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Simulations on Prevalence of *Echinococcus multilocularis* in Hokkaido on the Basis of Vole Population Dynamics

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In our study, we have investigated the influence of the intermediate host population density on the prevalence of *Echinococcus multilocularis* in the definitive host using a mathematical model of transmission. For the vole population (intermediate host) in Hokkaido, a model of population dynamics has been constructed in this paper which follows the seasonal and annual fluctuations. In the northeastern area, the vole density appears to fluctuate periodically with a 4 year cycle. The prevalence of *Echinococcus multilocularis* in the fox population (definitive host) can be affected by the density of vole through the fox ingesting infectious voles. Therefore we have prepared a food habit function of foxes and the logistic distribution has been proposed. The simulations which have been carried out using the mathematical model for transmission of *Echinococcus multilocularis* together with the vole dynamics have indicated that the prevalence in foxes is correlated and synchronized with the population dynamics of vole. In addition they have also made us recognize that it is necessary to introduce a suitable food habit function into the transmission model.

Key words: *Echinococcus multilocularis, food habit of foxes, Hokkaido, population dynamics, vole*

1. INTRODUCTION

The parasites *Echinococcus multilocularis* in fox populations prevail in almost all areas of Hokkaido, Japan. There are also signs of alveolar *Echinococcus* in the human population. Our paper focuses on the relationship between the prevalence of *Echinococcus multilocularis* in the definitive host population, fox, and the density of the intermediate host population, vole, based on a mathematical model of transmission.

There are various characteristics in the population dynamics of vole which depend on seasonal, annual and geographical factors (Kaneko et al., 1998; Saitoh et al., 1998a). The infection rate in foxes depends on the density of vole through its food habit, because a fox feeds on voles by preference but it does also have other available food. Yoneda (1981) reported on the diversity of food habits for seasons and areas. The winter food habit of foxes which is influenced mainly by snowfall plays an important role in the infection rate of foxes (Kondo et al., 1986). The fluctuation in the infection rate of foxes is either synchronized with that of the vole density or follows it with a one year leg (Saitoh et al., 1998b). In this paper, we formulate a mathematical model for the population dynamics of the vole as well as a function which describes the food habit of foxes, and then combine them with a model for transmission of *Echinococcus multilocularis* (Ishikawa et al., in preparation).

We have carried out the simulations on the prevalence of *Echinococcus multilocularis* in two typical areas: the northeastern area in Hokkaido and the southwestern area using the field data of Nemuro and Oshima, respectively. The comparative study on the food habit of foxes shows that it is necessary to introduce a suitable food habit function into the transmission model.

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2. MATERIALS AND METHODS

Seasonal Population Dynamics of Vole

The population dynamics of the vole is under the influence of the breeding season, a breeding coefficient and a survival rate which is seasonally swayed by meteorological conditions. It is well known (Kaneko et al., 1998) that the breeding time covers three seasons, that is, from April to October, that the pregnancy rate is higher in spring and fall than in summer, and that the survival rate is higher in winter than in the other seasons, so that the population density curve has two peaks a year.

We need several assumptions to deal with a model for the population dynamics of vole. We assume that the breeding season begins on the first day when the move in the average temperature with a band width of 20 days is in excess of 5 °C (Stenseth et al., 1998). We may assume that spring runs for two months from this day, and this is followed by summer and fall each for two months. In our study, we adopted the temperatures in the northeastern part of Hokkaido from Nemuro the data of which was measured by the Meteorological Agency, Japan. The breeding rate R of the vole is written by the form

$$R = LS \cdot SR \cdot P_{rep}$$

where LS, SR and P_{rep} denote litter size, sex ratio and percentage of breeding females, respectively. We adopt that $LS = 5.3$ and $SR = 0.5$. The other parameters, such as P_{rep} and the survival rate are discussed in next section.

Annual Population Dynamics of Vole in Hokkaido

To investigate annual population dynamics of vole, we used the census data on vole populations in Hokkaido carried out by the Forestry Agency of the Japanese Government. Saitoh et al. (1998a) reported that a periodic fluctuation in the vole population with a 3.5 - 4.5 year cycle was found in the northern and eastern area in Hokkaido whereas an aperiodic fluctuation was found in the southernmost area. The proportion of breeding voles was higher during the increase phase than during the decline phase (Nakata, 1989). It is assumed that both percentage P_{rep} of breeding females and survival rate depend on age and season, therefore we arranged some sets of data which consisted of parameters concerned with age (0, 1, 2, 3 months old and more than 4 months old) and each season as shown in Table 3 of Yoccoz et al. (1998). We make suitable combinations of these parameter sets in a model of vole population to realize a periodic or aperiodic situation.

