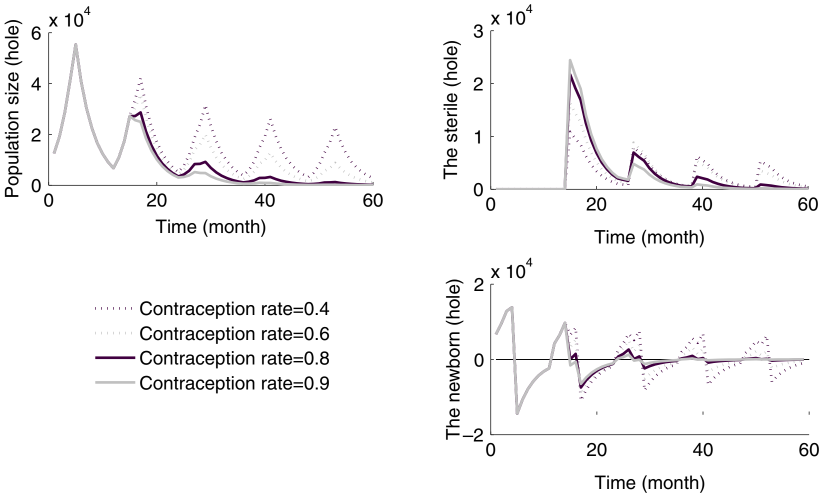

Fig. 5. Effect of contraception rate on the pika population size, numbers of sterile individuals, and the newborns, where the non-disseminating contraceptive control is implemented in every April starting from the second year.

4.2. The contraceptive control

We first consider the non-disseminating contraceptive control.

The larger contraception rate produces a better control effect, that is, along with the increase of contraception rate, the pika population size declines, the number of sterile individuals increases, the number of the newborns decreases, and the damaged time of alpine grassland is shortened. This is confirmed in Fig. 5, where control is implemented in every April starting from the second year.

To further study the effect of space manners and time manners in non-disseminating contraceptive control, we take the contraception rate to be 0.6.

Due to similar reasons as those in lethal control, for non-disseminating contraceptive control, the effect of uniform control is distinctly better than that of mosaic control. This can be seen from Fig. 6, where the state-dependent impulsive contraceptive control is applied in April of the second year and after as needed. Here, in uniform control, the population size, the number of newborns, the number of damaged cells, and dispersed active burrows all are smaller than the corresponding ones in mosaic control. Therefore, in the practice of contraceptive control, uniformity of space is also strongly recommended. Hereafter, the space manner of non-disseminating contraceptive control is always assumed to be uniform.

Obviously, a single contraceptive control could not root up the damage of plateau pika. Following a single contraceptive control, sterile individuals would die gradually and the remnant population would reach the previous level again rapidly. If impulsive contraceptive control at fixed time is employed, plateau pika population would diminish tardily and hence it may require more time to eliminate the damage caused by plateau pika. When state-dependent impulsive contraceptive control is used, the damage caused by plateau pika would vanish rapidly, but the number of controls may be large. Fig. 7 shows the effect of time manners on pika population size. The first control starts in April of the second year.

When contraceptive control is carried out in the non-growing season of plateau pika, the population develops in a similar way whenever contraceptive control is implemented. In the non-growing season, both sterile and fertile plateau pika individuals die with the same death rate. Contraceptive control only proportionally transforms fertile individuals to sterile individuals. Hence, whenever contraceptive control is implemented, the plateau pika population enters the growing season with the same number of sterile individuals and with the same number of fertile individuals. However, implementing contraceptive control at a fixed time in the growing season has a better control effect. In the growing season of plateau pika, earlier implementation of state-dependent impulsive contraceptive control produces a better control effect.

