

SUGGESTED RUNNING HEAD TITLE  
DYNAMICS OF POPULATION SCRAMBLING FOR TERRITORY SITES

**Dynamics of Population Scrambling  
for  
Limited Number of Available Territory Sites**

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## Abstract

In this paper, we consider a mathematical model for the territorial population scrambling for the territory. In our modelling, we classify the considered population into two subpopulations: *territorial* and *non-territorial*, and further, do each of these subpopulations into *non-fighting* territorial population and *fighting*. The considered region is assumed to involve the suitable habitats and unsuitable ones for the successful reproductive activity. We consider the effect of change of the availability of suitable habitat, that is, the proportion of suitable habitats in the considered region, on the persistence and the structure of population scrambling for the territory. Especially, we discuss the threshold for the availability of suitable habitats according to the persistence of population, and the dependence of the structure of population and the occupancy ratios of the suitable habitats at the equilibrium state on the availability of suitable habitats.

*Keyword:* Territory; Habitat; Fight

## 1. Introduction

Territory is established for the various purposes, for example, for the foraging and for the mating. In many cases, the territory is established as the region with a size. So, as a result, the habitat space is divided into the region with some size. Therefore, the decreasing habitat space considerably effects on the territorial species according to its persistence.

For example, the Northern Spotted Owl (*Strix occidentalis caurina*) inhabits in the mature and old growth coniferous forest land in the United States Pacific Northwest. This forest land is very valuable timber land, and in recent year, the felling has been done. With the fragmentation of the preferred habitat, the population of the spotted owl has decreased rapidly. For territorial species, like the Northern Spotted Owls, the effect of loss or fragmentation of preferred habitat on the population persistence has been studied (Lande, 1987; Lande, 1988; Doak, 1989; Thomas *et al.*, 1990; Fahrig and Merriam, 1992; Lamberson and Carrol, 1992; Lamberson *et al.*, 1992). Such studies suggested the necessary proportion of preferred habitat in the whole region for the population persistence.

Lamberson and Carrol (Lamberson and Carrol 1992) constructed a mathematical model of the population dynamics for the territorial bird. It consists of the territorial and the non-territorial populations which have not yet secured a home range. They suggested that there would be the threshold for the availability of suitable habitats, that corresponds to the proportion of suitable habitats in the considered region, for the population persistence. With the suitable habitats less than the threshold, the population must decrease toward extinction, and with those more than it, the population tends to have a stable equilibrium size. Furthermore, they suggested that the proportion of reproducible territorial individuals in the whole population at the equilibrium state would be independent of the proportion of preferred habitats, and the reproducible territorial population per suitable habitat decreases as the availability of suitable habitats gets smaller.

Some fights for keeping the territory would occur in such population scrambling for the territory. As for the extent of fight, there would be such fights that it continues just for a short time, and that territorial individuals fight intensely. With such fighting, each of the individuals may be damaged, so that the amount of the energy and the time for the mating may be lost. That is, it could be suggested that the fighting effects the death rate or the reproduction rate.

In this paper, we construct a mathematical model for the population scrambling the territory. We classify the considered population into two subpopulations: *territorial* and *non-territorial*, and furthermore, do these subpopulations into *non-fighting* and *fighting* subpopulations. The considered region is assumed to involve the suitable and the unsuitable habitats for the successful reproductive activity. We consider the effect of change of the availability of suitable habitats on the persistence and the structure of population scrambling for the territory.

## 2. Model System

In our model, we focus only female population without taking account of age structure. Population is classified into two subpopulations: *territorial* and *non-territorial*. Territorial individual keeps its territory and fights against invaders, while non-territorial individual searches the site appropriate for its territory, and if it encounters such a site kept by a territorial individual, it is likely to fight to get the territory.

Let  $t_a(t)$  denote the total population of territorial individuals at time  $t$ .  $t_k(t)$  and  $t_f(t)$  respectively denote *non-fighting* territorial population and *fighting* one at time  $t$ . So  $t_a(t)$ ,  $t_k(t)$  and  $t_f(t)$  have the following relation among them:

$$t_a(t) = t_k(t) + t_f(t). \quad (1)$$

Next, let  $n_a(t)$  denote the total population of non-territorial individuals at time  $t$ .  $n_s(t)$  and  $n_f(t)$  respectively denote non-territorial population *searching* territory and that *fighting* against territorial to get territory at time  $t$ . Hence,  $n_a(t)$ ,  $n_s(t)$  and  $n_f(t)$  have the following relation:

$$n_a(t) = n_s(t) + n_f(t). \quad (2)$$

Let  $w(t)$  denote the whole population at time  $t$ :

$$w(t) = t_a(t) + n_a(t).$$

On the other hand, we assume that there totally exist  $s$  spatial sites, of which  $h$  sites are suitable and available for the habitat for the successful reproductive activity. In our model,  $t_a(t)$  suitable sites of  $h$  are occupied at time  $t$ . If searching *non-territorial* individual encounters an unoccupied site of  $h$ , it can change to *territorial* to keep it. With the random searching, the probability of such encounter for a searching non-territorial is assumed to be proportional to the frequency of unoccupied sites:

$$\frac{h - t_k - t_f}{s}. \quad (3)$$

When and only when searching non-territorial individual encounters a site occupied by a non-fighting territorial, the fight between them occurs with a probability. In such case, the searching non-territorial changes to the fighting non-territorial, and the counter territorial does to the fighting territorial. The probability of such encounter for a searching non-territorial is assumed to be proportional to the frequency of territories with non-fighting territorials:

$$\frac{t_k}{s}. \quad (4)$$

In our model, we assume that the fight between territorial and non-territorial is always one-to-one. The sites with fight are neglected by any searching non-territorial. So, we consider that  $t_f(t) = n_f(t)$  at any time  $t$ . Hereafter, we

consider the dynamics just among  $t_k(t)$ ,  $t_f(t)$  and  $n_s(t)$ . Each fight finishes with a probability per unit time, and fighting non-territorial can defect the counter territorial at probability  $\beta$ . We assume that the loser is damaged to die with a probability. The survival rates of the loser territorial and non-territorial are respectively given by  $\sigma_T$  and  $\sigma_N$ . Reproductive activity can be allowed only for *non-fighting territorial* population, and the recruited population is supplied as *searching non-territorial*. The reproduction rate  $b$  is such that new born female survives from its birth till joining to searching non-territorial population. We consider the natural death rates only for non-fighting territorial and for searching non-territorial, given respectively by  $p_k$  and  $p_s$ .

With the above assumptions (see Fig. 1), the population dynamics can be described by

$$\frac{dt_k(t)}{dt} = \frac{a(h - t_k - t_f)n_s}{s} - r\frac{t_k}{s}n_s + \delta t_f - p_k t_k \quad (5)$$

$$\frac{dt_f(t)}{dt} = r\frac{t_k}{s}n_s - \delta t_f \quad (6)$$

$$\frac{dn_s(t)}{dt} = -\frac{a(h - t_k - t_f)n_s}{s} + bt_k - r\frac{t_k}{s}n_s + \sigma\delta t_f - p_s n_s, \quad (7)$$

where  $a$ ,  $r$  and  $\delta$  are positive constants, and

$$\sigma = \sigma_T\beta + \sigma_N(1 - \beta). \quad (8)$$

With the following non-dimensional variables,

$$T_k \equiv \frac{t_k}{h}; \quad T_f \equiv \frac{t_f}{h}; \quad N_s \equiv \frac{n_s}{h}; \quad A \equiv \frac{a}{\delta};$$

$$R \equiv \frac{r}{\delta}; \quad P_k \equiv \frac{p_k}{\delta}; \quad P_s \equiv \frac{p_s}{\delta}; \quad B \equiv \frac{b}{\delta};$$

$$H \equiv \frac{h}{s}; \quad \tau \equiv \delta t,$$

the system of (5), (6) and (7) can be rewritten as follows:

$$\frac{dT_k(\tau)}{d\tau} = AH(1 - T_k - T_f)N_s - RHT_kN_s + T_f - P_kT_k \quad (9)$$

$$\frac{dT_f(\tau)}{d\tau} = RHT_kN_s - T_f \quad (10)$$

$$\frac{dN_s(\tau)}{d\tau} = -AH(1 - T_k - T_f)N_s + BT_k - RHT_kN_s + \sigma T_f - P_sN_s, \quad (11)$$

where  $T_k$  and  $T_f$  are not beyond 1. Variables  $T_k$ ,  $T_f$  and  $N_s$  mean the corresponding populations per suitable habitat. Parameter  $H$  not beyond 1 corresponds to the availability of suitable habitats in the considered region. Now,  $T_a$ ,  $N_a$  and  $W$  are respectively defined as follows:

$$T_a \equiv T_k + T_f$$

$$N_a \equiv N_s + N_f$$

$$W \equiv T_a + N_a.$$

Variables  $T_s$ ,  $N_a$  and  $W$  mean the territorial, the non-territorial and the total population per suitable habitat. These variables per suitable habitat indicate the ratios of the suitable habitat occupancy by the corresponding subpopulations.

### 3. Analysis

#### 3.1. EXISTENCE AND LOCAL STABILITY OF EQUILIBRIUM STATES

In this section, we consider the equilibrium state  $(T_k^*, T_f^*, N_s^*)$  for the system of (9), (10) and (11). It satisfies the following equations:

$$\begin{cases} AH(1 - T_k^* - T_f^*)N_s^* - RHT_k^*N_s^* + T_f^* - P_kT_k^* = 0 \\ RHT_k^*N_s^* - T_f^* = 0 \\ -AH(1 - T_k^* - T_f^*)N_s^* + BT_k^* - RHT_k^*N_s^* + \sigma T_f^* - P_sN_s^* = 0. \end{cases} \quad (12)$$

From (12), we can explicitly obtain the equilibrium states  $(T_k^*, T_f^*, N_s^*)$  expressed as follows:

$$\left( \frac{AHN_s^*}{P_k + AHN_s^* + ARH^2N_s^{*2}}, RHT_k^*N_s^*, N_s^* \right), \quad (13)$$

where  $N_s^*$  is given as zero or the positive root for the following equation:

$$ARH^2P_sN_s^{*2} + \{ARH^2(1 - \sigma) + AHP_s\}N_s^* + AH(P_k - B) + P_kP_s = 0. \quad (14)$$

