

# Effects of the Prey Refuge Distribution on a Predator-Prey System

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The existence of prey refuges in a predator-prey system is known to be strongly related to the ecosystem's stability. In this study, we explored how the prey refuge distribution affects the predator-prey system. To do so, we constructed a spatial lattice model to simulate an integrative predator (wolf) - prey (rabbit) - plant (grass) relationship. When a wolf (rabbit) encountered a rabbit (grass), the wolf (rabbit) tended to move to the rabbit (grass) for foraging while the rabbit tended to escape from the wolf. These behaviors were mathematically described by the degrees of willingness for hunting ( $H$ ) and escaping ( $E$ ). Initially,  $n$  refuges for prey were heterogeneously distributed in the lattice space. The heterogeneity was characterized as variable  $A$ . Higher values of  $A$  equate to higher aggregation in the refuge. We investigated the mean population density for different values of  $H$ ,  $E$ , and  $A$ . To simply characterize the refuge distribution effect, we built an  $H$ - $E$  grid map containing the population density for each species. Then, we counted the number of grids,  $N$ , with a population density  $\geq 0.25$ . Simulation results showed that an appropriate value of  $A$  positively affected prey survival while values of  $A$  were too high had a negative effect on prey survival. The results were explained by using the trade-off between the staying time of the prey in the refuge and the cluster size of the refuge.

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## I. INTRODUCTION

The dynamic relationship between predators and their prey in ecosystems has fascinated mathematical biologists for a long time [1,2] and will continue to be one of the dominant themes in both ecology and mathematical ecology. Understanding the dynamics of this relationship is essential for comprehending the resilience and stability of ecosystems.

The first mathematical model to represent the dynamics of the predator-prey population is the Lotka-Volterra model [3,4]. This model provides an intuitive understanding of the predator-prey system and clarifies the main feature of species interactions: the periodic oscillation of the population density in predator-prey systems. However, the population cycle is strictly unrealistic in real ecosystems. Changing the birth and the death rates does nothing but change the period of the oscillation; *i.e.*, no population can dominate, and there is no possibility of either population being driven to extinction. Holling [5, 6] solved this problem by suggesting three types of functional responses for different species of predators: Holling type I, II, and III. The function indicates the number of prey killed by one predator at various prey densities, which is useful for capturing the characteristic features

of predator-prey interactions. However, this function is likely to be violated in the field because the response type assumes that the predator and the prey randomly encounter each other. In many cases, prey avoid being killed by predators either by defending themselves or by escaping. One way to escape is to move into a refuge where the predation risk is reduced [7,8]. The refuge can be a habitat that is spatially separate [9], a phase of the prey's life history that is temporally separate [10,11], a collective behavior of the prey, such as aggregation into herds [12,13], *etc.* For this reason, a prey refuge provides a more realistic prey-predator model.

In previous studies, researchers considered two types of refuges: those that protected a constant fraction and those that protected a constant number of prey. Many of the studies reported that the refuges that protect a constant number of prey led to a stable equilibrium and have a stronger stabilizing effect on population dynamics than refuges that protected a constant proportion of prey [14–19]. These studies are helpful in understanding how the prey refuge influences predator-prey systems. However, previous studies only focused on the type of refuge and the presence / absence of a refuge, not the refuge distribution. In fact, the spatial distribution of a refuge is likely to strongly affect predator-prey systems because a landscape containing a refuge affects the predator and prey populations [20].

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Table 1. Summary of the variables, symbols, and values used in the predator-prey-plant model.

Symbol	Variable name	Values used in the simulations
$L$	Lattice space size	100
$h$	Ecological preference of a site	0.0 – 1.0
$H$	Willingness for hunting	Varies from 0.0 to 1.0
$E$	Willingness for escaping	Varies from 0.0 to 1.0
$W$	Initial density of predators	0.3
$R$	Initial density of prey	0.3
$G$	Initial density of grass	0.3
$n$	The number of prey refuges	1000, 3000, and 5000
$A$	Heterogeneity of refuge distribution	Varies from 0.0 to 1.0
	Growth probability for grass	0.2
	Predator (prey) reproduction rate	0.2
	Predation probability	0.2
	Maximum value of predator's (prey's) health state	5

In this study, we constructed a spatial lattice-based model to simulate predator-prey dynamics. The lattice-based model is known not only to be considerably more stable than non-spatial models [21] but also to be able to be used to examine many interesting features of individuals that are found in nature [22–24]. Compared with the existing predator-prey lattice models (including the work in Ref. [25], our simulation model has two distinguished points: one is that predators and prey employ hunting and escaping behavior, respectively, and the other is that the heterogeneous distribution of prey refuges is incorporated. Using this model, we explored the effects of the refuge distribution on the predator-prey system.

## II. MODEL DESCRIPTION

In this model, for ease of reference, we referred to predators as wolves, prey as rabbits, and plants as grass. These species do not represent the actual animal or plant species. They are general agents used to represent predation interactions.