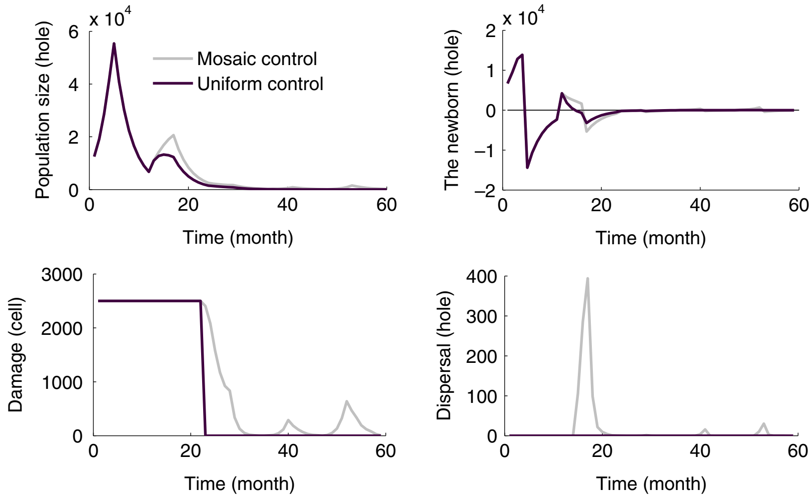

Fig. 6. Effects of mosaic and uniform non-disseminating contraceptive controls on population size, amount of dispersal, number of the newborns, and damaged area, where state-dependent contraceptive control starts in April of the second year.

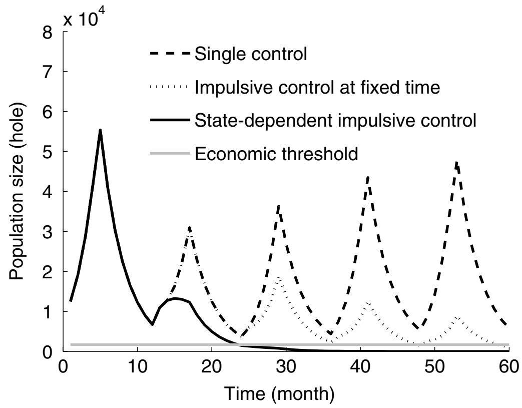

Fig. 7. Effect of time manners in uniform non-disseminating contraceptive control, where the control starts in April of the second year.

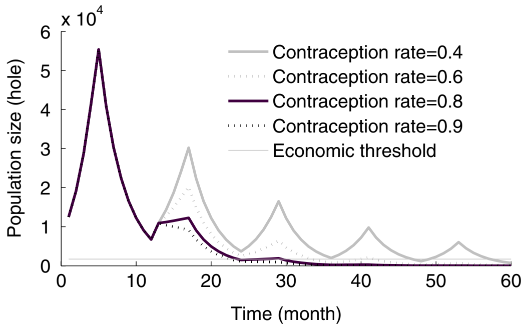

Fig. 8. Effect of contraception rate on pika population size with uniform self-disseminating contraceptive control.

Next, we consider the self-disseminating contraceptive control. As in the non-disseminating contraceptive control, the uniformity in space and larger contraception rate yield a better control effect, see Fig. 8. If the control is conducted during the growing season of plateau pika, earlier implementation gives a better control effect; if the control is carried out during the non-growing season of plateau pika, the population develops in a similar way. Fig. 9 shows us the similarity and difference, where the implementing times of control are April, June, September and December, respectively.

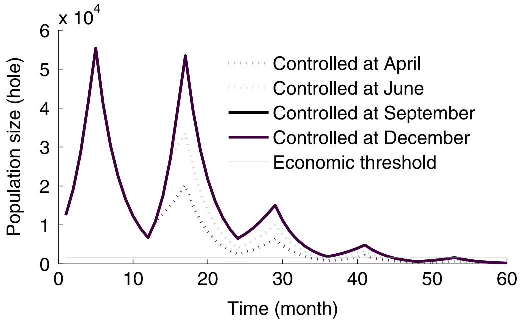

Fig. 9. Effect of the implementing time on the population size with uniform self-disseminating contraceptive control.

