Hystrix, (n.s.) 11 *(2)* (2000): 103-114

MANAGING CHAMOIS *(RUPICAPRA RUPICAPRA)* POPULATIONS: A MODEL WITH MACROPARASITES INFECTION AND HOST DYNAMICS

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ABSTRACT - The following paper contains a mathematical model for the analysis of temporal variations of a chamois *(Rupicapra rupicapm* L.)-Trichostrongylidae free-living system in the Brenta area (Trentino, Italy) under different harvesting regimes. The numerical values of the parameters of the model were obtained through the analysis of population counts and the parasitological surveys obtained during a four year study. Different harvesting regimes could affect differently the dynamics both of the host population and its parasites. Simple demographic analysis seems to suggest that the culling of older individuals is appropriate. However, if we insert a parameter into the system which considers immunity to parasitic infection then the culling of younger individuals becomes more appropriate for the maintenance of health and population size.

Key words: mathematical model, population dynamics, *Rupicapra rupicapra* L., macroparasitic infection, harvesting.

INTRODUCTION

Many authors now recognise that the wide distribution of pathogens among wild populations plays an important role both in the structuring of animal communities and in their temporal and spatial dynamics and that mathematical models could become powerful tools in the analysis of such variations (Grenfell and Dobson, 1995). Theoretical studies and experiments with laboratory animals have demonstrated that some macroparasites (helminths and arthropods) (Anderson and May, 1978) can regulate host populations but, apart from the well documented example of *Trichostrongylus tenuis* in Red Grouse (Hudson and Dobson, 1995), evidence coming from free living host-parasite systems are still limited. This is mainly due to the difficulties arising in empirical data collection. Macroparasite infections are commonly recorded in chamois populations of the Alps (Meneguz *et al.*, 1996) but apart from parasitological and pathological investigation, no manipulative experiment has been performed to assess the impact of such parasites on the vital rates of the chamois as has been done, for example, for other ungulate-macroparasite systems (Gulland, 1992). Generally, mathematical models used in wildlife management do not include the impact of macroparasites on the host population dynamics; thus, if the macroparasites affect the vital rates of the host, the number of harvestable individuals could be overestimated. This paper presents a deterministic mathematical model (for an age-structured population of herbivorous hosts) that in-

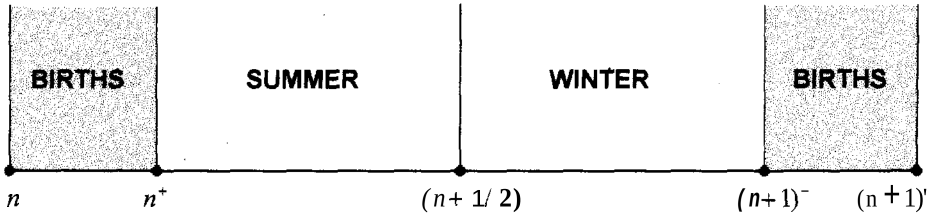

Figure 1 - Subdivision of the year into three phases as considered with the seasonal model: summer, period of parasite infection; winter, period in which infective free-living stages are not present on pastures; births, calving season at the beginning of summer.

cludes the impact potential of macroparasites on the direct life cycle of the host. Model parameters and assumptions contained here are calibrated to the Trichostrongylidae-chamois (*Rupicapra rupicapra* L.) system. This model was used to simulate the effect of different hunting regimes on the dynamics of a chamois population and considers two situations in which the parasite affects or not the vital rates of the host.

