MATHEMATICAL MODELS AND WILDLIFE DISEASES: TECNIQUES OF PARAMETERS ESTIMATION FOR NEMATODES INFECTIONS

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Abstract - The use of mathematical models in the study of wild host-nematodes interaction is still limited since the estimate of the numerical values of many parameters of the models are usually difficult to be quantified empirically. In this paper we present a technique of parameter estimation based on a mathematical model for macroparasitic infections using a Bayesian updating method. As a case- study we considered a Trichostrongylidae, principally *Teladorsagia circumcinta*, infection in a chamois population (*Rupicapra rupicapra* L.). Using these estimates a value of the basic reproduction ratio (R_0) equal to 2.4 was obtained.

Riassunto - L'utilizzo dei modelli matematici nello studio delle interazioni tra ospiti vertebrati e nematodi parassiti è ancora limitato poiché la stima dei valori numerici di molti parametri in essi contenuti risulta spesso difficoltosa. In questo lavoro viene presentata una tecnica di stima parametrica che utilizza un approccio di tipo Bayesiano. E' stato utilizzato un modello matematico per infestazioni macroparassitarie a ciclo diretto implementato su dati di tipo empirico relativi a un'infestazione da Trichostrongylidae, soprattutto *Teladorsagia circumcinta*, in una popolazione di camoscio (*Rupicapra rupicapra* L.). Le stime dei parametri ottenute forniscono un valore di R_0 (tasso base di riproduzione del parassita) pari a 2.4.

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1. Introduction

Mathematical models play a significant role in our understanding of epidemiology and dynamics of parasite-host interactions (Anderson & May, 1991; Scott & Smith, 1994; Grenfell & Dobson, 1995) but their use in the analysis of many macroparasites (as nematodes) -wildlife systems is still limited (Barlow, 1995).

One reason is that the estimate of the numerical values of many parameters used in such models require long-term studies on host demography and manipulative experiment to understand parasite induced effects (Gulland, 1992; Hudson *et al.*, 1992; Hudson *et al.* 2002.; McCallum & Dobson, 1995). Environmental complexity, in terms of geomorphology and climate, and species behaviour that affect their observation and monitoring (these characteristics are common in Alpine ecosystems and many of their wildlife species) often represent a limitation for the development of epidemiological and ecological studies on nematodes infections in wildlife with the application of mathematical models.

Our theoretical approach to these constrains is to use mathematical models as exploratory tools (Damaggio *et al.*, 1996; Rosà *et al.*, 1997) for obtaining a first estimate of some fundamental parasite population parameters and parameters regarding the host-parasite interaction using only few measures of parasitological and demographic variables of the two populations.

These estimate will be derived by simulating the relationship between parasite dynamics and host dynamics with the use of a mathematical model. They will represent a guidance for further study and they will prove useful only if there is a reasonable agreement between the dynamics simulated by the model and the temporal changes actually observed in the host and parasite populations under study.

In this paper we present the estimate of the numerical values of some parameters regarding a Trichostrongylidae infection in a chamois (*Rupicapra rupicapra* L.) population obtained by the application of a 4-dimensional deterministic model (Pugliese *et al.*, 1998) to a set of empirical estimate of parasite and host demographic variables (Rizzoli, 1995; Damaggio *et al.*, 1996; Rosà *et al.*,1997).

2. Material and methods

2.1 Case study

Epidemiological investigations on a chamois population (*Rupicapra rupicapra* L.) of the Province of Trento (Italy) were carried out

after a population crash (Rizzoli, 1995). Pulmonary and abomasal nematodes, principally *Neostrongylus linearis* (Marotel, 1913) and *Teladorsagia circumcinta*, Stadelmann, 1894, were recorded as highly prevalent and abundant. Under the hypothesis that the parasite intensity of infection was related with changes in the vital rates of the host population, a 4-dimensional deterministic model was constructed. In this study only direct transmitted parasites were considered. Measure of abomasal nematodes abundance and aggregation were recorded during a 4 year surveys; host demography was studied over 10 years population counts (Rosà *et al.*, 1997).