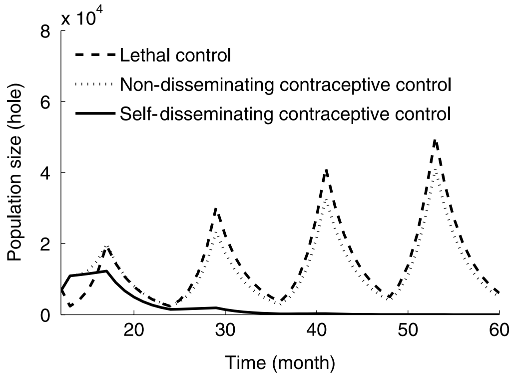

Fig. 10. Effect of three controls on the population size with each control being implemented at the second April. It turns out that the self-disseminating contraceptive control has the best control result.

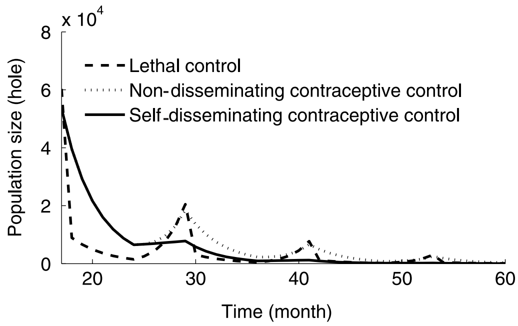

Fig. 11. Effect of three controls on the population size, where the controls are implemented impulsively at every April except the first one. Then lethal control has the best control result.

4.3. Comparison of effects of lethal control and contraceptive control

For the sake of comparison, we let the killing rate and the contraception rate all be 0.8, the space manner is uniform control.

Since new sterile plateau pika individuals come into the world continuously, self-disseminating contraceptive control possesses a good control effect. It could drive the plateau pika population almost to extinction.

Compared with lethal control, after non-disseminating contraceptive control, the plateau pika population changes in a more placid way and could not decrease to a small size rapidly. But non-disseminating contraceptive control has a better control effect in the long run. For a single control, the aforementioned 'good' characteristic of non-disseminating contraceptive control is obvious. When control is too frequent to reflect the 'good' characteristic, lethal control may have a better control effect. This is confirmed in Figs. 10 and 11.

However, if state-dependent impulsive control is implemented, after some time, the plateau pika population develops in a similar way no matter what control measure is used (Fig. 12).

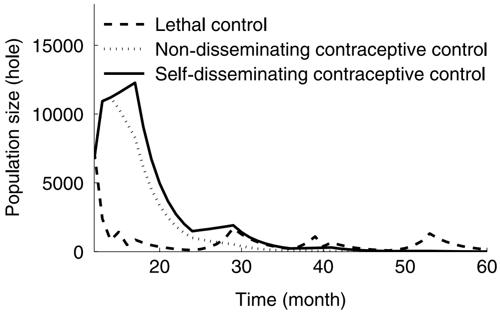

Fig. 12. Effect of three state-dependent impulsive controls on pika population size. After some time, there is no great difference of the population size among lethal control, non-disseminating contraceptive control, and self-disseminating contraceptive control.

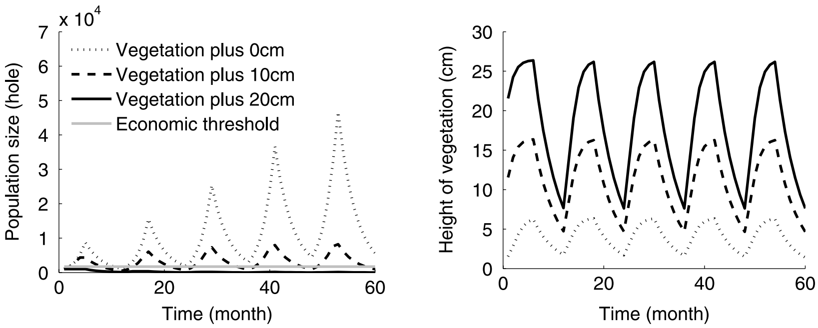

Fig. 13. The effect of vegetation restoration on pika population size (left) and vegetation height (right). Here vegetation plus a number means that the grassland is restored with the result that the vegetation height is increased in the first April by that number. This will affect the carrying capacity accordingly. In the simulation the other parameters are kept unchanged. It is obvious that the larger the degree of restoration is, the better is the control effect.