In case of  $N_s^* = 0$ , (13) gives the trivial equilibrium  $(0, 0, 0)$ . On the other hand, in case of  $N_s^* > 0$ , it gives the non-trivial equilibrium state. For these equilibria, we can easily obtain the condition for its existence and local stability (Appendix A): If

$$H \leq \frac{P_kP_s}{A(B - P_k)}, \quad (15)$$

the trivial equilibrium  $(0, 0, 0)$  is locally stable, and then the non-trivial equilibrium can not exist. Otherwise, if

$$H > \frac{P_k P_s}{A(B - P_k)}, \quad (16)$$

the trivial is unstable, and the non-trivial equilibrium state uniquely exists locally stable. (16) represents the necessary availability of suitable habitats for the population persistence. This result from (15) and (16) on the  $(P_k, P_s)$ -dependence of the population persistence is shown in Fig. 2.

### 3.2. POPULATION STRUCTURE AT THE EQUILIBRIUM STATE

In this section, we consider how the population structure at the equilibrium state depends on the availability of suitable habitats  $H$ . We show the result that the dependence in Table. 1. Table. 1 shows how the population structure changes as the availability of suitable habitats  $H$  decreases.

$T_f^*/W^*$  represents the proportion of fighting territorial in the whole population, and it monotonically decreases as the availability of suitable habitats  $H$  gets smaller.

$T_k^*/T_a^*$  represents the proportion of reproducible territorial in the whole territorial population.  $T_k^*/T_a^*$  monotonically increases as the availability of suitable habitats  $H$  gets smaller.

The  $H$ -dependence of the proportion  $T_a^*/W^*$  of territorial population in the whole population changes according to the parameters  $P_k$  and  $P_s$  (see Fig. 3 and Appendix C). When the natural death rate  $P_s$  for non-territorial is large enough to satisfy the following:

$$P_s > B - P_k + 1 - \sigma, \quad (17)$$

the proportion of territorial monotonically decreases as the availability of suitable habitats  $H$  gets smaller, while, when  $P_s$  is small to violate the condition (17), it monotonically increases.

Contrarily to the case of  $T_a^*/W^*$ , the proportions  $N_a^*/W^*$  and  $N_a^*/T_a^*$  of non-territorial in the whole population and in the whole territorial population have the exactly inverse dependence on  $H$ , related to the condition (17).

The  $H$ -dependence of the proportion  $T_k^*/W^*$  of non-fighting reproducible territorial population in the whole population changes according to the parameters  $P_s$  and  $\sigma$  (see Fig. 3 and Appendix B). Fig. 3 indicates that, in the case when there is no damage in fight, that is, when  $\sigma = 0$ ,  $T_k^*/W^*$  always monotonically increases as the availability of suitable habitats  $H$  gets smaller. In the case when there is some damage in fight, when the death rate for non-territorial is small enough to satisfy the following:

$$P_s < \frac{1 - \sigma}{2}, \quad (18)$$

$T_k^*/W^*$  monotonically decreases as  $H$  gets smaller.

### 3.3. OCCUPANCY OF SUITABLE HABITATS

In this section, we consider the occupancy ratios of suitable habitats. We show the dependence of the occupancy ratios of suitable habitats on the availability of suitable habitat  $H$  in Table. 2.

$T_a^*$  which represents the territorial population per suitable habitat monotonically decreases as the availability of suitable habitats  $H$  gets smaller (see Fig. 4 and Appendix D). The parameter  $A$  represents the level of the efficiency of searching the suitable habitat. As  $A$  gets larger, the efficiency becomes higher. Fig. 4 shows that, for the population with the higher searching efficiency, when the availability of suitable habitat  $H$  is small, the territorial population per suitable habitat decreases rapidly with small reduction of  $H$ .

$T_k^*$  represents the reproducible territorial population per suitable habitat. We show the  $H$ -dependence of  $T_k^*$  in Fig. 5. It is shown that, when the searching efficiency is high, the reproducible territorial per suitable habitat does not necessary decreases as the availability of suitable habitat  $H$  gets smaller. That is, it is implied that there would be the case in which decreasing the availability of suitable habitat is better in order to maximize the reproducible territorial per suitable habitat.

Now, we suppose that the availability of suitable habitat  $H$  could be controlled. For the population at the equilibrium state with an availability of suitable habitat  $H_0$ , the relation between  $H_0$  and  $H$  with which  $T_k^*$  has the maximum is shown in Fig. 6. For  $P_k$  and  $P_s$  in the region of  $\Gamma_1$  shown in Fig. 6,  $T_k^*$  can increase by decreasing  $H$ , however, with too small  $H$ , it becomes smaller. For  $\Gamma_2$  and  $\Gamma_3$  in Fig. 6,  $T_k^*$  increases as  $H$  gets larger, however, for  $\Gamma_2$ , with too large  $H$ , it becomes smaller.

## 4. Discussion

In this paper, we made the mathematical model for the population scrambling territory, and considered the effect of change of the availability of suitable habitat for the population. Our model is the expanded model of Lamberson and Carrol (1992). The threshold for the availability of suitable habitat for persistence of population obtained in this paper was the same result to them. This means that the fighting for keeping territory does not effect on the persistence of population.

