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BASIC REGULATORY PARAMETERS OF THE HOST-PARASITE SYSTEM FOR WARBLE FLIES OF FARM ANIMALS USING HYPODERMA BOVIS AS AN EXAMPLE

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Abstract. While studying the consistent patterns in the host-parasite relationships on the model of warble flies infesting cattle, a firm internal regulatory system governing the number of parasites on the host and reflected in the level of populations, has been demonstrated. This regulatory system is governed by mathematical-statistical laws and therefore can be modelled and its different features expressed mathematically. The distribution of parasites in the host population agrees with the negative binomial distribution. Main mathematical formulations of the regulatory system (parameters) and defensive responses of the host to the invasion of parasites are analyzed. From the above consistent patterns important conclusions are drawn for the control of cattle hypodermatosis in practice. The mathematical model elucidates two stages of control — the first stage conforms to the natural regulatory system leading to a marked decrease of the degree of infestation, and the second stage is aiming at the eradication of the disease. It may be deduced from the above said that the control of hypodermatosis is expedient primarily in juvenile cattle, as shown by the results of the control carried out in Czechoslovakia.

1. Logical structure of the host-parasite regulatory system

While developing the basic control measures against pest insects a greater attention has been lately paid to the studies on the regulations in the population processes (Breev 1968, 1971, Viktorov 1969, Frisman et al. 1972, Anderson 1974, Breev and Minář 1976, Bart et al. 1976, Bart and Zagretdinov 1980, Bart 1981 etc). The necessity of such studies does not give rise to any doubt and is urgent. This can be explained by two reasons.

First, the basic natural control of the species numerousness created during its evolution, takes place on the level of its population. The intervention of man with the natural regulatory system of interrelationships in the species leads to the distortion of regulations in it and may result in different, mainly negative consequencies for the control measures to be undertaken. Therefore, in order to select an effective strategy of control it is essential to understand the degree of the interrelationship stability in the regulatory system and the range within which it is operating.

On the other hand, due to the increasing importance of the studies on logical structure of regulations, modern mathematical methods may be used. The mathematical methods embrace achievements of different fields of natural science. Their application makes it possible to view the problem from different angle and thus to disclose the logical essence of the phenomenon. If concrete biological systems are studied such an approach is a considerable improvement.

At the same time this more accurate, mathematical approach to the studies on regulatory processes requires a higher attention to all problems involved — scientific, methodological, organizational and experimental which make the studies and the application of the results in practice truly effective. Particularly, this approach requires a sufficient store of biological knowledge on the problem studied, because the application of mathematical methods is a most objective form of systematization of such knowledge.

For example, the compilation of the original factual material on the populational ecology of parasites in vertebrates is connected with considerable methodological difficulties (Breev 1967, Minář and Breev 1978, 1981, 1983). This is due to the fact that mathematical modelling of regulatory processes for these species is practically at its beginning.

Another difficulty in the construction of mathematical models for the populational processes studied is connected with the necessity of changing classical methods for the description of regulatory systems, which mainly concern free-living species (Volterra 1976). These methods are namely suitable for the studies on the dynamics of the process of density regulation. In the systems studied, however, the dynamic picture is considerably distorted by the process itself on one hand and concealed for immediate observation on the other. Here first and foremost is the total structure of the process, described by the probability distribution of the parasite number per host. The basic information on the species interrelationships consists in the type of distribution and in the structure of its parameters. For instance, we may refer to the different mathematical ways of describing the regulations in the populations of warble flies presented in the paper by Bart and Zagretdinov (1981).

Consequently, the basic task in the studies on regulations in the populations of parasitic species lies in an analysis of the construction of the total distribution of parasite numbers studied and in the explanation of the structure of parameters determining this distribution. While solving the problems of this type an essential role is played by the semantic and interpretational aspects requiring close joint activities of biologists and mathematicians.

2. Experience in the warble fly control

In the light of the above said, of interest is the long experience in the control of the cattle warble fly *Hypoderma bovis* in the Soviet Union and Czechoslovakia where essential theoretical and practical results have been lately obtained (Bart et al. 1976, Breev 1981, Breev and Minář 1981). In the USSR the occurrence of *H. bovis* has been distinctly reduced, and in some regions this species was completely eradicated (Breev 1980, Minář 1974). Until now *H. bovis* has been practically eliminated throughout the territory of Czechoslovakia (Minář 1980).