4.4. The vegetation restoration

In this subsection, we consider the effect of vegetation restoration. We only present the results for lethal control as the results for the other two control measures are similar. The degree of restoration absolutely affects the control effect, see Fig. 13. If the vegetation condition does not change, the plateau pika population would recover rapidly. If some restoration is made, the remnant population would recover at slow speed. When vegetation is restored to a certain degree, the plateau pika population would be suppressed timelessly and the damage caused by it would vanish.

5. Discussion

The degradation of alpine grassland is mainly caused by climate warming, overgrazing, rat damage, etc. [28]. The degraded alpine grassland is almost impossible to restore naturally, even without the presence of plateau pika. In practice, no control measures can eradicate plateau pika completely because of dispersal of plateau pika. In most cases, the reason that vertebrate pests are brought under control by humans is that human activities completely destroy their habitat, and the reason that vertebrate pests cannot be brought under control is that control measures used by human only directly reduce their population size. Both lethal control and non-disseminating contraceptive control cannot eliminate damage caused by plateau pika because they do not change the habitat of plateau pika. The self-disseminating contraceptive control cannot change the habitat of plateau pika, either. However, the control is persistent and can eliminate damage caused by plateau pika. Higher vegetation is not suitable to plateau pika, so restoring vegetation can eliminate damage caused by plateau pika and can settle the matter once and for all. However, restoring all degraded alpine grassland is unrealistic due to fund shortages, material requirement and old-fashioned ideas. The degraded alpine grassland would exist in a wide area and for a long time. On degraded alpine grassland, the self-disseminating contraceptive control is a suitable measure to control plateau pika and thus to slow down the degradation of alpine grassland.

Acknowledgments

This research was supported partially by the Natural Science Foundation of Shanxi Province (2009011005-3), by the National Natural Science Foundation of China (11071283), by the Natural Sciences and Engineering Research Council of Canada (NSERC), by the Ontario Early Researcher Award Program, by the One Hundred Talents Project of Shanxi Province, and by the Research Project Supported by Shanxi Scholarship Council of China (2011-093).