MATERIAL AND METHODS

The mathematical model

The model by Anderson and May (1978) for macroparasites with direct life-cycles has been adapted to examine the population biology of Trichostrongylidae in chamois. The main changes have been considering aggregation to be a dynamic variable, introducing the carrying capacity for the host, and assuming that infections will generally occur with several larvae at the same time (Damaggio *et al.*, 1996). The resulting deterministic model (Pugliese *et al.*, 1998) consists of four coupled differential equations describing changes in the host population size, N; the mean adult parasite burden, x; the aggregation of parasite distribution, **A** (defined as the ratio of the variance to the mean of adult parasite burden) and in the number of free living larvae, L. This model, like most deterministic models describing macroparasite infection, assumes that time is a continuous variable and that processes of reproduction, birth and death, occur continuously. However, both the dynamics of most populations in temperate environment, and their interaction with parasites are highly conditioned by seasonal effects (White *et al.*, 1996). Hosts generally reproduce in a narrow period within each year (May and June for the chamois) and become infected mainly during summer. In winter, the parasite uptake strongly decreases. For these reasons we developed a model for macroparasitic infection with discrete-continuous dynamics. We also took into account the age structure of the host population. In this model infections occur continuously during the summer, while in winter free-living stages are not active on pastures. Host births occurs instantaneously at the start of each summer (Fig. 1). All the model parameters and their biological interpretation are listed in Table 1. Details of the model are given in Appendix 1.

Parameters choice

Mean fertility and mortality (both natural and caused by harvesting) were estimated from census data on chamois populations in the Brenta area (Trentino, Italy) (Rizzoli, 1995; Rosà *et al.*, 1997). These mean values were distributed through the various age classes, following the general pattern shown in Pedrotti *et al.* (1996), and shown in Table 2. In this model the sex ratio is considered to be 1:1 and the birth rate represents the number of new born over the total host population.

Table 1 - Meaning and numerical values of parameters of the model. Numerical values are referred to the case B model where all host-parasite interaction parameters are independent from host age.

Parameter	Description	Numerical values
β	Instantaneous birth rate of hosts	see Table 2
μ	Instantaneous death rate of hosts	see Table **2**
V	Density-dependent increase in host mortality	$\nu = 3.5 \cdot 10^{-5}$
σ	Instantaneous death rate of adult parasite within the host	$\sigma = 6$
λ	Mean number of free-living stages forming a single infecting "parcel"	$\lambda = 363$
h	Number of infecting larva produced by an adult	$h = 100$
6	Instantaneous death rate in free-living stages	6 = 3
ψ	Proportion of ingested larvae that develop to adult stage	$\psi = 1$
a	Instantaneous death rate of hosts due to parasite	$\alpha = 1.67 \cdot 10^{-4}$
5	Reduction in chamois fertility due to parasite	$\xi = 1$
8	Average instantaneous rate of infection of host by parasite	$8 = 3 \cdot 10^{-4}$

Table 2 - Birth (β_i) and natural death rate (μ_i^{NAT}) of hosts divided into different age cohorts as considered in the age-structured seasonal model.

Age cohort	0	1	2	3	4	5	6	*7*	8	9	10	11	12	13	14	15
β_i	*0*	0	0.3	0.3	0.45	0.45	0.45	0.45	0.45	0.45	0.45	0.45	0.45	0.45	0.45	0.45
μ_i^{NAT}	0.3	0.05	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.05	0.1	0.1	0.1	*0.3*	*0.6*

As for the parameters concerning parasites, estimates of most of them are difficult to obtain, even in domestic animal systems (Smith and Grenfell, 1985). From the data on population size, mean and variance of parasite burden observed over 4 years in the chamois populations in Brenta area (Rizzoli, 1995; Rosà *et al.*, 1997), we followed a Bayesian procedure to estimate parasitological parameters. Starting from the best estimates existing in the literature (Grenfell *et al.*, 1995; Gulland, 1992; Michel, 1970; Smith and Grenfell, 1985), we obtained the estimates a *posteriori* shown in Table 1. The procedure is described in greater detail in Hudson *et al.*, in press.

We made two different assumptions based on the effect of host age on macroparasite. Firstly (case **A)**, all parameters concerning host-parasite interactions do not depend on host age, and are those reported in Table 2. This assumption ignores host acquired immunity to parasites, which is generally thought to be a very important factor (Wakelin, 1994). Detailed modelling of immunity as acquired through exposure to

Table 3 - Adult parasite mortalities (σ_i) and proportions of ingested larvae that develop to adult stage (ψ_i) in different age cohorts of hosts in case B.

Age cohort	1	2	3	4	5	2 6
σ_i	4	5	6	7	8	12
ψ_i	1	0.5	0.45	0.4	0.3	0.25

parasite leads, however, to very complex and intractable system of equations (Grenfell *et al.*, 1995). Therefore, secondly we assume, as a tractable approximation of acquired immunity, that some parameters (case B) depend on host age; and we assume that older hosts develop resistance to new infections (lower) and induce a higher mortality rate in adult parasites (higher), as shown in Table 3.