H. bovis is a suitable object for the detection and investigation of regulatory systems in the parasite populations. This is a species with a relatively simple life cycle, its numbers are strictly regulated by defensive responses of the hosts (Bart et al. 1976). At the same time, the logical structure of the regulatory system is typical of many other parasitic species.

The mathematical approach to the description of the regulatory system in the warble fly density (numbers) was preceded by long-term studies on the data acquisition of their ecology. Particularly, the species composition, mutual relationships among species and distribution of all warble fly species parasitizing farm and wild animals in the USSR and the adjoining countries were studied. The biology of the natural regulatory systems, determining the level and dynamics of the cattle warble fly numbers was studied and the most incriminating link — the first instar larvae, was determined. Finally, it was noted on the material on hand that the distribution of the number of second and third instar larvae of warble flies agrees with the negative binomial distribution (Breev 1968 a, b).

In this manner the basic goal of the mathematical analysis of the regulatory system of the parasite numbers was outlined. It consisted in the study, comparison and interpretation of different mathematical constructions of negative binomial distribution, in the detection and analysis of the structure of parameters, which are most informative about the process of density regulations and which determine this distribution.

A detailed description of results obtained by such analysis is found in the papers of Bart (1981), Bart and Zagretdinov (1980), Bart et al. (1976). We shall dwell only on those conclusions which are directly connected with the practice of control measures and with the fundamental principles of the theory on the regulations in the host-parasite system.

3. Model of negative binomial distribution

The first essential conclusion consists in the fact that the type of distribution of parasite number on the host (the negative binomial) is determined mainly by populational level of their interrelationships, while the individual level is reflected in the parameters of this distribution.

We shall designate the negative binomial distribution by the symbol $\beta_-(j|k, p)$ denoting the probability of having second and third instar warble fly larvae on the fixed host animal (j). The basic parameters of ditribution are interpreted analogically as the number or larvae which have died on the host (k) and the probability of death of one larva (p).

Concretely, this distribution has the form of

$\beta_-(j/k, p) = \frac{(k + j - 1)!}{(k - 1)!\, j!} p^k q^j$; $j = 0, 1, 2 \ldots$ where the symbol j! designates a product of integer numbers from 1 to j. For example, 5! = 1. 2. 3. 4. 5 = 120. It should be noted that a series of positive numbers whose sum equals 1 is called probability distribution. In every fixed values k and p the series of numbers ($\beta_-(j|k, p)$; $j = 0, 1, 2 \ldots$) forms the probability distribution. If k and p are not fixed, then $\beta_-(j|k, p)$ designates the family of probability distributions, k and p are called parameters of this family of distributions (briefly — parameters of the distribution). k may receive arbitrary integer numbers, while p means any number between 0 and 1. The number of larvae on the fixed host is a random variable and its concrete values are denoted by j. In the used designations of the probability distribution the parameters are separated from the values of random variable by a vertical line. If the distribution has several parameters, they are separated from each other by a comma.

If k equals 1, the negative binomial distribution is called geometric distribution $\beta_-(j \mid, p) = pq^j$; $j = 0, 1, 2 \ldots$. It has a sense of probability of accumulating j (survived) larvae in the host organism until the moment of death of one larva. The sum total of independent random variables similarly distributed according to the geometric distribution has a negative binomial distribution $\beta_-(j \mid k, p)$. The negative binomial is closely connected with the Poisson distribution $P(n \mid \lambda) = \frac{\lambda^n}{n!} e^{-\lambda}$ describing the oviposition, and anti-Poisson distribution (particular case of the so-called gamma distribution), associated with actions of the hosts defensive reactions: $\gamma(\lambda \mid n) = \frac{\lambda^{n-1}}{(n-1)!} e^{-\lambda}$. $P(n \mid \lambda)$ means probability of n eggs laid by the warble fly female per a unit of time at an average speed of oviposition λ, while $\gamma(\lambda \mid n)$ is the distribution of average speed of oviposition necessary for the accumulation of n eggs on a fixed host animal.