References

[1] V.H. Heywood, Global Biodiversity Assessment, Cambridge University Press, Cambridge, 1995.
[2] C.H. Lai, A.T. Smith, Keystone status of plateau pikas (*Ochotona curzoniae*): effect of control on biodiversity of native birds, Biodiversity and Conservation 12 (2003) 1901–1912.
[3] W.J. Li, Y.M. Zhang, Impacts of plateau pikas on soil organic matter and moisture content in alpine meadow, Acta Theriologica Sinica 26 (2006) 331–337.
[4] A.T. Smith, J.M. Foggin, The plateau pika (*Ochotona curzoniae*) is a keystone species for biodiversity on the Tibetan plateau, Animal Conservation 2 (1999) 235–240.
[5] Z. Yang, X. Jiang, The harm of plateau pika on grassland vegetation and its control threshold value, Pratacultural Science 19 (2002) 63–65.
[6] S.X. Xu, X.Q. Zhao, Y. Sun, W. Zhao, T.B. Zhao, The situation of the grassland rodent harms and measures of elimination in the Qinghai province, Ecology of Domestic Animal 23 (2002) 47–49.
[7] Y. Wang, X.M. Wang, Z.H. Wang, P. Giraudoux, K. Takahashi, G. Alastair, Primary study on habitat choice of plateau pika (*Ochotona curzoniae*), Journal of Sichuan University (Natural Science Edition) 41 (2004) 1041–1045.
[8] J.R. Liang, L. Zhou, S.W. Wei, Z.W. Wang, R.Y. Sun, Mathematical models for recovery of the number of remnant rodent population, Acta Ecologica Sinica 4 (1984) 88–98.
[9] C.H. Tyndale-Biscoe, Virus-vectored immunocontraception of feral mammals, Reproduction, Fertility and Development 6 (1994) 281–287.
[10] Y.Z. Shi, On the influences of range land vegetation to the density of plateau pika (*Ochotona curzoniae*), Acta Theriologica Sinica 3 (1983) 181–187.
[11] H.W. Liu, L. Zhou, Modeling dispersal of the plateau pika (*Ochotona curzoniae*) using a cellular automata model, Ecological Modelling 202 (2007) 487–492.
[12] J. von Neumann, A.W. Burks, Theory of Self-Reproducing Automata, University of Illinois, Chicago, 1966.
[13] G.B. Ermentrout, L. Edelstein-Keshet, Cellular automata approaches to biological modeling, Journal of Theoretical Biology 160 (1993) 97–133.
[14] A.K. Dewdney, Computer recreations: sharks and fish wage an ecological war on the toroidal plant Wa-Tor, Scientific American (1984) 14–22.
[15] E. Klopfer, A. Begel, StarLogo under the hood and in the classroom, Kybernetes 32 (2003) 15–37.
[16] B.J. Cole, D. Cheshire, Mobile cellular automata models of ant behavior: movement activity of *Leptothorax allardycei*, The American Naturalist 148 (1996) 1–15.
[17] B. Schönfisch, M. Kinder, A fish migration model, in: S. Bandini, B. Chopard, M. Tomassini (Eds.), Cellular Automata: 5th International Conference on Cellular Automata for Research and Industry, ACRI 2002 Geneva, Switzerland. October 9-11, 2002 Proceedings, Springer, Berlin/Heidelberg/New York/Hong Kong/London/Milan/Paris/Tokyo, 2002, pp. 210–219.
[18] R.A. Feagin, X.B. Wu, F.E. Smeins, S.G. Whisenant, W.E. Grant, Individual versus community level processes and pattern formation in a model of sand dune plant succession, Ecological Modelling 183 (2005) 435–449.
[19] K. Ioannis, A model for the influence of the greenhouse effect on insect and microorganism geographical distribution and population dynamics, Biosystems 45 (1998) 1–10.
[20] Y.G. Matsinos, A.Y. Troumbis, Modeling competition, dispersal and effects of disturbance in the dynamics of a grassland community using a cellular automaton model, Ecological Modelling 149 (2002) 71–83.
[21] J.H. Wang, M.J. Kropff, B. Lammert, S. Christensen, P.K. Hansen, Using CA model to obtain insight into mechanism of plant population spread in a controllable system: annual weeds as an example, Ecological Modelling 166 (2003) 277–286.
[22] W.H. Wei, Y.F. Cao, Y.M. Zhang, B.F. Yin, J.L. Wang, Influence of the predation risk on the behavior of the plateau pika, Acta Zoologica Sinica 50 (2004) 319–325.
[23] X.L. Jiang, Relationship of population quantities of plateau pika with vegetation homogeneity, Acta Prataculturae Sinica 7 (1998) 60–64.
[24] H.W. Liu, L. Zhou, W. Liu, H.K. Zhou, Study on dispersal of plateau pika in degraded alpine meadow, Prataculture & Animal Husbandry 153 (2008) 8–11.
[25] Z.L. Yan, L. Zhou, Y. Sun, W. Liu, H.K. Zhou, A research about the population dynamics model of Ochotona curzoniae in alpine meadows of source region of Yangtze and Yellow river, Journal of Sichuan Grassland 114 (2005) 17–19.
[26] J.K. Liu, Y.Z. Zhang, G.W. Xin, Relationship between numbers and degree of harmfulness of the plateau pika, Acta Zoological Sinica 26 (1980) 378–385.
[27] X.G. Wang, A.T. Smith, On the natural winter mortality of the plateau pika (*Ochotona curzoniae*), Acta Theriologica Sinica 8 (1988) 152–156.
[28] Z.H. Shang, R.J. Long, Formation reason and recovering problem of the "black soil type" degraded alpine grassland in Qinghai–Tibetan plateau, Chinese Journal of Ecology 24 (2005) 652–656.