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USING A CELLULAR-AUTOMATA MODEL TO INVESTIGATE THE EFFECTS OF GRAZING ON PLATEAU PIKA POPULATION DYNAMICS

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The plateau pika is a keystone species of Qinghai–Tibet plateau, but its overabundance aggravates the degradation of alpine meadow. Grazing is the most convenient manner to utilize alpine meadow. Grazing would change vegetation condition, that is, change the habitat of plateau pika and so lead to variation of plateau pika population. Based on ecological characteristics of plateau pika and alpine meadow, a cellular-automata model is established to investigate the influence of grazing on dynamics of plateau pika population. Vegetation shortens with the increase of grazing intensity. When grazing intensity is light, the height of vegetation under summer grazing, continuous grazing, rotational grazing and winter grazing decrease in turn. The ACC (average carrying capacity of plateau pika) is higher on degraded meadow and is lower on undegraded meadow. On undegraded meadow grazing affects the value of ACC, whereas, on degraded meadow grazing has slight effect on it. On undegraded meadow, plateau pika occupies all cells speedly, the amount of damaged cells and the average amount of live holes in occupied cells decrease or hold the line on temporal dimension. On degraded meadow, the dispersal of plateau pika is restrained, the amount of damaged cells and the average amount of live holes in occupied cells increase on temporal dimension.

Keywords: Cellular-automata model; grazing; plateau pika; alpine meadow.

Mathematics Subject Classification 2010: 37B15, 68Q80

1. Introduction

The plateau pika (*Ochotona curzoniae*) is small, non-hibernating, diurnal lagomorphs, whose distribution largely coincides with alpine meadow of the Qinghai–Tibet plateau of China. The degradation of alpine meadow results in increasing of its abundance, and at the same time, increase of its abundance aggravates the degradation of alpine meadow. The plateau pika reduces palatable herbage available for domestic livestock (e.g. yak (*Bos grunniens*), Tibetan sheep (*Ovis aries*)), destructs soil structure, and it is the intermediate host of cysticerci. Even so, plateau pika is a keystone species of the Qinghai–Tibet plateau. The burrows constructed by plateau pika are functioned as breeding habitat for small birds (e.g. Hume's ground jay (*Pseudopodoces humilis*), snowfinch (*Montifringilla*)) and lizards (*Phrynocephalus vlangalii*, *Eremas multiocellata*). The plateau pika serves as principal prey for nearly all of the plateau's predators (e.g. golden eagles (*Aquila chrysaetos*), upland buzzards (*Buteo hemilasius*), saker falcons (*Falco cherrug*), goshawks (*Accipiter gentilis*), black kites (*Milvus migrans*), little owls (*Athene noctua*)). The burrowing activity of plateau pika may minimize soil erosion, enhance the ability of soil to absorb precipitation, accelerate the available nutrient cycling, and create microhabitats resulting in high plant species richness [11, 13, 22]. Furthermore, plateau pika became one new experimental animal recently [14]. Just because of the dual role of plateau pika we ought to reinforce monitoring and managing its population in order to bring it to appropriate spatio-temporal distribution and make it play the role of keystone species and be harmless to alpine meadow.

Grazing is the most economic and convenient manner to utilize the alpine meadow. The activity of grazing brings two completely contrary effects to meadow vegetation, it can decrease the growth rate of vegetation owing to, e.g. reduce photosynthetic area, it also can increase the growth rate owing to, e.g. enhance photosynthetic rate. Thus, the effect of grazing on meadow vegetation is mainly determined by the net efficiency of "decrease" and "increase" [1, 18, 20]. The browse and trample of grazed herbivores have important influence on the component, structure, function of plant community and on the physical–chemical features of soil. Change of vegetation would directly and/or indirectly change the habitat of plateau pika and so lead to variation of plateau pika population. The influence of grazing on vegetation is extensively studied, however, the influence on rodents rarely.

Following increase of grazing intensity, the area damaged by plateau pika and the density of plateau pika increase [4], the amount of *Microtus oeconamus* and *Ochotona cansus* decrease, the amount of *Myospalax baileyi* increase [17]. *Meriones meridianus* and *Cricetulus barabensis* adapted to habitats under farming disturbance and forbidden grazing disturbance very well, *Phodopus roborovskii* adapted to habitat under rotational grazing disturbance very well and *Dipus sagitta* adapted to habitat under over-grazing disturbance very well.