2.2 The mathematical model

A classical model for studying host-macroparasite interactions was introduced by Anderson and May (1978) for the case of macroparasites with direct life-cycles. This model has been modified by letting the aggregation be a dynamic variable (Adler & Kretzschmar, 1992), introducing a carrying capacity for the host (Pugliese & Rosà, 1995) and assuming that infections will generally occur with several larvae at the same time (Damaggio *et al.*, 1996). The resulting model (Pugliese *et al.*, 1998) has a reasonable flexibility in explaining observed values of aggregation, and all its parameters have a biological interpretation and are, at least in principle, passable of independent measurement. Mathematically, it consists of four coupled differential equations (equations 1) describing changes in the host population size, ***N***; the mean adult parasite burden, χ; the aggregation of parasite distribution, ***A*** (defined as the ratio of the variance to the mean) and the number of free living larvae, *L*.

1)

$$\frac{dN}{dt} = N(\beta[1+(A-1)(1-\xi)]^{\frac{-}{A-1}} - \mu - (\beta-\mu)N/N_{\xi} - \alpha x)$$

$$\frac{dx}{dt} = x(-\sigma - \alpha A - \beta[1+(A-1)(1-\xi)]^{\frac{-}{A-1}}) + \theta\psi L$$

$$\frac{dA}{dt} = -(A-1)(\sigma + \alpha A + \frac{\theta\psi L}{x}) + \beta x[1+(A-1)(1-\xi)]^{\frac{-}{A-1}} + \frac{\theta\psi L}{x}\lambda$$

$$\frac{dL}{dt} = hNx - \delta L - \theta L N$$

The parameters of the model are described in Table 1. Equations of the model (1) can be examined when the parasite is first introduced to the host populations to produce an expression for the basic reproduction ratio (R_0) of the parasite. When λ=0 we obtain the following expression:

2)

$$R_0 = \frac{h\psi\theta N_{\xi}}{(\delta+\theta N_{\xi})(\beta+\sigma+\alpha)}$$

When the basic reproduction ratio equals unity, equation (2) can be rearranged to provide an expression for the threshold number of hosts required to continuously sustain an abomasal infection:

3)

$$N_T = \frac{\delta(\beta+\sigma+\alpha)}{\theta(h\psi-(\beta+\sigma+\alpha))}$$

When λ>0 an extra term appears in the denominator of R0 because the infection occur with several larvae at the same time; consequently, also the expression of will differ somewhat (for details see Pugliese *et al.*, 1998).

2.3 Estimating parameters: techniques

A standard method in parameter estimation is the minimisation of the sum of squared deviations between model predictions and observed data. Without aiming at a precise estimate with an error margin, we suggest here instead two simpler methods, based on a single (or few) static measure; these methods give a quick idea of the values of model parameters that are compatible with data, and of the sensitivity of model predictions on parameter values.

2.4 Backward deterministic estimation

In the simplest method, we simply assume that the observed values correspond to an equilibrium of the model. We then use the model backwards, finding from the equilibrium the parameter values. More precisely, we start from the equations for the endemic equilibrium, obtained setting equal to 0 the right hand sides of the model (1). With some algebraic manipulations, we obtain, if ξ=0, the following equations to estimate α, λ, θ, and *h*:

4)

$$\alpha = \frac{\beta-\mu}{x^*}(1-\frac{N^*}{N_{\xi}})$$

5)

$$\lambda = \frac{(A^*-1)(2\alpha A^*+2\sigma+\beta)-\beta x^*}{\alpha A^*+\beta+\sigma}$$