Harvesting regimes

For the hunting management of chamois populations, generally a culling of approximately 1/3 of yearlings, 1/3 of adult males and 1/3 of adult females is suggested (Schroder, 1992). Such a regime should preserve the social structure of the population and its status (Tosi and Toso, 1992). More quantitative approaches to management have also been considered. For instance, Capurro (1991) considered different hunting regimes in a stochastic demographic model for chamois population (Capurro *et al.*, 1996). The objectives of management are the maximisation of minimum population size, of average yield (number of culled animals), and minimisation of the variance of the yield. Regimes considered are proportional yield (culling a fixed proportion of the stock), constant reproductive stock (culling all the animals beyond a target population size), and a so-called traditional regime, approximating current practices. Their result is that "constant reproductive stock" are much more effective in terms of conservation of the population, and its mean yield: On the other hand, "proportional yield" regimes give a lower variance. Within such regimes, the most effective ones are those that preferentially cull older individuals. These are more effective than "traditional regimes" according to all criteria.

An interesting application of macroparasite models is to investigate whether such predictions change when host-parasite interactions are considered. We simulated the effects of three different hunting regimes (Regime 1, 2 and 3) on the model shown in Appendix 1, using all the parameter values for the chamois and parasite population, as described above. The three regimes are all of the "proportional yield" type. The first is meant to simulate current practice in the Brenta area: the culling is distributed through all age classes so that the hunting bag consisted of 1/3 yearlings and 2/3 adults (individuals older than two years). In Regime 2 we consider a higher hunting pressure on yearlings, and in Regime 3 only adults were shot. The exact values (shown in Tables 4 and 5) are adjusted so that the mean hunting pressure is around 7-8% and that, not considering the impact of parasites on the vital rates of the hosts, all regimes maintain the same equilibrium value for total host population.

RESULTS

Without parasites

First, we simulated the three different regimes without considering the impact of the parasite on the vital rates of the host. As

Table 4 - Death rates due to hunting under three simulated harvest regimes.

Age cohort	Regime 1	Regime 2	Regime 3
Kids	0	0	0
Yearlings	0.1575	0.25	0
2-5 years	0.072	0.079	0.075
>5 years	0.072	0.01	0.16

Table 5 - Hunting bags under the different simulated harvest regimes.

Age cohort	Regime 1	Regime 2	Regime 3
Kids	0	0	0
Yearlings	1/3	6/10	0
≥2 years	2/3	4/10	1

mentioned above, we chose the regimes in order to obtain the same equilibrium value for total host population when parasites are not considered (Fig. 2 and Table 6). In Figure 3 the total number of culled animals is shown for the different regimes. The third regime yields the highest number of culled animals, though only slightly higher than the first one while the second regime is clearly the worst (Table 6). This result is in agreement with the usual results on the optimal harvesting regimes (see above).