In order to deeply understand the influence of grazing on plateau pika population dynamics, a cellular-automata (CA) model is established and performed.

In [21], Von Neumann and Burks completed the fundamental work on CA model and then this method is extensively used in fields of sociology, economics, strategics and scientific research. CA model for simulating ecological process, in practice, is little easier for being built and giving the simulation results. The behavior of this simpler model is qualitatively and quantitatively similar to that of much more complex model [5].

CA model is one kind of dynamic system where space, time and state are discrete and interactions are local. The states of each cell are updated simultaneously at discrete time steps, based on states of itself and its neighborhoods at the preceding time step. The algorithm used to compute the cell states at next time step is referred to as the CA local rule. Usually the same local rule applies to all cells of the CA model. More detailed description about CA model may be found in [7, 27, 28].

In ecology, CA models have been used for simulating the ecological process of rabbit–grass [10] and shark–fish [3] and satisfying dynamics are exhibited, CA models have also been used for simulating animal group behavior, e.g. ants [2], and migration of fishes [23]. At present, simulating dispersal of community based on CA models is focused. Used CA model, Ioannis [8] determined the geographical distribution and population dynamics of a hypothetical species in a scenario of global warming, Wang *et al.* [24] obtained insight into mechanism of plant population spread in a controllable system, Matsinos and Troumbis [19] showed that longer dispersing plants may have a competitive advantage in their colonization success as compared to the better competitors, especially in the cases of a disturbance-mediated creation of gaps in the landscape, Feagin *et al.* [6] demonstrated that both an environmental gradient and facilitative succession resulted in the formation of characteristic sand dune patterns.

In this paper, a CA model was established to investigate the influence of grazing on plateau pika population dynamics. This CA model is developed based on the ecological characteristics of plateau pika and alpine meadow, so it can be applied in practice. On the other hand, the CA approach evolved, the state of cells is no longer discrete.

2. Materials and Methods

2.1. *The CA model*

The factors that affect plateau pika selecting its habitat are habitat position, soil texture, water distance, shrub coverage, height of broad leaf vegetation [25], distribution of natural enemy [26] and human activities [9]. Environment transition, predation pressure [26] and nidifugity drive the plateau pika to disperse. The natality and mortality of plateau pika are regulated according to ratio of population density to carrying capacity and food availability. All aforementioned factors are not mutually exclusive, for simplicity, here only height of vegetation and the ratio of plateau pika density to carrying capacity are considered. As a result of special geographical environment and meteorological condition, the vegetation of alpine meadow vegetates during period from April to September, and not during period from October to the next March, correspondingly, the herbivorous plateau pika breeds during period from April to August, and not during period from September to the next March.

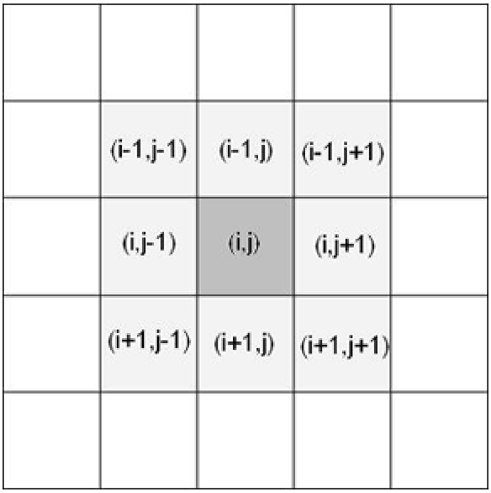

Fig. 1. The eight neighborhoods (the light gray part) of cell (i, j).

Homogenous 870 m × 870 m alpine meadow was divided into 50 × 50 squares with side-length of 17.4 m [15], each square is regarded as a cell. In simulation, eight neighborhoods (Fig. 1), one month time step and periodic boundary conditions are employed.

From April to September, the height of vegetation h(cm) satisfies logistic model [15]

$$h = \frac{6.4}{1 + 204.1 \exp(-0.93t)} \tag{2.1}$$

and from October to the next March h(cm) satisfies Malthusian model $h = 39.13 \exp(-0.21t)$ [15]. The h is directly proportional to dry biomass $x(g)$ of vegetation, here $h = 0.42x$ in 25 cm × 25 cm area [15].