Lamberson and Carrol (Lamberson and Carrol 1992) suggested that the proportion of territorials in whole population at equilibrium state does not depend on the proportion of preferred habitat, and the reproducible territorial population per suitable habitat decreases as the availability of suitable habitat gets smaller .



While, our results show that the structure of population at the equilibrium state changes according the availability of suitable habitats. Furthermore, we obtained the result that the reproducible territorial population per suitable habitat does not necessary decrease as the availability of suitable habitat gets smaller. It is those points that our results is considerably different from Lamberson and Carrol (Lamberson and Carrol 1992).

In our model, we consider that, when individuals are defected in the fight, they are damaged to die. However, individuals must spent the energy by fighting, and the decrease of the survival rates of not only individuals be defected but also one won in fight should be considered. Also, we regard the reproduction as the continuous process where in most case it should be handled as the discrete annual event. It is necessary to consider the model taking account of these points.

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## Appendix A Existence and Local Stability of Non-trivial Equilibrium State

In this appendix, we show the analyzing way of the existence and the local stability of the equilibrium states. At first, we consider the existence of the non-trivial positive equilibrium state given by (13). Since the coefficient of  $N_s^{*2}$  and  $N_s^*$  of (14) are positive, it can be easily proved that, if and only if (16) is satisfied, (14) has a positive root.

Next we consider the local stability of equilibrium state. Jacobi matrix for the equilibrium  $(T_k^*, T_f^*, N_s^*)$  of the system (9), (10) and (11) is obtained as follows:

$$\begin{pmatrix} -AHN_s^* - RHN_s^* + P_k & -AHN_s^* + 1 & AH(1 - T_k^* - T_f^*) - RHT_k^* \\ RHN_s^* & -1 & RHT_k^* \\ AHN_s^* - RHN_s^* + B & AHN_s^* + \sigma & -AH(1 - T_k^* - T_f^*) - RHT_k^* - P_s \end{pmatrix}. \quad (19)$$

At first, we consider the case when the non-trivial positive equilibrium does not exist. The characteristic polynomial for  $(0, 0, 0)$  is given by

$$p_0(\lambda) = (\lambda + 1)\{\lambda^2 + (P_k + AH + P_s)\lambda + AH(P_k - B) + P_k P_s\}. \quad (20)$$

It is easily found that the roots of  $p_0(\lambda) = 0$  are not beyond 0 when and only when (15) is satisfied. Therefore, it can be proved that  $(0, 0, 0)$  is locally stable when and only when (15) is satisfied.

Next, we consider the non-trivial positive equilibrium. The characteristic polynomial of (19) for the non-trivial equilibrium appears in the following form:

$$p_*(\lambda) = \lambda^3 + a_1\lambda^2 + a_2\lambda + a_3, \quad (21)$$

where

$$\begin{aligned} a_1 &= 1 + P_k + AHN_s^* + RHN_s^* + \frac{AHB + ARH^2\sigma N_s^*}{P_k + AHN_s^* + ARH^2N_s^{*2}} \\ a_2 &= P_k + AHN_s^* + AHP_sN_s^* + P_sRHN_s^* + AHP_sN_s^{*2} \\ &\quad + \frac{AHB + ABRH^2N_s^* + 2ARH^2P_kN_s^* + ARH^2P_k\sigma N_s^* + A^2RH^3N_s^{*2}}{P_k + AHN_s^* + ARH^2N_s^{*2}} \\ a_3 &= \frac{AHN_s^*\{AH(B - P_k)(1 + 2RHN_s^*) + RH(1 - \sigma)(P_k - ARH^2N_s^{*2})\}}{P_k + AHN_s^* + ARH^2N_s^{*2}}. \end{aligned}$$

With some cumbersome estimation, we can show that  $a_1$ ,  $a_2$  and  $a_3$  satisfy the Jury criteria when and only when (16) is satisfied (as for the Jury criteria, for instance, see Murray, 1989), so that the non-trivial positive equilibrium is locally stable when it exists.

## Appendix B $H$ -dependence of The Proportion of Territorial

Since  $T_k^*$ ,  $T_f^*$  and  $N_s^*$  satisfy (12),  $T_a^*/W^*$  can be rewritten as follows:

$$\begin{aligned} \frac{T_a^*}{W^*} &= \frac{T_k^* + T_f^*}{T_k^* + 2T_f^* + N_s^*} \\ &= \frac{P_s(1 + RN_s^*)}{P_s + 2RP_sN_s^* - R(1 - \sigma)N_s^* - P_k + B}. \end{aligned}$$

The derivative of  $T_a^*/W^*$  in terms of  $H$  can be obtained as follows:

$$\frac{\partial(T_a^*/W^*)}{\partial H} = \frac{P_s R(\partial N_s^*/\partial H)(-P_s + B - P_k + 1 - \sigma)}{\{P_s + 2RP_sN_s^* - R(1 - \sigma)N_s^* - P_k + B\}^2}.$$

Since  $N_s^*$  satisfies (14),  $\partial N_s^*/\partial H$  is obtained as follows:

$$\frac{\partial N_s^*}{\partial H} = -\frac{2RP_sN_s^* + RH(1 - \sigma) + P_s}{R(1 - \sigma) + P_k - B}.$$

From (12),  $N_s^*$  satisfies

$$(1 - \sigma)RN_s^* + P_k - B = -(RP_sN_s^{*2} + P_sN_s^* + \frac{P_kP_s}{A}) < 0.$$

So  $\partial N_s^*/\partial H > 0$ . Therefore, if

$$P_s > B - P_k + 1 - \sigma,$$

then the derivative of  $T_a^*/W^*$  in terms of  $H$  is negative, and  $T_a^*/W^*$  monotonically decreases in terms of  $H$ . While, if

$$P_s < B - P_k + 1 - \sigma,$$

then the derivative of  $T_a^*/W^*$  in terms of  $H$  is positive, and  $T_a^*/W^*$  monotonically increases in terms of  $H$ .