This model consists of strategically moving a predator (wolf) and a prey (rabbit), a plant (grass), and a refuge for prey. We generated a lattice space in which the predator and the prey can move. A random value,  $h$ , was assigned to each lattice. The wolves and the rabbits prefer sites with higher  $h$  values. When a wolf (rabbit) met a rabbit (grass), the wolf (rabbit) tended to move to the rabbit (grass) for foraging while the rabbit tended to escape from the wolf. These behaviors were mathematically described by the degree of willingness to hunt ( $H$ ) and escape ( $E$ ). Initially,  $n$  refuges for the prey were heterogeneously distributed in the lattice space. The heterogeneity was characterized as the variable  $A$ . Higher

values of  $A$  equated to higher aggregations in the refuge. The variables and their values used in this model are shown in Table 1.

Interactions among species were included in the model; wolves eat rabbits, rabbits eat grass, and the grass grows by itself. Wolves and rabbits moved in the lattice space without stopping. When different species occupied the same site, predation could occur according to the predation probability. The health state decreased by one with every time step. When the state of an animal decreased to less than zero, the animal died and was removed from the system. All locational and biological variables were updated and scheduled at each time.

### 1. Lattice Space

In order to generate a lattice space in which individuals could randomly move, we assigned a random value,  $h$ , that ranged from 0.0 to 1.0 to each lattice site. The wolves and rabbits prefer sites with higher  $h$  values. Thus, the wolves and the rabbits were most likely to move into a neighboring site with the highest  $h$  value (Fig. 1(a)). The  $h$  value of each site was determined by using a uniform random function supported by MATLAB ver. 7.0 (Mathworks).

The probability that an individual would move to a given neighbor site was calculated as the ratio of the  $h$  value of that site to the summation of the  $h$  values of the remaining neighbor sites. For example (see the case of Fig. 1(a)), the probability that an individual would move in the top-right direction was calculated as  $0.8 / (0.8 + 0.7 + 0.4 + 0.3 + 0.5 + 0.2 + 0.1 + 0.3)$ . We call this probability the transition probability,  $P_{tran}$ . The value of  $P_{tran}$  for each direction is represented outside of the

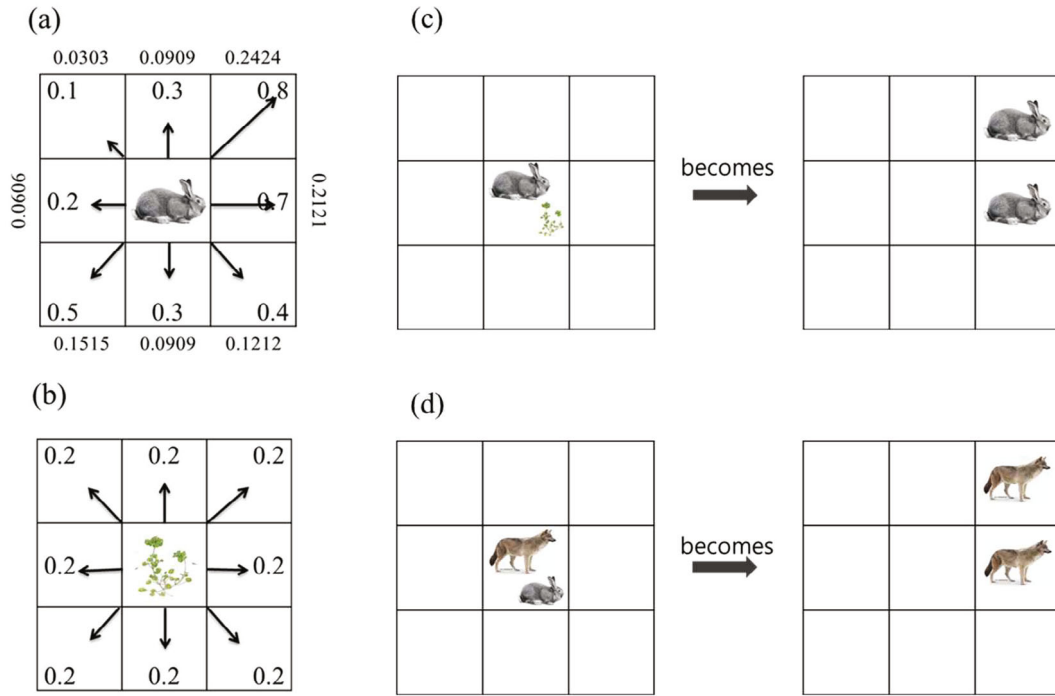


Fig. 1. (Color online) (a) Example of a prey (or a predator) surrounded by eight neighboring sites. Each neighboring site is labeled with its associated  $h$  value that reflects the landscape property. The length of each arrow indicates the probability that the prey (rabbit) will move into a specific site. (b) Growth process of grass that has a growth probability of 0.2. When (c) the prey eats the grass or (d) the predator eats the prey, the prey (or predator) may give birth to a single offspring.

lattice box shown in Fig. 1(a). Whenever the simulation is repeated, the values of  $h$  were renewed on the quenched randomness in the evolution of the predator-prey system.