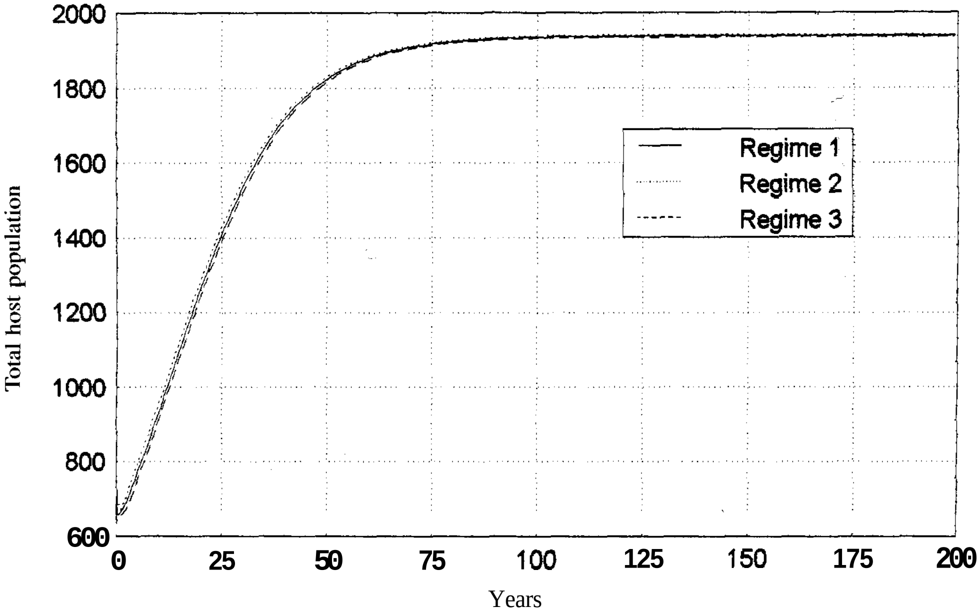

Figure 2 - Simulation of the host population dynamic for the three regimes when the parasites are not considered. The parameter values are those reported in Table 2.

Table 6 - Equilibrium values for the total host population and the total number of harvested chamois per year in the case without parasites.

	Total host population	Total number of harvested chamois per year	mean % of harvesting
Regime 1	1940	148	7.63
Regime 2	1942	140	7.21
Regime 3	1937	150	7.74

Table 7 - Mean vaiues for the total host population, the mean adult parasite burden, the aggregation (variance/mean) of parasite distribution and the total number of harvested chamois per year in the case **A** with parasites.

	Total host population	Mean parasite burden	Aggregation of parasites	Total number of harvested chamois per year	mean % of harvesting
Regime 1	784	193	182.24	60	7.65
Regime *2*	789	192	182.23	58	7.35
Regime 3	777	193	182.25	59	7.59

With parasites

When introducing the impact of parasites on host population dynamics in the model, we considered (as stated above) two different cases: **A** no age-dependence; B acquired immunity approximated as in Table 3. In case **A,** mean parasite burden of different age cohorts is almost the same (Fig. 4). Only the results for regime 2 are shown, because the behaviour is very similar for the other two regimes. The results concerning hunting management are shown in Figure 5. It can be seen that, in this case, the host population fluctuates (with damped oscillations) around an average value which is lower than without parasites (Table 7). The absolute reduction (here more than one half) depends on the choice of parameters, which are a little

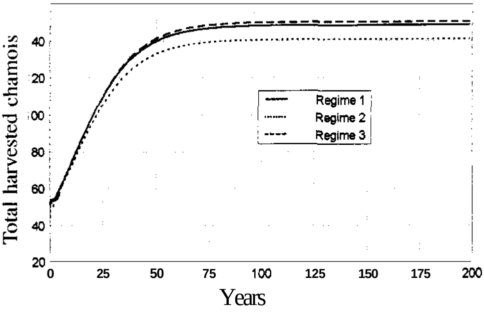

Figure 3 - Simulation of the total culled animals for the three regimes when parasires are not considered. The parameter values are reported in Table 2.

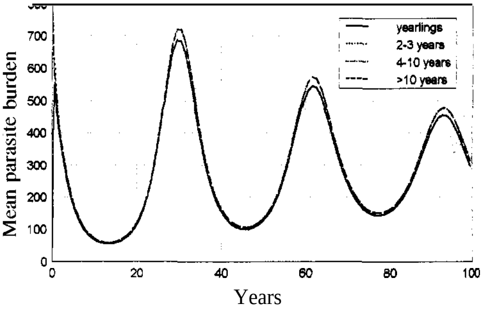

Figure 4 - Mean parasite burden for different age cohorts in the case **A** for regime 2. The parasite population parameter values are those reported in Table 1.