The above conclusion follows from the fact that the negative binomial distribution describes a steady stereotype of the host's and parasite's behaviour in the process of evolution, basically, at the moment of the flight and oviposition of warble flies, resulting from the analysis of the known gamma-Poisson construction

$$\beta_-(j \mid k, p) = \int_0^\infty P(j \mid \lambda q)\, \gamma(\lambda, p \mid k)\, d(\lambda p)$$

of this distribution, presented in the paper of Bart et al. (1976). The initial postulate for this model, which may be called the principle of reflexion, consists in the following. If the infestation is described by (random) function $n = \eta(\lambda)$ (the speed of oviposition λ determines the number of eggs on the fixed host animal), the action of defensive reactions of the host population is determined by the reverse functional dependence $\lambda = \eta^{-1}(n)$ (behaviour of hosts during the infestation determines the speed of oviposition necessary for the accumulation of n eggs on the fixed host animal).

In the mathematical statistics the mentioned operation of conversion of functions to the realizations of random process (in this case of the Poisson's) corresponds with the P. Fischer's idea of construction of the so-called fiducial distributions. The distribution of random variable $\eta^{-1}(n)$, when n is fixed (in this case anti-Poisson's) will be fiducial, after Fischer, to the distribution of the initial random variable $\eta(\lambda)$ when λ is fixed (in our case to Poisson distribution (Kramer 1975).

In the mentioned construction of the negative binomial also the individual level of defensive responses is taken into account, where larvae in the host organism are divided into dead and survived ones $n = k + j$, according to the probability p and q, $p + q = 1$. Consequently, the Poisson distribution of the hosts' infestation with parasites causes defensive responses in host population (restless behaviour) leading to the distortion ("blurring up") of the oviposition speed after anti-Poisson distribution, which finally results in the negative binomial distribution of the number of survived larvae on the host.

This conclusion can explain the fact that the type of density distribution $\beta_-(j \mid k, p)$ is preserved in different sites of the species' range (Breev and Minář 1976a, b, 1978a, b, 1979, 1981, Minář and Breev 1977, Breev 1977). Next, the stable interrelationships of the parasite and host will be understood as the mentioned natural mode of regulation of *H. bovis* numbers, leading to the negative binomial distribution $\beta_-(j \mid k, p)$ of the number of second and third instar warble fly larvae on the fixed host animal.

It should be noted that among the probability models in parasitology, describing the numbers of parasitic species, in the focus of attention are the schemes directly or indirectly connected with the constructions of the negative binomial (Breev 1972, Bart et al. 1976, Kornikov et al. 1979). This may be explained mainly by the fact that this law is the simplest in the class of the so-called overdispersed distributions (dispersion greater than the expected value), whose leading role is noted in the very determination of the concept of parasitism (Crofton 1971, Kennedy 1978 etc.). From the viewpoint of overdispersion the Poisson distribution takes the extreme place — expected value equals dispersion. The other extreme is represented by the normal distribution, in which the expected value and dispersion are independent parameters. An interesting and important problem is the classification of distributions according to the form and the degree of connection between their expected value and dispersion. Finally, the mentioned gamma-Poisson scheme of construction of the

negative binomial exactly shows that overdispersion results from the interaction of species, i.e. because of the presence of regulations.

4. Regulatory parameters

Another essential conclusion is connected with the detection of distribution parameters and associations between them, which determine the stability of regulations in the system.

Common characteristics of infestation in parasitology are its extensity (E) (incidence of infestation) and intensity (I) (mean infestation per infested host) of infestation. This is accounted for by the simplicity of calculation of the evaluations of these parameters according to real observations. Analogically with the basic characteristics of continuous features whose distribution it is customary, as a rule, to describe by normal law, also mean population density (M) and dispersion (D) are considered. Both mentioned pairs of characteristics determine the negative binomial distribution, but are not decisive in the analysis of the activity of regulatory systems described by the negative binomial distribution. Here the basic characteristics are the parameter $q = 1 - p$ — the probability of the survival of first instar larva and — the number of dead larvae, while the basic emphasis is laid on the character of connection between them.