## 2. Interactions

When a wolf (rabbit) encountered rabbits (grass), predation between them could occur according to the predation probability. The following rules applied to predation and reproduction:

- Grass could grow into its neighboring sites (empty or refuge) according to its growth probability. Note that a single unit of grass could possibly grow into multiple neighboring sites during one iteration time step (Fig. 1(b)).
- When a wolf and a rabbit were present within the same site, the wolf could eat the rabbit with the predation probability. This rule was also applied to the relationship between a rabbit and grass. A wolf (rabbit) taking a rabbit (plant) gave birth to an offspring according to a birth probability. The offspring was introduced into one of the sites neighboring its parent site (Figs. 1(c) and (d)). If the parent site had no unoccupied neighboring sites, the wolf (or rabbit) could not give birth to offspring.

- The state of health of a wolf (or a rabbit) was represented by a value ranging from 0 to 5. When a wolf (or a rabbit) was first introduced, or born, its health state was assigned an initial value of 5. In the case that a wolf (or a rabbit) consumed food (grass for a rabbit; rabbit for a wolf) at any time before death, its health state was restored to the maximum value.
- When a wolf (or rabbit) moved to a new site, its health state decreased by 1. When its health state decreased to below zero, the wolf (or rabbit) was considered dead, and it was removed from the system.

Rabbits and grass were allowed to enter into the refuge sites while wolves were prohibited. In the refuge, the rabbit could reproduce by eating grass, and the grass could grow by itself.

## 3. Individual Behavior

We formulated the transition probability for an individual positioned at  $(i, j)$  to move to its neighboring site  $(i + \alpha, j + \beta)$ . Here,  $\alpha$  and  $\beta$  take values of  $-1$ ,  $0$ , or  $1$  to represent the neighboring sites to the site occupied by the individual. Rabbits had a willingness to both hunt (consume grass) and escape (avoid wolves),

while wolves had a willingness to hunt (consume rabbit). Therefore, the  $P_{trans}$  for the wolf and the rabbit were calculated as functions of the willingness. The  $P_{trans}$  for a rabbit,  $P_{trans}^{rabbit}(i + \alpha, j + \beta)$ , and the  $P_{trans}$  for a wolf,

$P_{trans}^{wolf}(i + \alpha, j + \beta)$ , were mathematically described as follows:

$$P_{trans}^{rabbit}(i + \alpha, j + \beta) = h(i + \alpha, j + \beta)(1 - \theta_{i+\alpha, j+\beta}^r) \\ \times \left( \frac{(1 - \tilde{H})(1 - \tilde{E})}{N_a - N_r} + \theta_{i+\alpha, j+\beta}^g \left( \frac{\tilde{H}}{N_g} \right) + (1 - \theta_{i+\alpha, j+\beta}^w) \left( \frac{(1 - \tilde{H})\tilde{E}}{N_a - N_w - N_r} \right) \right), \\ (\alpha, \beta = -1, 0, 1; \alpha^2 + \beta^2 \neq 0),$$

$$P_{trans}^{wolf}(i + \alpha, j + \beta) = h(i + \alpha, j + \beta)(1 - \theta_{i+\alpha, j+\beta}^w) \times \left( \frac{(1 - \tilde{H})}{N_a - N_w} + \theta_{i+\alpha, j+\beta}^r \left( \frac{\tilde{H}}{N_r} \right) \right),$$

where

$$\theta_{i+\alpha, j+\beta}^l (l = g, r, \text{ or } w) = \begin{cases} 1 & \text{for the presence of an individual (grass, rabbit, or wolf)} \\ 0 & \text{otherwise,} \end{cases}$$

$$N_m = \sum_{\substack{k, l = -1, 0, 1 \\ k^2 + l^2 \neq 0 \\ \text{for } m \text{ sites}}} h(i + k, j + l) \quad (m; \text{all, grass, rabbit, or wolf})$$

$$\tilde{E} = \begin{cases} E & \text{for the presence of any wolf at the neighborsites} \\ 0 & \text{otherwise,} \end{cases}$$

$$\tilde{H} = \begin{cases} H & \text{for the presence of any grass (rabbit) in the neighborsites of a rabbit (wolf)} \\ 0 & \text{otherwise,} \end{cases}$$

where  $H$  and  $E$  represent the degrees of willingness to hunt and to escape, respectively.  $H$  and  $E$  had values ranging from 0.0 to 1.0, and the degree of willingness increased in this value range. An example is illustrated in Fig. 2. If a rabbit was surrounded by other rabbits, the rabbit could not move into the occupied neighboring sites, but could only move into an empty site (Fig. 2(a)). This behavioral rule is stochastically represented as the first term on the right side for  $P_{trans}^{rabbit}(i + \alpha, j + \beta)$ . The  $h$  value of each site, representing how favorable a site is for wolves and rabbits, is represented in the lattice box, and the transition probability values for each direction are represented outside the lattice box. The value of  $P_{trans}^{rabbit}(i + \alpha, j + \beta)$  was calculated for the case where  $H = 0.9$  and  $E = 0.9$ . In this situation, the second and the third terms become zero because no neighboring sites contain either wolves or grass. In the case that a rabbit is surrounded by grass, the transition probability for the sites with grass was much higher (see Fig. 2(b)). This behavior is described by the second term of the right side in the formula,  $P_{trans}^{rabbit}(i + \alpha, j + \beta)$ . The third term describes a rabbit surrounded by several wolves (Fig. 2(c)). When a rabbit has both grass and wolves in its neighbor sites, the rabbit has a relatively high transition probability to-