Because that density of plateau pika is proportionate to density of live holes, in the present study, only density of live holes is considered. Higher vegetation (more biomass) can maintain more plateau pika. But when vegetation is too high plateau pika could not find predator effectively owing to visual limit, so plateau pika does not select habitat with higher vegetation. Therefore, along with increasing of height of vegetation, firstly the carrying capacity $K^t_{i,j}$ (amount of live holds per cell) of live holes in cell (i, j) at time t increases and then decreases, until equals zero. Here [15]

$$K^t_{i,j} = \begin{cases} 4.71h + 13.04 & (h < 4.82), \\ 35.99 & (h = 4.82), \\ -3.08h + 50.98 & (h > 4.82). \end{cases} \tag{2.2}$$

The dynamics of live holes originates from its birth and death within each cell and from dispersal among cells. The herbivorous plateau pika has growing season and non-growing season. In growing season (from April to August), the amount of live holes $m_{i,j}^t$ in cell (i,j) at time t satisfies logistic equation

$$m_{i,j}^{t+1} - m_{i,j}^t = 0.749 m_{i,j}^t \left(1 - \frac{m_{i,j}^t}{K_{i,j}^t}\right)$$

and in non-growing season (from September to the next March) $m_{i,j}^t$ satisfies Malthusian equation: $m_{i,j}^{t+1} - m_{i,j}^t = r_4 m_{i,j}^t$, where 0.749 is growth rate of plateau pika population during growing season [29] and r_4 is mortality during non-growing season.

Define $C_{i,j}^t = m_{i,j}^t / K_{i,j}^t$. If $C_{i,j}^t - C_{i,j+1}^t > \alpha$, then at the next time step $t+1$ cell (i,j) well transfer live holes to cell $(i,j+1)$, if $C_{i,j}^t - C_{i,j+1}^t < -\alpha$, then at the next time step $t+1$ cell (i,j) well accept live holes from cell $(i,j+1)$, and if $-\alpha < C_{i,j}^t - C_{i,j+1}^t < \alpha$, then at the next time step $t+1$ there is no migration of live holes between cell (i,j) and cell $(i,j+1)$. It is similar for cell (i,j) and its other seven neighborhoods. Where, α is a parameter that expresses the reluctance of plateau pika to leave its previous habitat. Larger α implies more reluctance. The plateau pika is gregarious animal, so in same natural environment living with family would ensure more advantage than living in exile.

The amount of live holes that migrate from cell (i,j) to its eight (usually less than eight, because not always the differences of C between cell (i,j) and its all neighborhoods are larger than α) neighborhoods can be got through solving system of linear algebraic equations. The system of linear algebraic equations is formulated based on that after migration the C of cells that accepted live holes from cell (i,j) is less α than the C of cell (i,j). But sometimes paradoxical result can be got. For example, if only the differences of C between cell (i,j) and its two neighborhoods $(i,j-1)$ and $(i-1,j)$ are larger than α, then the system of linear algebraic equations is

$$\frac{m_{i,j}^t - x - y}{K_{i,j}^t} = \frac{m_{i,j-1}^t + x}{K_{i,j-1}^t} + \alpha = \frac{m_{i-1,j}^t + y}{K_{i-1,j}^t} + \alpha,$$

where x and y are amounts of dispersed live holes. Its solution is

$$x = (K_{i,j}^t)^2 K_{i,j-1}^t (C_{i,j}^t - C_{i,j-1}^t - \alpha) - K_{i,j}^t K_{i,j-1}^t K_{i-1,j}^t (C_{i,j-1}^t - C_{i-1,j}^t),$$
$$y = (K_{i,j}^t)^2 K_{i-1,j}^t (C_{i,j}^t - C_{i-1,j}^t - \alpha) + K_{i,j}^t K_{i,j-1}^t K_{i-1,j}^t (C_{i,j-1}^t - C_{i-1,j}^t).$$

When $|C_{i,j-1}^t - C_{i-1,j}^t|$ is too large, x or y would be negative, this is illogical. If the aforementioned situation come forth, find out the one that is immediately larger than α from all difference of C between cell (i,j) and its eight neighborhoods, denote the difference as MIN, then replace α with MIN and calculate the amounts of dispersed live holes once again, repeat this process until the amounts of dispersed live holes are all positive.