6)

$$\theta = \frac{x^*(\alpha A^*+\beta+\sigma)}{\psi L^*}$$

Tab. 1 - Meaning of variables and parameters of the model

Parameter	Description
N	Host population size
x	Mean adult parasite burden
A	Aggregation of parasite distribution (defined as variance/mean)
L	Number of free living larvae
β	Instantaneous birth rate of hosts
μ	Instantaneous death rate of hosts
N_K	Carrying capacity for the host population
σ	Instantaneous death rate of adult parasite within the host
λ	Mean number of free-living stages forming a single infecting "parcel"
h	Instantaneous rate of production of infecting larva
δ	Instantaneous death rate of adult of free-living stages
ψ	Proportion of ingested larvae that develop to adult stage
α	Instantaneous death rate of host due to the parasite
ξ	Instantaneous reduction in chamois fertility due the parasite
θ	Average instantaneous rate of infection of host by parasite

7)

$$h = \frac{L^*(\delta + \theta N^*)}{x^* N^*}$$

If a numerical value for L is not known, but it may be assumed that it is relatively large, it is still possible to estimate the values of α, λ and the product of θ, h. In fact, the product of equations (6) and (7) gives

8)

$$\theta h = (\alpha A^* + \beta + \sigma)\left[\frac{\delta}{N^*} + \frac{x^*(\alpha A^* + \beta + \sigma)}{L^*}\right] \approx (\alpha A^* + \beta$$

With this method it possible to estimate a number of parameters equal to the number of equations of the model, if all the variables of the model are observable. The parameters to be estimated are those for which direct measures are lacking or are most uncertain. The other parameters are fixed at the best empirical estimates. While this method is certainly simplistic, it can be integrated through a sensitivity study (Fig. 1): one can vary the values of the parameters to be estimated, and see the effect on the equilibrium values.

2.5 Bayesian updating method

The previous method can be integrated with the standard method of minimising the squared deviations via a Bayesian technique.

In Bayesian methods, one starts from a prior distribution on parameters, reflecting initial uncertainties; following standard usage, the multidimensional parameter will be denoted by Θ, the observed data by X, the prior distribution by $P(\Theta)$. As a second ingredient, one has a likelihood function of the observed data, $P(X/\Theta)$, i.e. $P(X/\Theta)$ is the probability that the observed data occur given that the parameter is equal to Θ. Finally, Bayes' formula yields the posterior (after having observed the data) distribution $P(X/\Theta)$ of the parameters as

9)

$$P(\Theta / X) = cP(X / \Theta)P(\Theta)$$

where c is a normalising constant that ensures that $P(X/\Theta)$ is a probability distribution. In our case, the prior parameter distributions were chosen on the basis of literature data and our feeling for existing uncertainties. The choice is described in the Table 2.

The likelihood function will depend on the dynamical model we are using and there are several possible choices (Patwardhan and Small, 1992). Our choice was simply the Gaussian centred on the equilibrium values predicted by the model for a given value of the parameters.

Precisely, letting N, x and A denote the observed values of host population size, mean parasite burden, and aggregation of parasite distribution, we used

$$P(X / \Theta) = \exp(-2\, SS^2(\Theta))$$

where

$$SS^2(\Theta) = \frac{(N - N^*(\Theta))^2}{\sigma_1^2} + \frac{(x - x^*(\Theta))^2}{\sigma_2^2} + \frac{(A - A^*(\Theta))^2}{\sigma_3^2}$$

and $N^*(\Theta)$, $x^*(\Theta)$, $A^*(\Theta)$ represent the values of endemic equilibrium for our mathematical model when the multidimensional parameter is Θ. In words, this choice says that, if were known, a data point would be more likely, the closest (in the sense of least squares) it was to the equilibrium of the model with parameter Θ.

To obtain the posterior distribution on Θ, using (9), we need to compute $P(X/\Theta)$, and thus $N^*(\Theta)$, $x^*(\Theta)$, $A^*(\Theta)$, for a large number of possible values of Θ. Since Θ is multidimensional, the number becomes quickly very large: for instance, if Θ was 6-dimensional and we were