ward the top-right and the bottom-left sites according to the formula for  $P_{trans}^{rabbit}(i + \alpha, j + \beta)$  (Fig. 2(d)). For the case that the wolf was surrounded by several rabbits, the transition probability for the sites of the rabbits increased while the probabilities for empty sites decreased (Fig. 2(e)). In the present study, each combination of  $E$  and  $H$  was run for 500 iterations, and the results were averaged over 50 independent simulations.

#### 4. Refuge Distribution

To make heterogeneous refuge distributions on the lattice space, we introduced the function  $Amp(i, j)$ , such that  $Amp(i, j) = (i^2 + j^2)^{-(A+1)/2}$  on the space. Here, the position of  $(i, j) = (0, 0)$  was the center of the space. When  $A = -1$ , the value of  $Amp(i, j)$  becomes zero. The large values of  $Amp$  come together around  $(0, 0)$ .  $Amp(i, j) \times \exp(2\pi i\theta)$  corresponded to the element of a  $100 \times 100$  matrix.  $\theta$  is a number in the domain of  $[0, 1]$ . By applying the inverse Fourier transform to the matrix, we finally obtained a new matrix, which was projected to the lattice space. When the value of  $A$  was low



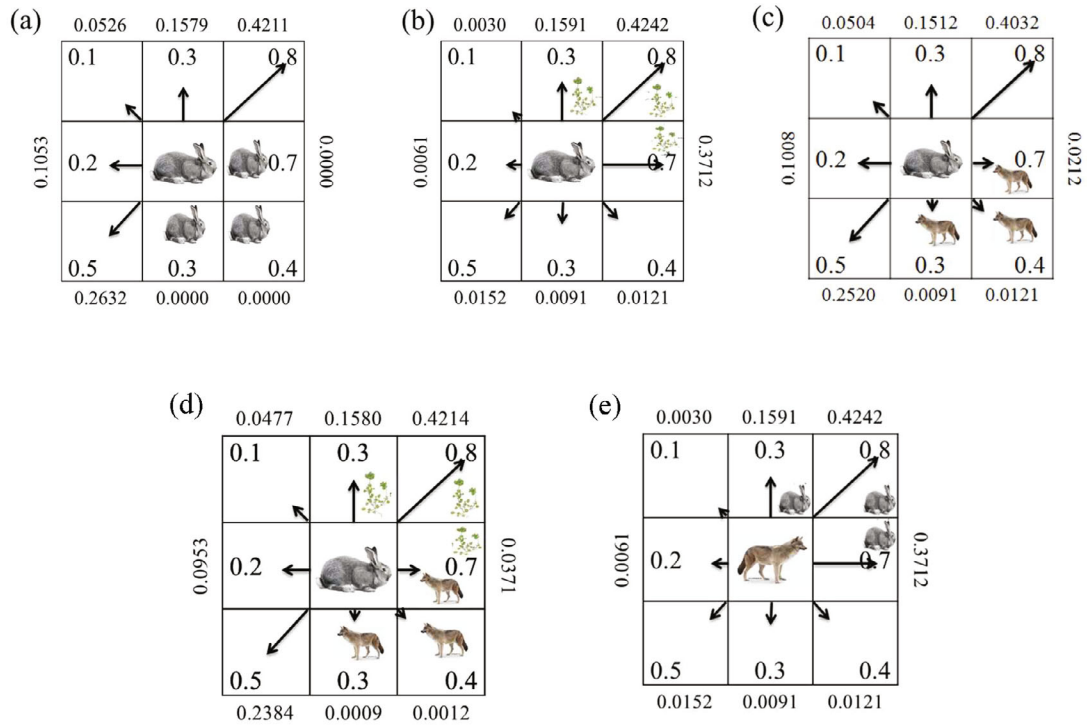


Fig. 2. (Color online) Transition probability,  $P_{trans}^{rabbit}$ , of a rabbit when its neighbor sites are occupied by (a) other rabbits, (b) grass, (c) wolves, or (d) both grass and wolves. The transition probability,  $P_{trans}^{wolf}$ , of a wolf when its neighbor sites are occupied by (e) rabbits and the  $h$  values, reflecting the landscape property, are provided within each grid cell. The values of the transition probability are provided outside each grid cell.