On average, from April to September 2.4 g dry biomass was consumed by one plateau pika in one day and from October to the next March 23.5238 g [30]. There is an economic threshold, when the amount of plateau pika is larger than this threshold, alpine meadow would be destroyed, otherwise there is no destruction. Liu *et al.* [16] suggested that this threshold is 9.05 head per hectare, meanwhile, they allude that there is 0.4 head plateau pika living in one live hole. So, the economic threshold is 0.69 holes per cell, from April to September 0.96 g dry biomass was consumed by one live hole in one day and from October to the next March 9.41 g.

2.2. *Simulating*

The aim of simulating is to investigate the influence of grazing on plateau pika population dynamics. The CA model was performed with MATLAB. There was no research on α, in simulating, take $\alpha = 0.1$ empirically. Through carefully calculating, take $r_4 = -0.26$, so that when each cell contains five live holes at April, the amount of live holes would recur year and year. Thus, in simulating, the difference between population dynamics of plateau pika must originate from different grazing intensity or different grazing system and not from the CA model itself.

Figure 2 shows the initial configuration of live holes, where only the dark cells were inhabited by plateau pika. Two scenarios are considered: there are 0.4 and five live holes in each dark cell, they mean few and many plateau pikas, respectively.

Two vegetation conditions are involved: degraded meadow and undegraded meadow. The meadow mentioned in the CA model is degraded. In the CA model, adding 20 cm to vegetation height of the initial April and the carrying capacity of vegetation height, respectively, while other parameters unfaltering yields the undegraded meadow, thus, Eq. (2.1) changes to

$$h = \frac{26.4}{1 + 14.53\exp(-0.93t)}.$$

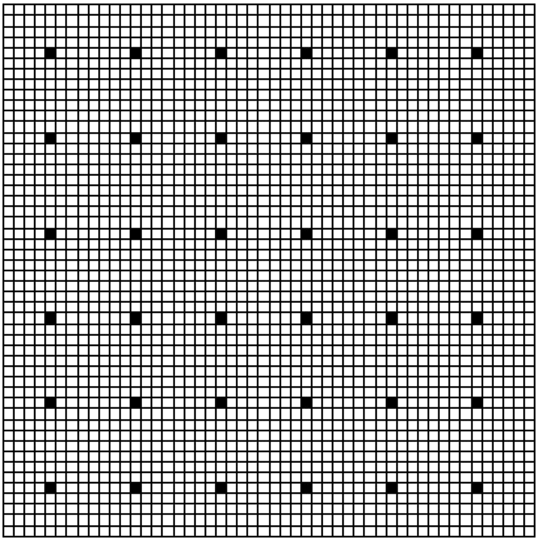

Fig. 2. The initial configuration, where only the dark cells were inhabited by plateau pika.

Table 1. Five grazing intensities.

Gradients	From April to September	From October to the next March
1	+30% (+4.5%)	−1% (−0.2%)
2	+15% (+2.4%)	−2% (−0.3%)
3	+0% (+0%)	−0% (−0%)
4	−15% (−2.7%)	−20% (−3.7%)
5	−30% (−5.8%)	−40% (−8.2%)

Four grazing systems are considered: continuous grazing, rotational grazing, summer grazing and winter grazing. For convenience, summer grazing refers to grazing from April to September, winter grazing refers to grazing from October to the next March, rotational grazing refers to grazing only in even months.

In virtue of compensation, from April to September, light grazing would increase vegetation biomass, but heavy grazing would decrease vegetation biomass [31]. From October to the next March, by lack of compensation, grazing results in decreasing of vegetation biomass affirmatively. Under same grazing intensity, if vegetation biomass decreases all year, then, without fail, the decrease during period from April to September is lighter than the decrease during period from October to the next March. For simplicity, the grazing intensity is expressed as the proportional increase or decrease of vegetation height. Consider five grazing gradients (Table 1), where the "+20%" means the height of vegetation being $1 + 20\% = 1.2$ times of height of vegetation with no grazing, and so forth. The amounts in parenthesis are monthly changing rates of vegetation height. From gradient one to five, the grazing intensifies by and by.

The two states of live holes, two vegetation conditions, four grazing systems and five grazing intensities combine into 80 cases and for each case, simulates for two years.