Before this conclusion will be elucidated, the dependencies of the mentioned pairs of characteristics, considered as parameters of the negative binomial distribution, on the parameters of this distribution must be discussed.

$$E = 1 - p^k; \qquad I = \frac{kq}{p(1 - p^k)} \qquad M = \frac{kq}{p} \qquad D = \frac{kq}{p^2} \qquad \frac{D}{M} = \frac{1}{p} > 1$$

It should be also noted that the basic methods of mathematical statistics were developed with a view to continuous distributions (primarily to normal), therefore the application of these methods for discrete distributions of the negative binomial is connected with certain difficulties. Consequently, if the construction of parameter estimates by method of maximal likelihood (Breev 1972, Bart at al. 1976) is possible by using a computer, the determination of the objective degree of reliability of these estimates poses a problem. All this presents additional difficulties for the analysis of regulatory systems.

In order to elucidate the above conclusion we shall consider the problem of possible effects due to the human interference with the natural regulatory system in the process of control. The basic method in the *H. bovis* control at the stage of first instar larvae is the treatment of herds with insecticides. In the scheme of the negative binomial this corresponds to the sharp increase of the k parameter value, and this fact causes different distortions of the negative binomial distribution. When the values of the k parameter tend to infinity, the following distributions may be limiting for $\beta_-(j \mid k, p)$, depending on the degree of connection between k and q parameters.

A. If $kq \to 0$, then $\beta_-(j \mid k, p)$ converges to singular distribution, i.e. with probability 1 the variable j equals zero.

B. If $kq \to a$, where a is an integer number, $(\beta_-(j \mid k, p)$ tends to Poisson distribution $P(j \mid a)$.

C. If $kq \to \infty$, then in the limit we obtain a normal distribution corresponding to the preceding case when $a \to \infty$.

The favourable effect, i.e. the eradication of all parasites is possible only in case A, and for this purpose it is necessary, due to the condition $kq \to 0$, that in the process of control the speed of the increasing tension of defensive responses of hosts be higher than the intensity of the control measures applied. If the intensity of treatments is not coordinated with the action of defensive reactions, i.e. kq does not tend to zero if k tends to infinity, then the natural regulatory system responds to such an interference by negative effects.

For instance, if the value of parameter k has increased due to the treatment of the herd τ times ($\tau > 1$), and the variable of parameter q has remained the same in agreement with the above case B, then the infection rate of herds increases as a result of such "control".

This is true. Let E_0 — be the extensity of herd infestation prior to treatment and the distribution of the parasite numbers $\beta_-(j \mid k_0, p_0)$. If the extensity of infestation of the same herd next year (following the treatment) is designated by E and the corresponding distribution of the numbers by $\beta(j \mid k, p)$, then from the above table we have: $E_0 = 1 - p_0^{k_0}$; $E = 1 - p^k$. As has been supposed $p = p_0$ and $k = \tau k_0$. Therefore, $E = 1 - p_0^{\tau k_0}$. Hence we immediately obtain $E = 1 - (1 - E_0)\ \tau > E_0$, E increasing to 1 while $\tau \to \infty$.

Thus, a more detailed analysis of the stability of regulations in the host-parasite system for *H. bovis* is connected with the analysis of the structure of the q parameter, describing the individual level of defensive responses of hosts.

5. Concept of thresholds and scale of immunity to infection

The biological nature of the host's immunity to the warble fly infection has not been adequately studied at present due to serious methodological difficulties in obtaining relevant information. So far it is only known that basic mortality (about 80 %) of larvae occurs at the first stage of development (Breev 1967). At the same time the study on the properties of the negative binomial distribution, reflecting the logical structure of the process of the density regulation (Bart et al. 1976, Bart and Zagretdinov 1980, Bart 1981) has led to the following conclusion. At the organism's level the given regulatory system is resistant within a certain framework, namely: for parameter q in such a system there exist certain limits of its possible values, beyond which the stability of the potential system is disrupted.