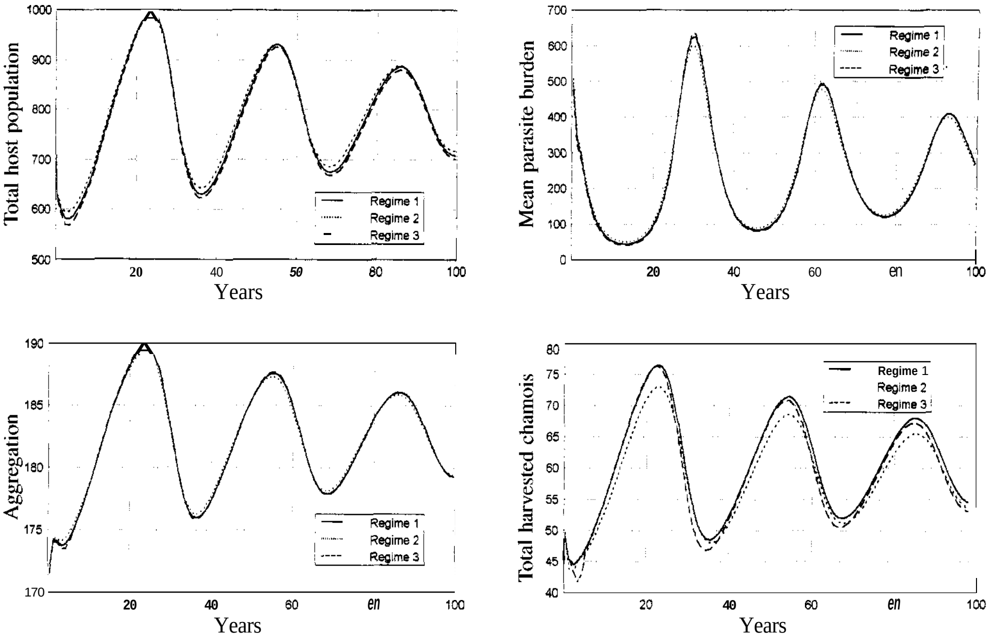

Figure 5 - Simulation of the temporal variations observed in the host population, mean parasite burden, aggregation and the number of the total harvested chamois for the three regimes in the case **A.** The parasite population parameter values are those reported in Table 1.

dubious, but the qualitative effect is robust with respect to parameter values. Under different hunting regimes the dynamics of host and parasite populations remain very similar (Fig. 6 and Table 7). **As** for the number of culled animals, the second regime still yields the lowest number of harvested chamois while the first is slightly better than the third, in particular at the minima of host population, even if in this case the differences are very small.

For case B, the results are shown in Figure 6. We can see that yearlings are the most heavily infected age class. The difference is especially visible at the peaks of infection. Again, we show only the dynamics for regime ***2,*** since the behaviour is similar for the other two regimes. In this case, the dynamics of total host and parasite population change with different hunting regimes (Fig. 7 and Table 8). Regime 2 keeps maintains the host population size at the highest values (more than 10% higher than in regime 3) with the mean parasite burden at the low-

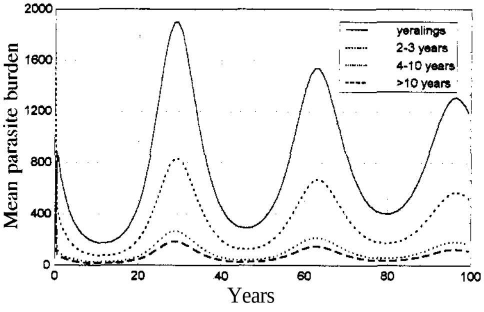

Figure 6 - Mean parasite burden for different age cohort in the case B for regime *2.* The parameter values are those reported in table 4 and in Table 1 except for h=205; this has been change so that the value of the basic reproductive ratio (R_0) is similar in the two cases.

Table 8 - Mean values for the total host population, the mean adult parasite burden, the aggregation (variance/mean) of parasite distribution and the total number of harvested chamois per year in the case B with parasites.

	Total host population	Mean parasite burden	Aggregation of parasites	Total number of harvested chamois per year	mean % of harvesting
Regime 1	820	111	179	63	7.68
Regime 2	856	106	181	61	7.13
Regime 3	772	118	176	60	7.77

est. Moreover, the aggregation of the parasite distribution is the highest in regime 2; since high aggregation is generally considered a positive index in macroparasitic infections (Genchi *et al.*, 1991), we can assume that regime 2, in this case, tends to maximise the host population health. On the other hand, it is not an efficient regime from the harvesting point of view, since it yields a lower number of culled animals than regime 1, although the population size is higher (Table **8).**