3. Results and Analysis

3.1. *Influence of grazing intensities on vegetation*

Regardless of whether the live holes is more or less initially, regardless of whether the alpine meadow is degraded or not, regardless of which grazing system is employed, the height of vegetation decreases with the increase of grazing intensity. On continuous grazing meadow, the influence of grazing intensity on vegetation height is the most remarkable one, and then on summer grazing meadow, rotational grazing meadow and winter grazing meadow, in turn. Figure 3 shows the influence of grazing intensity on vegetation height, where each dark cell of the initial configuration contains 0.4 live holes, continuously grazed on undegraded meadow.

3.2. *Influence of grazing systems on vegetation*

The influence of grazing systems relates to grazing intensity.

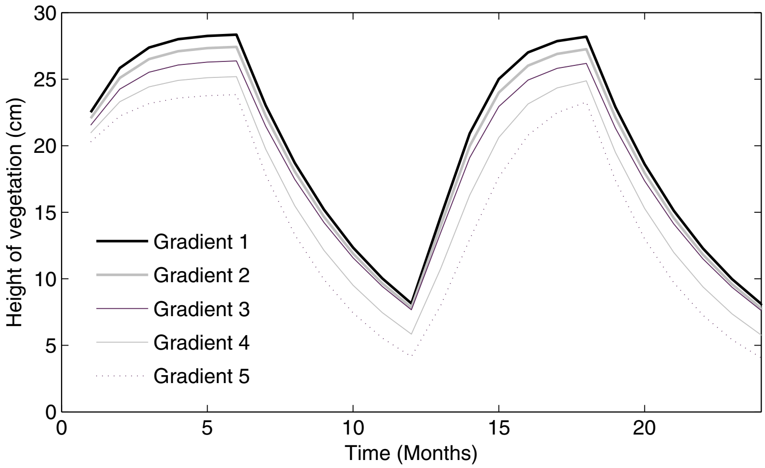

Fig. 3. The influence of grazing intensity on vegetation height.

When grazing intensity is light, that is, under the first or second gradient, from April to September, grazing can increase biomass (or height) of vegetation. This time, vegetation under summer grazing, continuous grazing, rotational grazing and winter grazing shortens in turn. This phenomenon is reasonable. In absolute value, the simulative effect during period from April to September is much greater than the dissipative effect during period from October to the next March (30 or 7.5 times), only simulative effect acts on summer grazing meadow, two kinds of effects continuously act on continuous grazing meadow, two kinds of effects intermittently act on rotational grazing meadow, only dissipative effect acts on winter grazing meadow. Figure 4 shows the influence of grazing system on vegetation height, where each

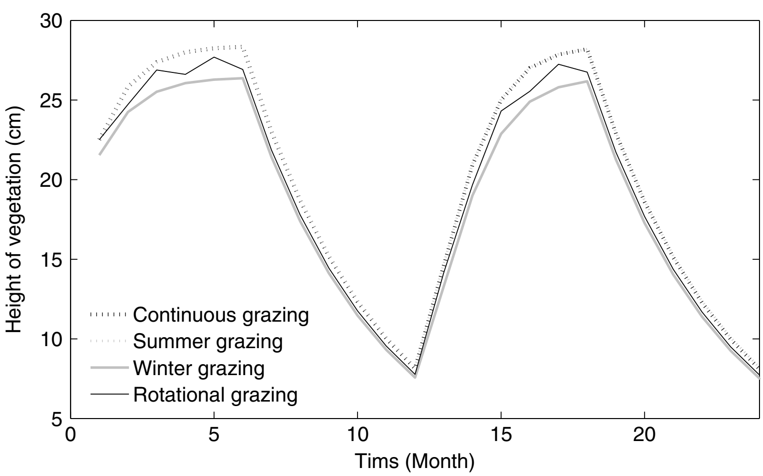

Fig. 4. The influence of grazing systems on vegetation height, where the grazing intensity is light.