Food Habit of Foxes Depended on Vole Population

Voles can transmit *Echinococcus multilocularis* to a fox when a susceptible fox ingests an infected vole. Therefore, it is important to know the food habit of foxes, that is, the number of voles which a fox ingests a day, hereafter referred to as NVF. A fox feeds on voles by preference but it does have other available food (Yoneda, 1981). NVF depends on the population density of vole and on meteorological conditions (Abe, 1975; Yoneda, 1981). Thus as NVF we introduce the food habit function $F(x)$ of vole population density x into our transmission model.

We assume that the food habit function $F(x)$ increases exponentially in low density, while the increasing degree of $F(x)$ is reduced in high density, and that $F(x)$ becomes saturated with the maximum of NVF in a fairly high density. We use the logistic distribution as the food habit function $F(x)$ conveniently, whose value is the number of vole ingested by fox a day:

$$F(x) = \frac{V_{\max}}{1 + \exp(-\frac{x-\mu}{\sigma})}$$

where x and V_{max} denote population density of vole per 0.5 ha and the maximum number of vole which are ingested by fox. The μ, and σ denote the median, and variance of the distribution.

3. RESULT

Simulation of Mathematical Model for Vole Population Dynamics

To simulate the vole population for the situation with a 4 year cycle of periodic fluctuation in the northeastern area of Hokkaido, we sorted the years into two groups: the years of increasing vole population and those of decreasing vole population. Next, we applied a suitable combination of the 7 parameter sets chosen from Table 3 of Yoccoz et al. (1998) to each group, while avoiding the eradication or explosion of the vole population. Fig. 1

shows the density curve for the vole population per 0.5 ha obtained by our model, which includes seasonal fluctuations, the annual periodic ones and a range of fluctuations from 6.0 to 24.0. For the purpose of a comparative study, we also prepared a model for the aperiodic situation observed in the southwestern area in Hokkaido, and these results are shown in Fig. 1.

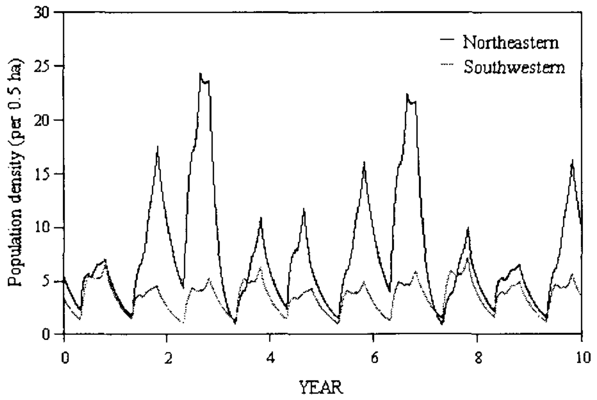

Fig. 1 The transition of vole population density by our model. The black line shows the density in the northeastern area of Hokkaido, and the gray line, that in the southwestern area of Hokkaido.

Food Habit Function for the Number of Vole Ingested by Fox

In the light of the census data on the vole population in Hokkaido (the Forestry Agency of the Japanese Government), we assigned the remaining parameters μ, and σ of the food habit function $F(x)$ as $\mu = 8.0$, and $\sigma = 2.5$ ($x \leq 8.0$), or $\sigma = 1.0$ ($x > 8.0$). The maximum V_{max} of NVF was chosen as 7.0 (Yoneda, 1981). Fig. 2 shows the transition of NVF derived by the simulation which associates the vole population dynamics with the food habit function as mentioned above.

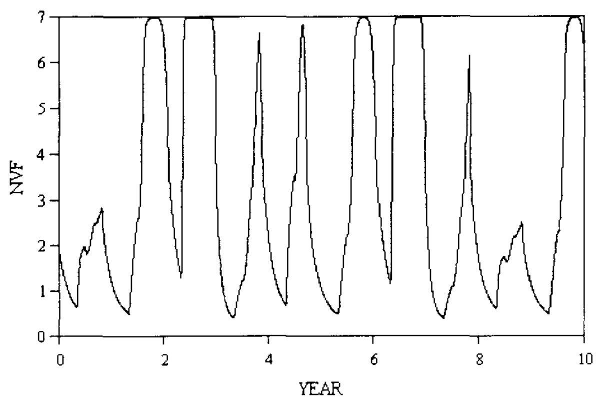

Fig. 2 The transition of the number of voles which the fox ingest (NVF) using the logistic distribution as the food habit function.