## Appendix C $H$ -dependence of The Proportion of Reproducible Territorial

Since  $T_k^*$  and  $T_f^*$  satisfy (12),  $T_k^*/W^*$  can be rewritten as follows:

$$\frac{T_k^*}{W^*} = \frac{T_k^*}{T_k^* + 2T_f^* + N_s^*}$$

$$= \frac{A}{A + 2ARN_s^* + ARN_s^{*2} + AN_s^* + P_k}.$$

Since  $N_s^*$  satisfies (14), the derivative of  $T_a^*/W^*$  in terms of  $H$  can be obtained as follows:

$$\frac{\partial(T_k^*/W^*)}{\partial H} = \frac{A^3 R \{(1 - \sigma)RN_s^* + P_k - B\}}{P_s(A + 2ARN_s^* + ARN_s^{*2} + AN_s^* + P_k)^2} \{2P_s - (1 - \sigma)\}.$$

From (14),  $N_s^*$  satisfies

$$(1 - \sigma)RN_s^* + P_k - B = -(RP_s N_s^{*2} + P_s N_s^* + \frac{P_k P_s}{A}) < 0.$$

Therefore, if

$$2P_s > 1 - \sigma,$$

then the derivative of  $T_k^*/W^*$  in terms of  $H$  is negative, and  $T_k^*/W^*$  monotonically decreases in terms of  $H$ . While, if

$$2P_s < 1 - \sigma,$$

then the derivative of  $T_k^*/W^*$  in terms of  $H$  is positive, and  $T_k^*/W^*$  monotonically increases in terms of  $H$ .

## Appendix D $H$ -dependence of Territorial Population per Suitable Habitat

Since  $T_k^*$  and  $T_f^*$  satisfy (12),  $T_a^*$  can be rewritten as follows:

$$T_a^* = \frac{AN_s^* + ARN_s^{*2}}{ARN_s^{*2} + AN_s P_k}.$$

The derivative of  $T_a^*$  in terms of  $H$  can be obtained as follows:

$$\frac{\partial T_a^*}{\partial H} = \frac{AP_k(\partial N_s^*/\partial H)(1 + 2RN_s^*)}{(ARN_s^{*2} + AN_s P_k)^2}.$$

Since  $N_s^*$  satisfies (14),  $\partial N_s^*/\partial H$  can be obtained as follows:

$$\frac{\partial N_s^*}{\partial H} = -\frac{2RP_s N_s^* + RH(1 - \sigma) + P_s}{R(1 - \sigma) + P_k - B}.$$

From (14),  $N_s^*$  satisfies

$$(1 - \sigma)RN_s^* + P_k - B = -(RP_s N_s^{*2} + P_s N_s^* + \frac{P_k P_s}{A}) < 0.$$

So  $\partial N_s^*/\partial H > 0$ . Therefore, the derivative of  $T_a^*$  in terms of  $H$  is positive, and  $T_a^*$  monotonically increases in terms of  $H$ .

## Figure and Table Caption

Fig. 1. Scheme of population dynamics for the model with four groups.

Fig. 2. The dependence of existence and local stability of the trivial and the non-trivial equilibrium states on the parameter region of  $P_k$  and  $P_s$ .

Fig. 3.  $T_k^*/W^*$  and  $T_a^*/W^*$  have the different monotonicity in terms of  $H$  according to the parameter  $P_k$  and  $P_s$ .  $A = 2.0$ ;  $R = 0.5$ ;  $H = 0.4$ ;  $B = 2.0$ ;  $\sigma = 0.2$ . The change of them for the decrease of  $H$  is shown.