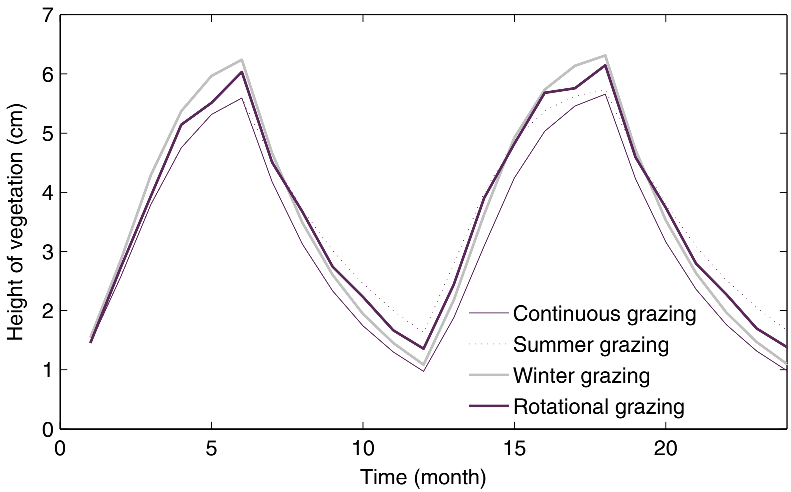

Fig. 5. The influence of grazing systems on vegetation height, where the grazing intensity is heavy.

dark cell of the initial configuration contains five live holes, grazed on undegraded meadow with the first intensity gradient.

When grazing intensity is heavy, that is, under the fourth or fifth gradient, grazing can decrease biomass (or height) of vegetation all year. The dissipative effect during period from October to the next March is greater than during period from April to September (1.33 times). Dissipative effect acts on continuous grazing meadow all year and intermittently acts on meadow with other three grazing systems, so vegetation height of continuous grazing meadow is the shortest. Figure 5 shows the influence of grazing system on vegetation height, where each dark cell of the initial configuration contains 0.4 live holes, grazed on degraded meadow with the fifth intensity gradient.

3.3. *Influence of grazing on carrying capacity of plateau pika*

Equation (2.2) illustrated the relation between height of vegetation and carrying capacity of plateau pika, so, grazing would alter the carrying capacity of plateau pika through altering the height of vegetation. Other than grazing intensity and grazing system, the carrying capacity of plateau pika also relates to other factors, such as, height of vegetation. In specific time, the carrying capacity of plateau pika is not explicitly related with grazing intensity and grazing system, however, the average carrying capacity (ACC) of plateau pika during period from April to September within simulating is influenced by grazing.

On the whole, ACC is higher on degraded meadow and is lower on undegraded meadow, the amount of live holes at the initial April has little effect on ACC, on undegraded meadow grazing intensity and grazing system affect value of ACC and on degraded meadow the effect is little. See Tables 2–5.

Table 2. The ACC on degraded meadow with less initial live holes.

Grazing intensity	1	2	3	4	5
Continuous grazing	31.27	31.53	31.59	31.11	29.80
Summer grazing	31.27	31.57	31.59	31.62	31.61
Winter grazing	31.56	31.55	31.59	31.05	30.46
Rotational grazing	31.50	31.53	31.59	31.37	31.07

Table 3. The ACC on undegraded meadow with less initial live holes.

Grazing intensity	1	2	3	4	5
Continuous grazing	1.13	1.48	1.77	3.40	6.71
Summer grazing	1.06	1.39	1.77	2.18	2.66
Winter grazing	1.83	1.86	1.77	2.85	4.87
Rotational grazing	1.37	1.58	1.77	2.56	3.63

Table 4. The ACC on degraded meadow with more initial live holes.

Grazing intensity	1	2	3	4	5
Continuous grazing	31.26	31.46	31.52	31.02	29.64
Summer grazing	31.27	31.50	31.52	31.55	31.50
Winter grazing	31.49	31.48	31.52	30.98	30.33
Rotational grazing	31.43	31.46	31.52	31.30	30.93

Table 5. The ACC on undegraded meadow with more initial live holes.

Grazing intensity	1	2	3	4	5
Continuous grazing	1.12	1.49	1.77	3.41	6.72
Summer grazing	1.06	1.39	1.77	2.19	2.66
Winter grazing	1.83	1.86	1.77	2.85	4.88
Rotational grazing	1.37	1.59	1.77	2.57	3.64

On undegraded meadow, ACC increases along with grazing intensifying, see Tables 3 and 5. It is because, at this time, vegetation is higher than 4.82 cm in most of time and when grazing intensifies vegetation shortens, ACC enlarges. On degraded meadow, vegetation varies around 4.82 cm, when vegetation shortens ACC may increases and also may decreases, see Tables 2 and 4.

On undegraded meadow, when grazing intensity is light the ACC under summer grazing is the smallest one, and then under continuous grazing, rotational grazing, winter grazing, when grazing intensity is heavy the ACC under summer grazing is also the smallest one, and then under rotational grazing, winter grazing, continuous grazing (Tables 3 and 5).