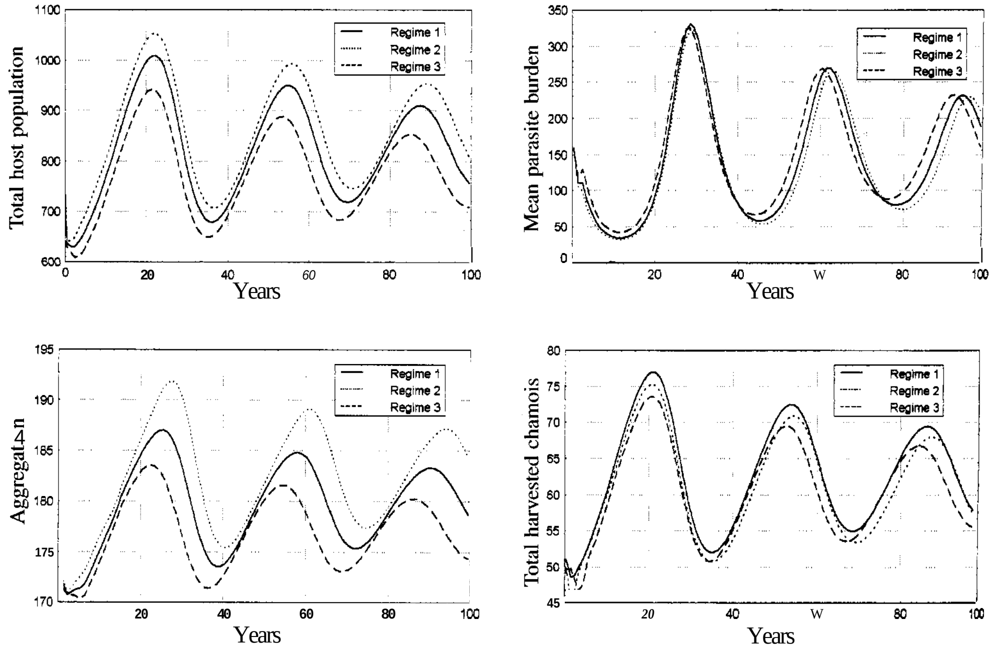

Figure 7 - Simulation of temporal variations observed in the host population, mean parasite burden, aggregation and the number of the total harvested chamois for the three regimes in the case B. The parameter values are those reported in Table 4 and in Table 1 except ofr *h*=205; this has been change so the value of the basic reproductive ratio (R,) is similar in the two cases.

DISCUSSION

Macroparasitic infections are commonly recorded in the Alpine chamois populations of Italy (Meneguz ***et** al.*, 1996). There have been some parasitological and pathological examinations carried out in the past but available information on the possible role of such a parasite in regulating host abundance remains scarce. Moreover, the importance of macroparasites could often be underestimated because of simple investigation and sampling bias (Hudson ***et** al.*, in press). Therefore, the possible consequences of host-parasite interaction should be carefully considered when harvesting plans are developed (Genchi ***et** al.*, 1991). The results obtained through our simulations showed the possible effects of different harvesting regimes on a model population affected and not affected by macroparasites. Since exact results depended on the parameter values, many of which are still largely unknown, these results are not meant to support, at the moment, a specific type of empirical management. Rather, they suggest the potential effects of macroparasites on host population dynamics and give a theoretical background from a comparison of empirical observation arising from repetitive harvesting records can be made.

A simple demographic analysis seems to suggest that the culling of older individuals would be effective. This has also been observed by other authors (Capurro, 1991). However, inserting immunity to parasitic infection into the model makes the culling of younger individuals a more appropriate choice for the maintenance of health and population size. Obviously, the quantitative differences depend on the assumptions made about how much acquired immunity depends on host age. The greater the age-dependent immunisation of the host, the larger the differences between the results of this model for macroparasitic infection and those of a pure demographic model will be. So more empirical and theoretical information is needed on the effect of macroparasites on host fecundity and survival and on the development of immunity in host populations, in order to use mathematical models as a quantitative tool for a better management of wildlife.

ACKNOWLEDGEMENTS

We would like to thank the Wildlife Service and the Hunting Associations of the Autonomous Province of Trento, the Administration of the Adamello Brenta Natural Park, the hunters and the rangers that collaborated in collecting data and information here presented.