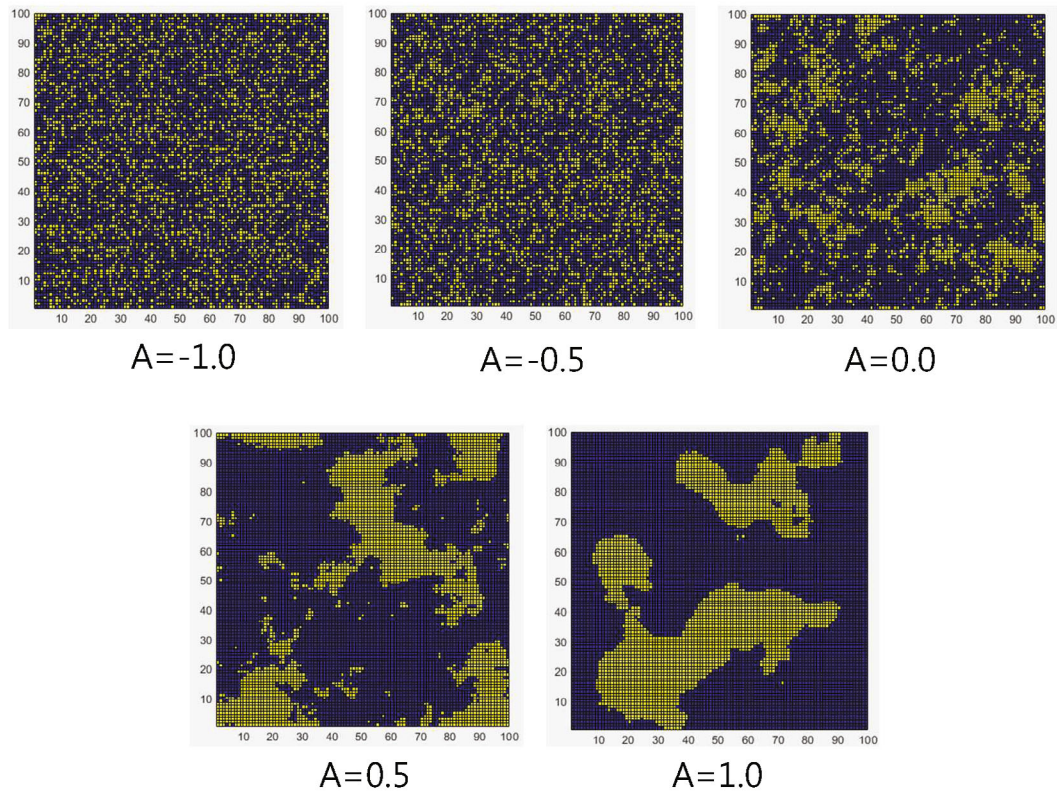


Fig. 3. (Color online) Spatial distribution of refuges for different heterogeneities.

in the range of  $[-1, 1]$ , lattices with relatively higher values were dispersively located. On the other hand, for high values of  $A$ , the lattices were clustered together (see Fig. 3). We introduced refuges ( $n = 1,000, 3,000$ , and  $5,000$ ) on the lattice space in descending lattice value order.

### 5. Initialization

A square lattice  $L \times L$  ( $= 100$ ) with periodic boundary conditions was considered. Each site of the lattice

$$\begin{aligned} n_w(i, j), \\ n_r(i, j), \\ n_g(i, j), \end{aligned} = \begin{cases} 1, & \text{when } \text{rand}(i, j) < W \text{ (for wolves), } R \text{ (for rabbits), } G \text{ (for grasses)} \\ 0, & \text{otherwise} \end{cases}$$

where  $\text{rand}(i, j)$  represents a randomly generated number with a value of  $[0, 1]$  at the site of  $(i, j)$ . Thus, the initially-assigned species densities were represented by the probabilities  $W$ ,  $R$ , and  $G$ . Through a preliminary study, we selected each initial density that guarantee the coexistence of a wolf, a rabbit, and grass under the condition of no refuge.

### 6. Input

In our preliminary study, we investigated the initial species density ( $W$  for wolf,  $R$  for rabbit, and  $G$  for grass) required for the coexistence of the three species under the condition of no refuge. The values of 0.3 for each species guaranteed the coexistence with a stable fluctuation in the population density. The number of refuges was initially considered in three cases: low ( $n = 1,000$ ), appropriate ( $n = 3,000$ ), and high ( $n = 5,000$ ). In addition, the value of the heterogeneity of the refuge distribution,  $A$ , was given a value ranging from 0.0 to 1.0

## III. RESULTS

Figure 4 shows the typical population dynamics for the wolf, rabbit, and grass for  $0 \leq t \leq 500$ , for  $A = 0.0$  and  $n = 3,000$ , where  $H = 0.0, 0.2, \dots, 1.0$  and  $E = 0.0, 0.2, \dots, 1.0$ . In the inset figures, the domain of the  $y$ -axis is the population density, which ranges from 0.0 to 1.0 for each species. The population density was calculated by dividing the number of individuals by the system size.

contained predator, prey, or plant, or remained empty. Before the simulation was run, wolves, rabbits, and grass were introduced on the lattice space by assigning 1 (present) or 0 (not present) to each lattice site. The assignment of 1 or 0 was determined by  $n_w(i, j)$  for wolves,  $n_r(i, j)$  for rabbits, and  $n_g(i, j)$  for grass, and these parameters denoted the number of individuals at the lattice site  $(i, j)$ .