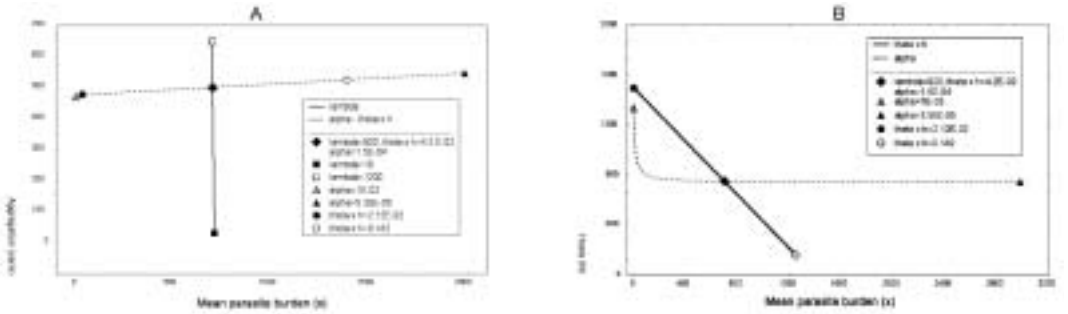

Fig. 1 – Sensitivity study on the method of fixed parameters for the estimation of α , λ and θh. Other parameters are β= 0.44, μ= 0.23, N_K=1500, (Rosà et al., 1997); δ =3, σ =6, ψ =0.65 (Smith and Grenfell, 1985; Michel, 1970); ξ =1 . The endemic equilibrium is assumed to be N^*=750, x^*=700, A^*=500 (Rosà et al., 1997). A) Projection on the (A, x) plane; B) Projection on the (N, x) plane. The point of intersection between two curves, (α=1.5·10^{-4}, λ=920 , θh=4.2·10^{-2}) is the same for both figures and represents the backward deterministic estimate.

content with a very coarse subdivision of each one-dimensional component of Θ in 10 parts, we would have 10^6 combinations to consider. In order to improve the efficiency, we did not computed all possible combinations, but followed the Latin Hypercube sampling scheme: see McKay *et al.* (1979) or Blower and Dowlatabadi (1994) for details.

The posterior distribution is genuinely multidimensional: even if in the prior distribution parameters are assumed to be not correlated, they will generally be correlated in the posterior distribution. In order to have a grasp of the posterior distribution, we will show its one-dimensional marginal distributions (the distributions of each single uncertain parameter of the model) and some descriptive statistics (mainly mean and variance of each parameter, and their correlations).

3. Results

The results of the sensitivity study on the backward deterministic estimation are presented in Fig. 1. Part A shows the effect of variations of parameter values on the mean parasite burden and the aggregation of the parasite distribution: λ (the mean number of free-living stages forming a single infecting parcel) influences only the aggregation, and basically the aggregation depends only on λ.

Part B shows the effect of variations of parameter values on the mean parasite burden (x) and the host population size (N): α (death rate of host due to the parasite) influences, over a large range, only the mean parasite burden and not the host population, where the increase of x reduces the mean parasite burden. θh (the product of the transmission rate and the parasite fecundity) moves N and x on a fixed line, where the increase of θh increases the mean parasite burden and decreases the host population size. This results was explained by the increase of the basic reproduction ratio of the parasites (R_0).

Fig. 2 shows the marginal distributions of the posterior distribution for each parameter, compared with the prior distributions. The estimates of the mean values, the variance and some correlation coefficient of the distribution of the estimated parameters are reported in Table 3. Using these values we obtained the basic reproduction ratio (R_0) equal to 2.4 and the threshold number of hosts required to continuously sustain the infection (N_T) around 600 (Tab.4).

In Table 5 the values of the increasing in mortality $\alpha \cdot i$ (additive effect $\mu_{tot}=\mu_{nat}+\mu_{prel}+\alpha \cdot i$) and reduction in fertility ξ^i (multiplicative effect $\beta_{tot}=\beta_{nat} \cdot \xi^i$) related to different values of the mean parasite burden using the estimated values of α and ξ are reported.

4. Discussion

One limitation to the use of mathematical models for studying the dynamical interaction among nematodes parasites and their wild host is that the estimate of most of the numerical values of their parameters require long-term studies on host demography and manipulative experiment to understand parasite induced effects (Gulland, 1992; Hudson *et al.*, 1992; Hudson *et al.*, 2002; McCallum & Dobson, 1995) that in many natural populations and ecosystems, like those of the Alps, they result difficult to be carried out.