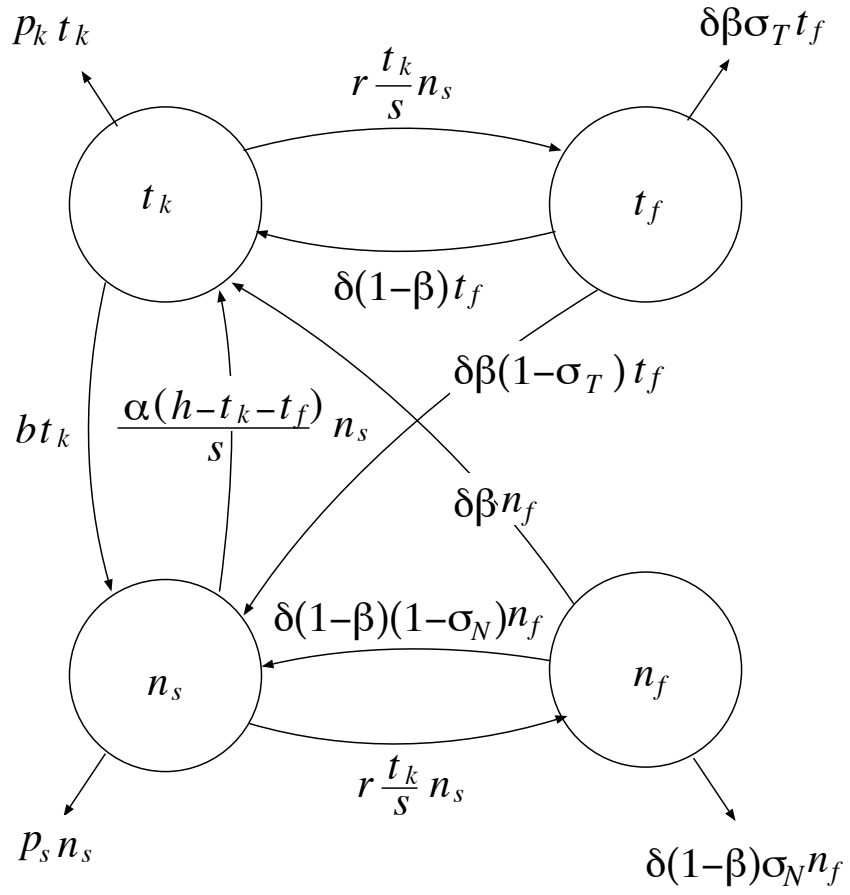
Fig. 4. The territorial population per suitable habitat  $T_a^*$  monotonically decreases as the availability of suitable habitat  $H$  gets smaller. For the population with the higher search efficiency  $A$ , when  $H$  is small,  $T_a^*$  decreases rapidly by the a little decrease of  $H$ .  $A = 1.0$ ;  $R = 1.0$ ;  $B = 0.5$ ;  $\sigma = 0.9$ ;  $P_k = 0.1$ ;  $P_s = 0.15$ .

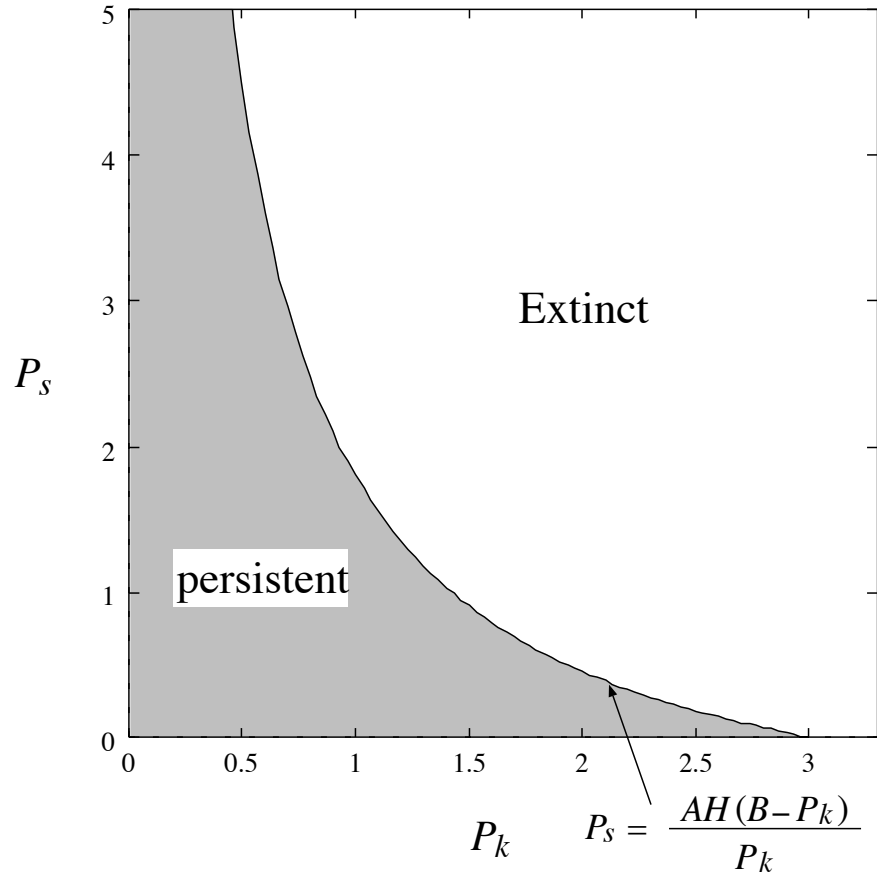
Fig. 5. The reproducible territorial per suitable habitat  $T_k^*$  has the maximum in terms of  $H$ . When the search efficiency  $A$  is high,  $T_k^*$  does not necessary decreases as the availability of suitable habitat  $H$  gets smaller.  $A = 1.0$ ;  $R = 1.0$ ;  $B = 0.5$ ;  $\sigma = 0.9$ ;  $P_k = 0.1$ ;  $P_s = 0.15$ .