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APPENDIX I: To obtain the seasonal model we modified the following continuous model (Pugliese *et al.,* 1998)

$$
\begin{aligned}
\frac{dN}{dt} &= N(\beta[1+(A-1)(1-\xi)]^{-\frac{}{A-1}}-\mu-\nu N-\alpha x)\\
\frac{dx}{dt} &= x(-\sigma-\alpha A-\beta[1+(A-1)(1-\xi)]^{-\frac{x}{A-1}})+\theta\psi L\\
\frac{dA}{dt} &= -(A-1)(\sigma+\alpha A+\frac{\theta\psi L}{})+\beta x[1+(A-1)(1-\xi)]^{-\frac{x}{A-1}}+\frac{\theta\psi L}{}\lambda\\
\frac{dL}{dt} &= hNx-6L-\theta LN,
\end{aligned}
$$

by assuming $\theta = h = 8 = \sigma = 0$ during winter. Hosts are divided into 16 classes with N_i, , x_i A_i indicating the host size, the mean parasite burden and the aggregation of the parasite distribution for the hosts which belong to the i class where i is equal to the age range from 0 to 14. Al the hosts which are older than 14 go in the class $i = 15$. A basic assumption of this model is that kids (class $i = 0$) do not take part in the parasite cycle; so that the parasitic mean and the aggregation for this class are equal to zero, that is $x_0 \equiv A_0 \equiv 0$. Considering the seasonal dynamics shown in Figure 1 the equations for the model with age structure assume the following form:

Summer: $t \in (n^+, n+1/2)$

$$
\begin{aligned}
\frac{dN_i}{dt} &= N_i(-\mu_i-\alpha_i x_i)-\nu(\sum_{i=0}^{15}N_i)^2\\
\frac{dx_i}{dt} &= x_i(-\sigma_i-\alpha_i A_i)+\theta_i\psi_i L_i\\
\frac{dA_i}{dt} &= -(A_i-1)(\sigma_i+\alpha_i A_i+\frac{\theta_i\psi_i L}{x_i})+\frac{\theta_i\psi_i L}{x_i}\lambda\\
\frac{dL}{dt} &= h\sum_{i=1}^{15}N_i\sum_{i=1}^{15}x_i-\delta L-\theta L\sum_{i=1}^{15}N_i
\end{aligned}
$$

with $i = 0,1,2,\ldots,15$

Winter: $t \in (n+1/2, (n+1)^-)$

$$
\begin{aligned}
\frac{dN_i}{dt} &= N_i(-\mu_i-\alpha_i x_i)-\nu(\sum_{i=0}^{15}N_i)^2\\
\frac{dx}{dt} &= -\alpha_i A_i x_i\\
\frac{dA}{dt} &= -\alpha_i A_i(A_i-1)
\end{aligned}
$$

Host births and winter survival of free-living stages appear only as a boundary condition, namely:

$$N((n+1)^+) = N((n+1)^-)\big[\beta(x((n+1)^-), A((n+1)^-))+1\big],$$

$$L((n+1)') = qL(n+1/2).$$

At the time of host births, all living hosts are ascribed to the older age class; N_i, x_i , A_i are thus recalculated as follows. Kids that have survived the winter become yearlings and they will be free of parasite, that is:

$$N_0((n+1)^+) = \sum_{i=1}^{15} \beta_i\,[x_i((n+1)^-), A_i((n+1)^-)]N_i((n+1)^-)$$
$$N_1((n+1)^+) = N_0((n+1)^-)$$
$$x_1 = A_1 = 0.$$

The individuals of an age range between 1 and 13 will pass to the successive class

$$N_i((n+1)^+) = N_{i-1}((n+1)^-)$$
$$x_i((n+1)^+) = x_{i-1}((n+1)^-)$$
$$A_i((n+1)^+) = A_{i-1}((n+1)^-). \qquad i = 2,3,4,\ldots,14$$

Finally to calculate the new values (at time $(n+1)^+$) of the class with $i = 15$ we have to aggregate the two class $i = 14$ and $i = 15$ at time $(n+1)^-$.