The occupancy of a lattice site by an individual of a species was given by a threshold that was based on the probabilities  $W$ ,  $R$ , and  $G$ :

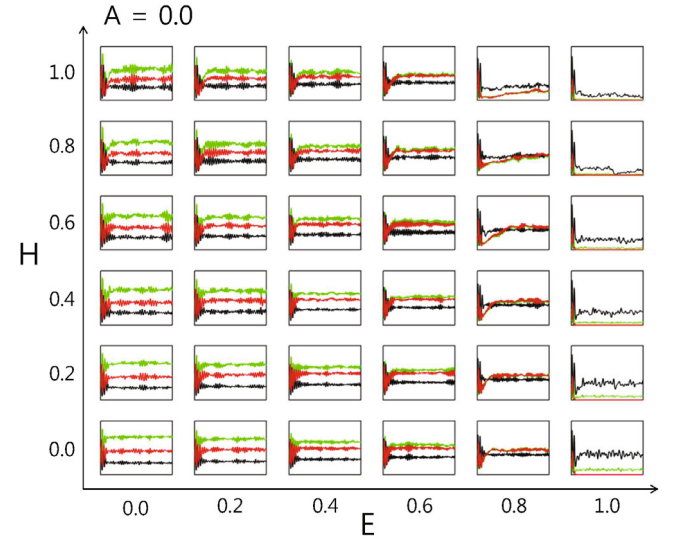


Fig. 4. (Color online) Plots of final population densities for  $E = 0.0, 0.2, 0.4, \dots, 1.0$  and  $H = 0.0, 0.2, 0.4, \dots, 1.0$ . In each plot, the  $x$ - and the  $y$ -axis represent the species density ranging from 0.0 to 1.0 and the simulation time ranging from 0 to 500, respectively. Red, green, and blue indicate wolf, rabbit, and grass, respectively.

The population density of wolves, rabbits, and grass are represented by red, black, and green plots, respectively.

For  $E = 0.0$  and  $0.2$ , the population density of each species strongly fluctuates with time because the rabbits with a low escape ability were easily eaten by the wolves. The rabbit decrease led to a decrease in the wolf density and an increase in the grass density. After that, the lower wolf density provided a chance for the rabbits to reproduce. The reproduction caused an increase in the

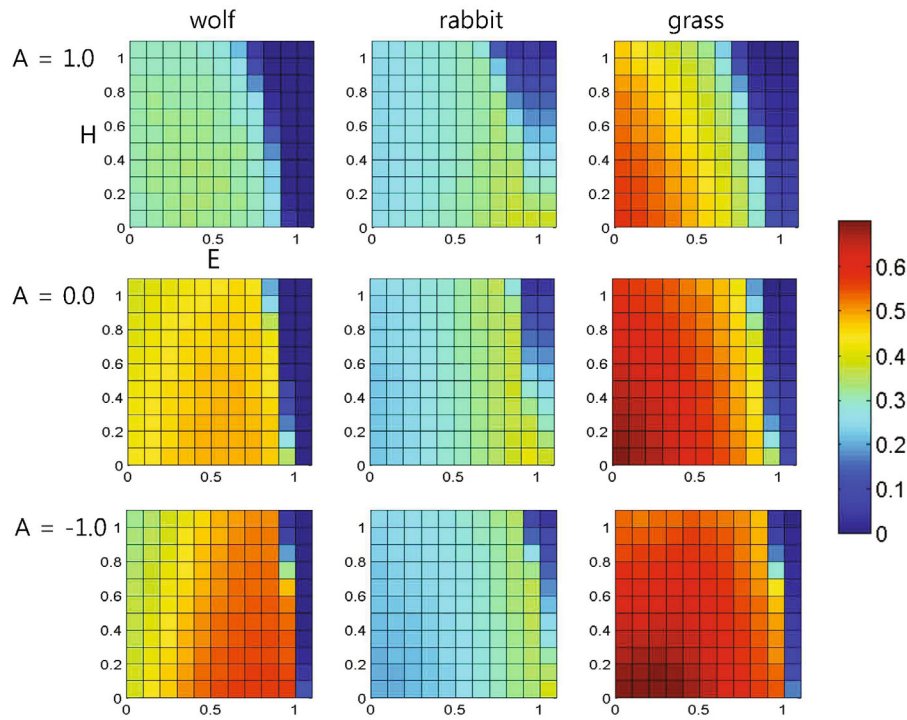
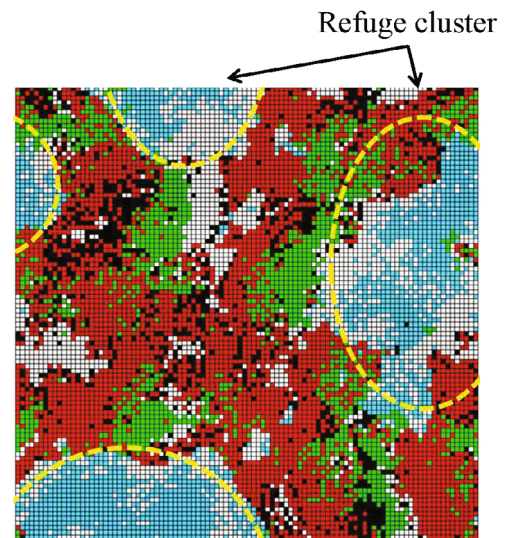