Simulation of Mathematical Model for transmission of Echinococcus multilocularis

We have carried out simulations using a model for the transmission of *Echinococcus multilocularis* (Ishikawa et al., in preparation), our model of vole population dynamics and a simple model of the fox population dynamics of foxes which considers only seasonal fluctuations. The prevalence curves of *Echinococcus multilocularis* in the fox population obtained by these simulations are shown in Fig. 3 for periodic and aperiodic vole density situations. According to our simulations, the prevalence rate ranges from 20% to 80% for the periodic situation while it only ranges limited from 40% to 60% for the aperiodic situation.

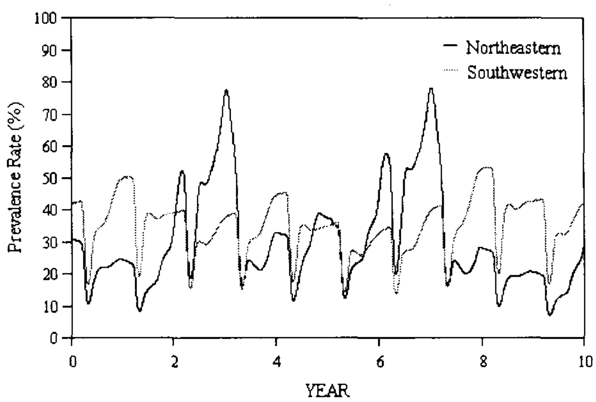

Fig. 3 Variation in the prevalence rate of the fox population by simulation. The black line shows the prevalence rate in the northeastern area of Hokkaido, and the gray line is that in the southwestern area of Hokkaido.

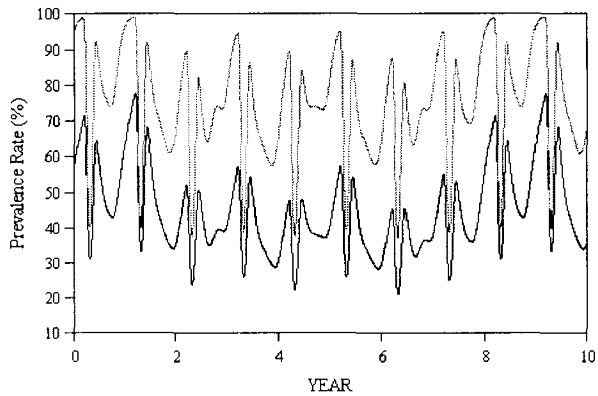

Fig. 4 Variation in the prevalence rate of the fox population using a constant as the food habit function. The black line shows the prevalence rate in the case with a value of 3.0, and gray line, with that of 6.0.

To investigate the effect of the food habit function on the infection rate of the fox population, we have compared the logistic distribution adopted in our model with the constant function (the two constant values were chosen 3.0 and 6.0) as the food habit function. The result of the simulations indicate that it has a small effect on the constant function case (Fig. 4).

4. DISCUSSION

In the population dynamics of vole, the annual population growth rate is given theoretically by the dominant eigenvalue of an annual matrix (Yoccoz et al., 1998). The dominant eigenvalues of the annual matrices corresponding to the parameter sets in our vole population model range from 0.90 to 5.07, although the actual growth rate can suffer a change according to the age distribution at the beginning of the study. The curve of population density in Fig. 1 satisfied the average range of the annual population densities at 8 observation points (from 3.0 to 23.0 per 0.5 ha) in the northeastern area of Hokkaido.

On using the constant function with the high constant value of 6.0 as the food habit function, for the situation of a high density of vole population, NVF is always assured a given quantity, that differs from the actual case, whereas for the situation of low density, the NVF should follow the result of the logistic distribution case. Its simulation yields an infection rate which is maintained with a narrow amplitude. On the other hand, using the low constant value of 3.0, it seems that the prevalence may only be influenced by the seasonal fluctuations of the fox population and may be independent of the annual fluctuation in vole density. If the prevalence in foxes was not reflected by the state of the intermediate host, then it would not realize the actual situation for transmission of *Echinococcus multilocularis*. The food habit of foxes should be affected by environmental conditions in their habitat, especially snowfall, but it is very difficult to incorporate them into the food habit function.

The simulations on the prevalence of *Echinococcus multilocularis* in fox carried out for the two typical fluctuations of vole densities show that, from the standpoint of the seasonal fluctuation, both of the prevalence curves have similar figures and reach their peaks in winter, while, from the standpoint of the annual fluctuation, the prevalence curve in the northeastern area has a higher peak and wider amplitude than that in the southwestern area. Therefore it follows from these simulations that there is a positive correlation and a synchronism between the population dynamics of vole and the infection rate in foxes.

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