Tab. 2 - Patterns of the prior distribution of parameters

Parameters	Distribution	Min	Max
α	Triangular	0	10-3
θ	Uniform	10-5	10-3
ξ	Uniform	0.998	1
ψ	Uniform	0.3	1
Parameters	Distribution	Mean	Varianceh
h	Normal	500	1000
δ	Normal	3	0.5
σ	Normal	6	2.5
λ	Log-normal	80	106

Tab. 3 - Mean and variance of the posterior distributions of parameters. Correlation coefficients (R) of some pairs of parameters. Only correlation coefficients greater than 0.1 in absolute value are reported.

Parameters	Mean value	Variance
α	1.02E-04	2.14E-09
θ	1.22E-04	3.20E-09
ψ	0.57	3.87E-02
h	499.11	511.84
δ	3.09	2.46E-01
σ	6.10	1.28
λ	756.36	7.49E+04
ξ	0.9998	1.64E-08
Pairs of parameters	*R*	
α,θ	0.12	
α,ξ	0.66	
θ,δ	0.38	
θ,σ	0.39	
θ,ψ	-0.71	

Mathematical models can be used as exploratory tools to give a first estimate of some fundamental parasite population parameters and parameters regarding the host-parasite interaction using only few measures of parasitological and demographic variables of the population and simulating the relationship between parasite and host dynamics with the use of the model. This methods give an initial estimate for the values of parameters difficult to estimate empirically thus allowing a first approximation of the basic reproductive ratio R_0 of the parasite and the threshold population density N_T necessary to continuously sustain the infection. These estimates, in absence of detailed empirical information, can provide an initial guidance for accept or exclude the hypothesis that macroparasites dynamics is related to the host dynamics allowing to take in account the potential relative impact of the parasite on the host, along with other ecological factors as climate and food shortage (Grenfell *et al.*, 1998). The empirical value of such parameters can be tested subsequently on the basis of population counts, necroscopic and parasitological examination on a sample of the population, along with experimental infections.

As example, in the Table 4 different values of the mean parasite burden, were related to an increase in host mortality and reduction in

Tab. 4 - Estimated values of the basic reproduction ratio (R_0) and the threshold number of hosts required to continuously sustain the infection (N_T)

Parameters	Estimated value
R_0	2.4
N_T	603

host fertility. Such values appeared comparable with the parasitological data obtained from a sample of the populations under study at different time when variation in host fecundity and mortality rates were observed (Rizzoli, 1995; Rosà *et al.*, 1997).

Moreover, after a posterior distribution has been obtained, new simulation can be performed by choosing parameter values randomly according to the posterior distribution; such simulations will yield an estimate of uncertainties in the forecast.

A second aim of these methods is to provide a starting point for empirical estimates of the parameters: if one expects, as example, the value of θ (the encounter rate between infecting larvae and hosts) to be around 0.0001, one would design an experiment to measure it differently (or would decide that such a measure would be altogether impossible) than if it were around 0.01. Via the sensitivity graphs (Fig 1), one can also see that a precise measure of some parameter is not needed if one is only interested in some variables of the model.

A third result of these estimates is to prove that the mathematical model is deficient at some stages: if the parameter values necessary to make the model compatible with data are completely different from empirical estimates, then something relevant is wrong with that model.