Fig. 5. (Color online) Grid maps of the population densities for each species where  $H = 0.0, 0.1, \dots, 1.0$  and  $E = 0.0, 0.1, \dots, 1.0$ . Dark red represents high density, and dark blue represents low density.

wolf density and a decrease in the grass density. Consequently, this cyclic process gave rise to a fluctuation. For  $E = 0.4$  and  $0.6$ , the degree of the fluctuation was decreased by the fact that an increase of the escape ability of rabbits decreased the degree of interaction. When  $E = 0.8$ , the fluctuation was largely decreased, and the wolf density decreased with the increasing  $H$ . This was caused by the rapidly decreasing interaction between the wolf and the rabbit. In addition, the decrease was enhanced by the presence of the refuge. When  $E = 1.0$ , rabbits successfully escaped from wolves, which caused the wolves to starve. After the extinction of the wolves, the density of the grass dramatically decreased with increasing  $H$  due to it being eaten by the rabbits.

In order to investigate the effect of the refuge distribution on the population density in the consideration of the individual behavior characterized by  $H$  and  $E$ , we built an  $H$ - $E$  grid map for each species. The population density of each species is represented by a different color on the grid map (see Fig. 5). The final population density was calculated by averaging the varying population density in the range of  $400 \leq t \leq 500$ . In this time domain, the population density was stabilized in fluctuation. For the wolf with  $E \leq 0.8$  and  $H \leq 1.0$ , the wolf population density decreased as  $A$  increased while the rabbit density was relatively stable. This indirectly reflects that the predation connection between the wolf and the rabbit became loose for higher  $A$  values. For the rabbit species, when the refuge was scattered ( $A = -1.0$ ), rabbits easily left the refuges and then were eaten by wolves, which led



In the clusters,  
 Blue sites: refuges with no rabbits  
 Gray sites: refuges occupied by rabbits

Fig. 6. (Color online) Snapshots of the spatial distributions of wolves (red dots), rabbits (gray dots), and grass (green dots) for  $A = 1.0$ . The yellow circles indicate the refuge clusters. In the clusters, blue dots represent refuges with no rabbits.

to a low rabbit density. On the other hand, when the



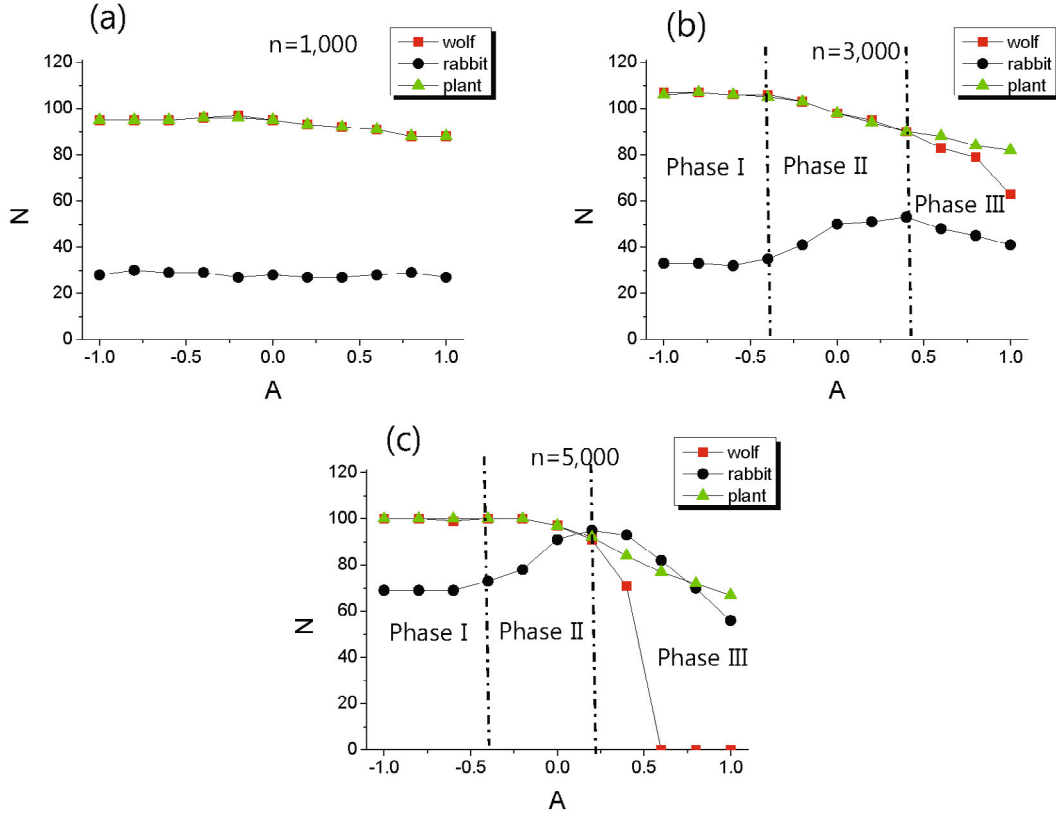


Fig. 7. (Color online) Plots of the number of grids,  $N$ , with a higher population density than 0.25 in the  $H$ - $E$  grid map against the heterogeneity of the refuge distribution for (a)  $n = 1,000$ , (b)  $n = 3,000$ , and (c)  $n = 5,000$ .