Fig. 6.  $T_k^*$  could change if  $H$  would be changed. For population with  $H = H_0$  and  $(P_k, P_s)$  of the region  $\Gamma_1$ ,  $T_k^*$  could take its maximum for an intermediate  $H = H^* < H_0$ . For  $\Gamma_2$ , it could take its maximum for an intermediate  $H = H^* > H_0$ . For  $\Gamma_3$ , for  $H = 1$ .  $A = 2.5$ ;  $R = 0.5$ ;  $H_0 = 0.1$ ;  $B = 0.7$ ;  $\sigma = 0.5$ .

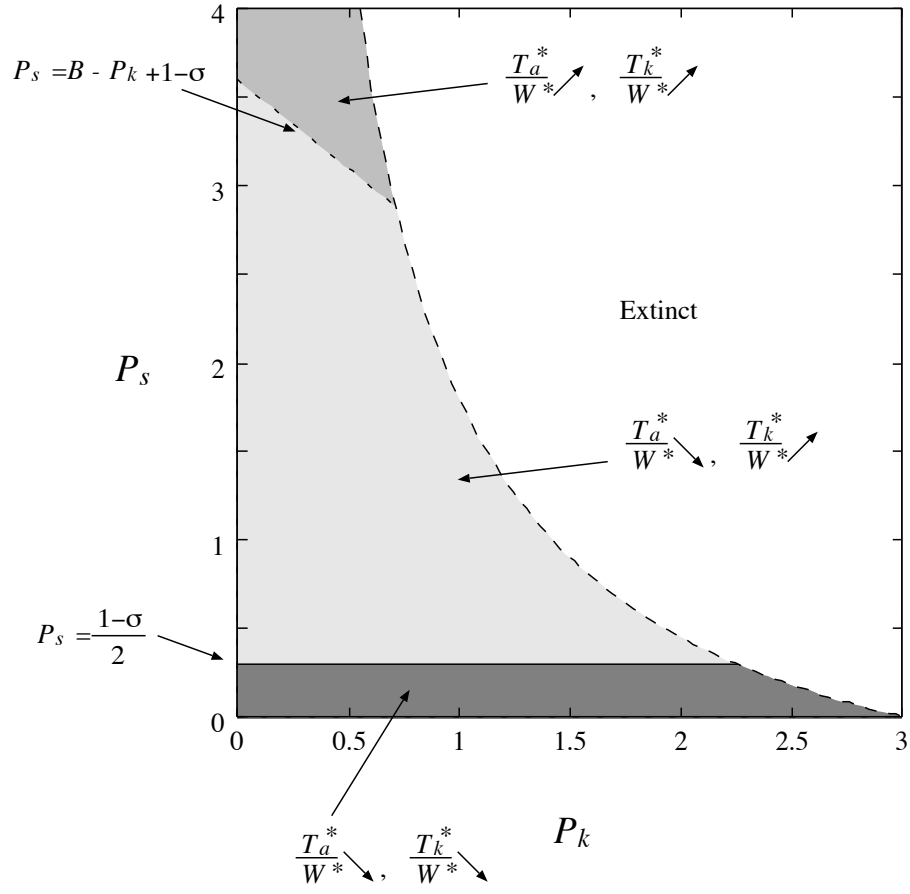
Table. 1. The structure of population at the equilibrium state depends on the availability of suitable habitats  $H$ .

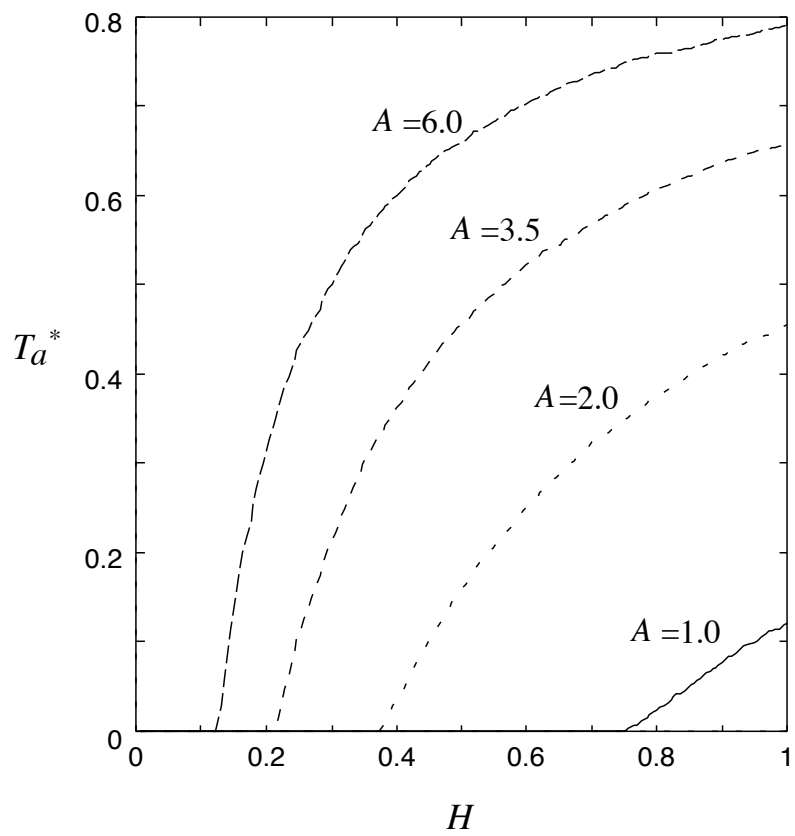
Table. 2. The dependence of the occupancy rate of the suitable habitats on the availability of suitable habitat  $H$  is shown.