3.4. *Influence of grazing on population dynamics of plateau pika*

Through affecting carrying capacity of plateau pika, grazing affects population size of plateau pika. Simulating indicates that population size of plateau pika coincides with ACC. For example, if continuously grazing on undegraded meadow where each dark cell of the initial configuration contains five live holes, the amount of total live holes increases in companying with grazing intensity and, correspondingly, the ACCs are $1.13, 1.49, 1.77, 3.41, 6.72$.

When the difference of C among cells is great enough plateau pika would disperse among cells. By dispersing, plateau pika not only can adjust amounts of live holes in all cells, but also can extend its habitat. During simulating, the area of habitat keeps its size in most of time, the extension of habitat happens now and then. Amount of occupied cells, amount of damaged cells and the average amount of live holes in occupied cells have no obvious relation with grazing, but they follow some laws on spatial dimension.

On undegraded meadow, the smaller carrying capacity of plateau pika induces greater C of cells occupied by plateau pika. Thus, in order to reducing survival pressure, plateau pika occupies all cells speedly. Simulating confirms this phenomenon and also shows that the amount of damaged cells and the average amount of live holes in occupied cells decrease or hold the line on temporal dimension.

On degraded meadow, the greater carrying capacity of plateau pika induces smaller C of cells occupied by plateau pika. The dispersal of plateau pika is restrained, the amount of damaged cells and the average amount of live holes in occupied cells increase on temporal dimension.

Figure 6 shows the dynamics of the amount of damaged cells (dotted line) and the average amount of live holes in occupied cells (solid line). Panel A shows the case where each dark cell of the initial configuration contains 0.4 live holes, rotationally grazed on degraded meadow. Panel B shows the case where each dark cell of the initial configuration contains five live holes, grazed on undegraded meadow in winter.

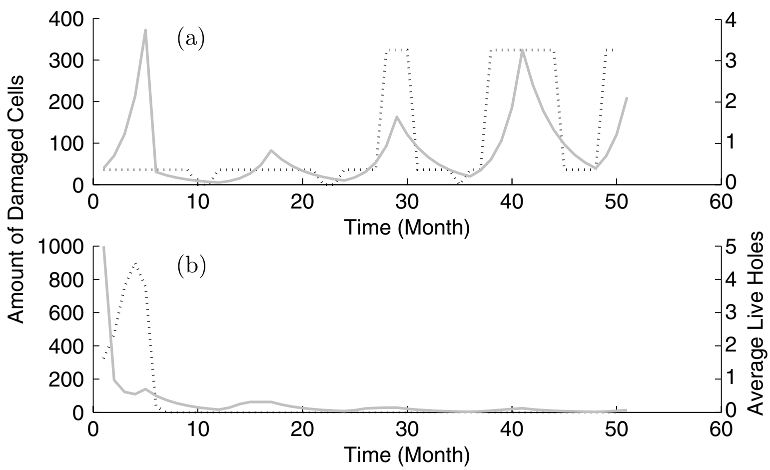

Fig. 6. The amount of damaged cells (dotted line) and damaged degree (solid line). Panel (a) shows the case where each dark cell of the initial configuration contains 0.4 live holes, rotationally grazed on degraded meadow. Panel (b) shows the case where each dark cell of the initial configuration contains five live holes, grazed on undegraded meadow in winter.

4. Discussion

Using a CA model, the influence of grazing on vegetation and population dynamics of plateau pika is studied. Vegetation shortens with the increase of grazing intensity. But, overgrazing and degradation are the most common reality of alpine meadow [12]. On degraded meadow, it is difficult to plateau pika to dispersal, this leads to aggregation phenomenon of plateau pika and further degradation of degraded alpine meadow. Thus, if there is not intervention of outside management the harmfulness caused by plateau pika would become more serious and could not vanish by itself. So, the restoring of degraded alpine meadow depends on reducing grazing intensity and controlling plateau pika.

In reality, after obtained the biomass of vegetation and the number of plateau pika at April, after known the grazing intensity and grazing system to be used, all volumes mentioned in this paper can be calculated and then the dynamics of vegetation and plateau pika can be predicted. Based this prediction, inappropriate grazing can be adjusted.

Acknowledgments

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