refuge was clustered ( $A = 1.0$ ), the grass in the clusters was rapidly consumed, which resulted in the starvation and death of rabbits traveling in the clusters (see Fig. 6). In the refuge clusters indicated by dotted yellow circles, gray and blue sites represent refuges with rabbits and refuges without rabbits, respectively. In the blue areas, rabbits died from starvation. Only moving rabbits near the boundaries of the refuge clusters survived.

In the  $H$ - $E$  grid maps, we counted the number of grids,  $N$ , with a population density  $\geq 0.25$ , where  $n = 1,000$ , 3,000, and 5,000 (Fig. 7). When the number of refuges was small ( $n = 1,000$ ), the refuge distribution did not affect the predator-prey system (Fig. 7(a)). When  $n = 3,000$  (Fig. 7(b)), three different phases were found: (I) no refuge effect phase ( $-1.0 \leq A < -0.4$ ), (II) refuge effect phase ( $-0.4 \leq A < 0.4$ ), and (III) habitat separation effect phase ( $0.4 \leq A < 1.0$ ). In phase I, rabbits were easily exposed to predation because the refuges were scattered. Subsequently, the wolf density became high, and the rabbit density was low. In phase II, large-sized refuge clusters were formed, which increased the survival probability of the rabbits. In phase III, the rabbits moving in the clusters were safe from wolf attacks, but they died because of starvation due to grass extinction in the clusters. In other words, a very large clustering of refuges led to an instability of the ecosystem due to habitat separation. The space was separated into two parts: one was

a habitat where the probability for rabbits to encounter wolves was high, and the other was a habitat in which no rabbits were killed by wolves, but where the grass was deficient. The separation played a negative role in the predator-prey system. When  $n = 5,000$  (Fig. 7(c)), the effect of the refuge distribution became stronger in each phase.

#### IV. DISCUSSION

Incorporating a refuge into predator-prey systems provides a more realistic model because many prey populations have some form of refuge available. When prey animals use refuges, they decrease their predation risk, which strongly affects the stability of the ecosystem. Thus, many researchers have studied the effects of the presence/absence of refuges on ecosystem stability and have revealed that refuges for prey have a stabilizing effect on the predator-prey population dynamics. However, they did not consider the influence of refuge distributions. In the present study, we explored how refuge distribution affected the ecosystem by using an integrative predator-prey model. The model was constructed based on the behavioral rules of individuals (hunting behavior of predators and escaping behavior of prey).



Through simulation experiments (see Fig. 4), we found that a stabilizing effect occurred with a higher escape ability of the prey, which indirectly showed that the stabilizing effect was closely related to the individual behavior of prey. A further investigation of how this relationship influences the effect would be interesting.

In this study, we appropriately set the values of the grass growth probability, individual health states, and the individual reproduction probabilities without any biological validation. However, the validation of the probability values could come from our preliminary simulation study. We confirmed that the change in the grass growth probability in the range of 0.1 – 0.3 did not statistically affect the simulation results shown in Fig. 7. For higher values of the reproduction probability ( $> 0.4$ ) and the health state ( $> 8$ ), the predator-prey ecosystem was broken by too many predators or prey. If grass were to be initially removed from the space, what would happen to the ecosystem? We carefully guess that the sub-ecosystems consisting of refuge and rabbits, shown in Fig. 5, would disappear which, in turn, would cause an easier extinction of rabbits. We leave this problem open for future study. As mentioned earlier, the initial density for each species was given in consideration of the coexistence condition among species.

In this study, we showed that when appropriate clusters of prey refuges were given, the probability of prey survival increased. Small, scattered refuges did not affect the predator-prey system while refuges that were too clumped played a negative role in ecosystem stability (Fig. 7). A comparison between simulation results and experimental data would be more probable if we could modify the model used in this study to be comparable with a real ecosystem by incorporating more variables to characterize individual behavior and biological properties [26].

In short, our model used two variables,  $H$  and  $E$ , to characterize escape and hunting behaviors. However, the behavior employed by real animals has more variables such as the predator's attack speed and attack direction, in the escaping and hunting behaviors. In addition, clearly, a prey with a high chance of escape is approached slowly while a prey with a low chance of escape is approached without such preventative measures.

Although these assumptions and behavior simplifications may not be realistic for animals in natural populations, our study is valuable because the simulation results not only highlighted the possible consequences of individual behavior in predator-prey-plant systems but also provided possible effects of the prey-refuge distribution on the ecosystems. Accordingly, this study could serve as a baseline for future empirical or observational studies on the dynamics of predator-prey systems with

refuges for prey. This may help to further narrow the gap between simulation models and experiments.

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