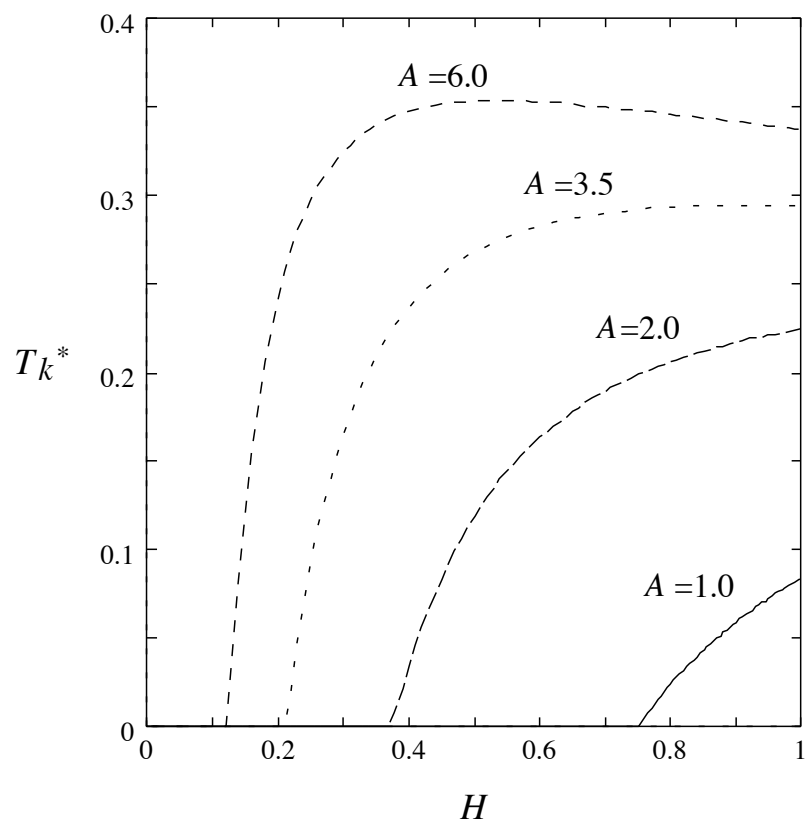


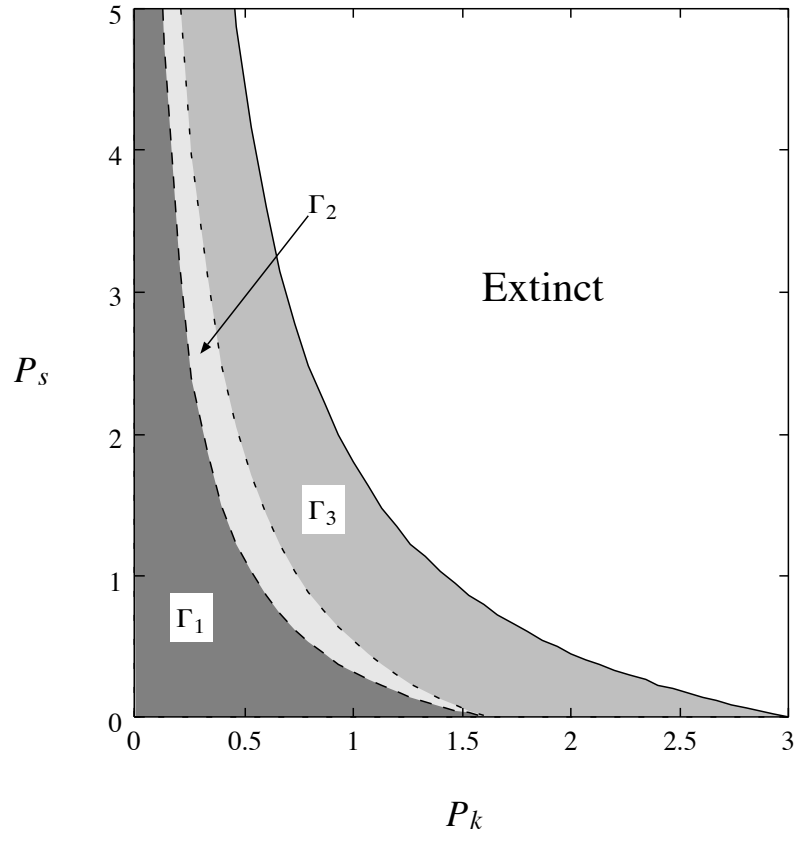







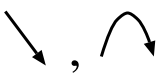








$\frac{T_a^*}{W^*}, \frac{N_a^*}{W^*}, \frac{N_a^*}{T_a^*}, \frac{T_k^*}{W^*}$	
$\frac{T_f^*}{W^*}$	
$\frac{T_k^*}{T_a^*}$	

$T_k^*, W^*, N_s^*$	
$T_a^*, T_f^*, N_a^*$	