We illustrate these points, referring to our case study. When the posterior distribution is similar to the prior distribution (as it is for ψ, h, δ, σ in Fig 2), our procedure has not been useful in resolving uncertainties: our empirical data are not sufficient to discriminate the value of these parameters. On the other hand, when it is different (the case of α, θ, λ and, to some

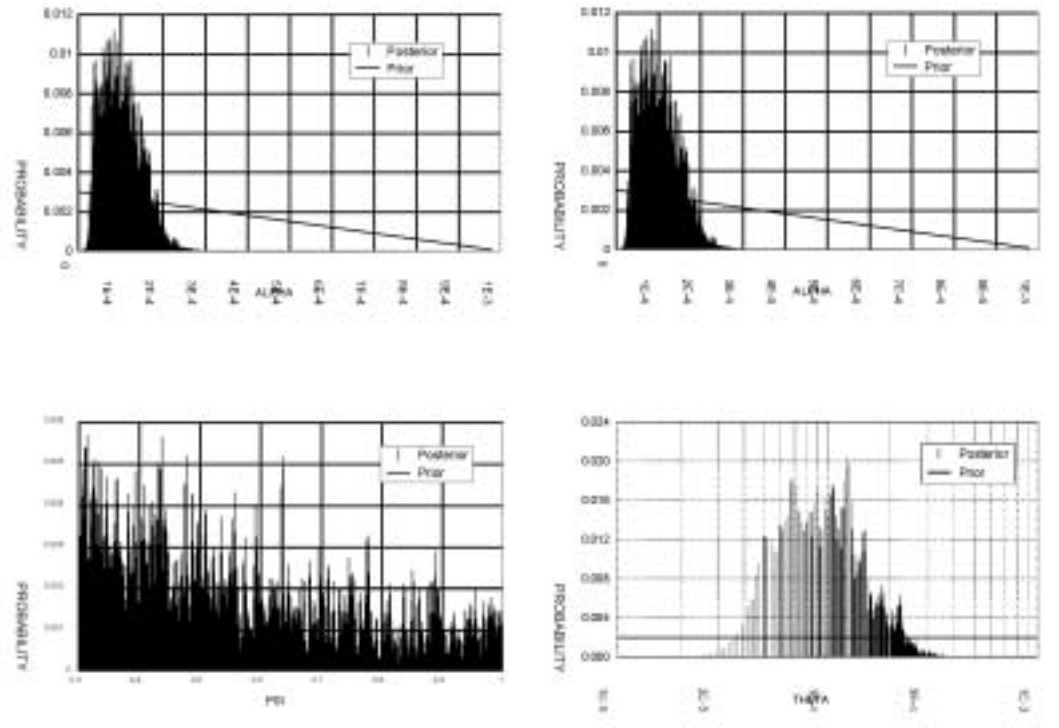

Fig. 2 – Marginal posterior distribution of the uncertain parameters according to the Bayesian updating method. The prior distribution of Box 4 was used. To evaluate the sum of squared deviations we used N=750, σ_1=200, x=700, σ_2=200, A=500, σ_3=250. The other parameters were fixed at β=0.44, μ=0.23 and N_K=1500.

Tab. 5 - Some values of the increasing in mortality $\alpha \cdot i$ (additive effect $\mu_{tot}=\mu_{nat}+\mu_{prel}+\alpha \cdot i$) and reduction in fertility ξ^i (multiplicative effect $\beta_{tot}=\beta_{nat} \cdot \xi^i$) related to different values of mean parasite burden (i) using the estimated values of α and ξ of Table 3. For comparison, fertility rate β_{nat} is 0.44, mortality rate $\mu_{nat}+\mu_{prel}$ is 0.23 at population size N=1500.

Mean parasite burden (i)	$\alpha \cdot i$	ξ^i
500	0.05	0.9
1000	0.1	0.82
5000	0.5	0.37

degree, ξ), the uncertainty has actually decreased: our new estimates (Table 3) can be a starting point for empirical studies.
Finally, one can compare the posterior distribution obtained for λ with some empirical estimated, obtained by Rosà *et al.* (1997), that estimate λ in the range 60-100. We must conclude that the model (1) can not account for the amount of aggregation measured in the chamois population: some other mechanism of generating aggregation must be considered.
This last point emphasises the difference between using this model and the classical model by Anderson and May (1978); in the latter, the aggregation is simply a parameter of the model while in our model aggregation is a dynamic variable; its value are predicted by the model on the basis of the parameter values, which are susceptible of independent measures. Thus, it become possible to falsify the model on the basis of small sample size and few empirical data.

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