Omitting the mathematical details of these studies, it should be noted that as a result a generalization of the class of geometric distributions was obtained by introducing a new supplementary parameter α, $0 \leq \alpha \leq 1$ into them. The generalized geometric distribution has the form

$$\beta_-(j \mid 0, p, \alpha) = q\left[\frac{j}{\alpha}\right]^+ - q\left[\frac{j+1}{\alpha}\right]^+$$

where the symbol $[x]^+$ designates the iteger number nearest to the number x to the right. For example,

$[3.5]^+ = 4$; $[2] = [2] = 2$; $[3.5] = 3$.

If we sum up k of independent random variables regularly distributed according to the generalized geometric distribution, we obtain a distribution which we shall name generalized negative binomial and designate by the symbol $\beta_-(j \mid k, p, \alpha)$. The concrete form of this distribution is quite complex, but we shall have no need of it.

The distribution possesses one important property. If $\alpha = \frac{1}{m}$, where m is an integer, then the generalized binomial is converted into the usual negative binomial, but with a different structure of parameters.

$$\beta(j \mid k - 1, p, \alpha) = \beta(j \mid k, 1 - q^{mj})$$

E.g. $\beta_-\left(j \mid 0, p, \frac{1}{2}\right) = q^{2j} - q^{2(j+1)} = q^{2j}(1 - q^2) = \beta(j \mid 1, 1 - q^2)$, i.e. the parameter $q = 1 - p$ in the generalized negative binomial is converted into the parameter q^m in the usual binomial.

Let us return to the biological interpretations. As shown in paragraph 3, the stable regulations in the system correspond to the usual negative binomial. In order to examine a wider class of interrelationships with different levels of regulation stability, the distribution of the parasite's numbers on the host should be described by the generalized negative binomial. The probability of the parasite's survival in the organism of the host is designated by the parameter q_0. Then, the stable regulations described by the negative binomial distribution correspond to the case when an integer number m is found, such as $q = q_0^m$, the member q^j in the distribution $\beta_-(j \mid k, p)$ taking the form q_0^{mj}.

For a better understanding of the seemingly simple transformations examined in the structure of negative binomial distribution the defensive reactions of the hosts should be interpreted at the level of organisms.

The penetration of every warble fly larva into the host's organism causes an increase of tension in the field of its immune responses when a certain level of intensity is reached, these responses become apparent and the larva dies. This mechanism is repeated again and again. It should be kept in mind that any change of the intensity of the host's defensive responses occur in its rhythm determined by the biological nature of immune processes of the host's organism. The existence of the integer number m, converting the generalized binomial into the usual one indicates that the rhythm, in which the immune system of the host's organism operates, is commensurable with the rhythm of larval penetration and thus, the mechanism of defensive responses is adjusted and can be repeated many times without any change. The adjustment of this mechanism occurs at the first phase of infection, when larvae accumulate until the death of the first larva. The numbers of these accumulated larvae are distributed according to the geometric law. The repetition of the mechanism mentioned corresponds to the summation of random variables geometrically distributed, resulting in the usual negative binomial, if the regulations are stable, and in the generalized negative binomial, if the immune and infective mechanisms are not in agreement. In the latter case the parameter $\alpha \neq \frac{1}{m}$, where m is an integer, i.e. it has a more complex theoretical-numerical structure. For instance, $\alpha = \frac{s}{m}$ is irreducible fraction or α — irrational number.

The parameter m was named the scale, and q_0 — the upper threshold of immunity to infection, α — the quantitative degree of compatibility (tolerance) of infective and immune processes (Bart et al. 1976).

As the concrete form of the distribution $\beta_-(j \mid k, p, \alpha)$ is generally quite complex, the study of its properties, particularly the estimates of its parameters really observed is a complicated mathematical problem. This is natural, because in the generalized negative binomial are included, except stable regulations, also their different distortions, for whose uniform descriptions it is hardly possible to construct a simple theory. Therefore, in order to select the estimate of the parameter q_0, qualitative considerations have to be basically used in real observations.

The stability of the effects of the host's defensive responses depends on many factors: the age of animals, the condition of their organisms, the previous experience of control etc. Apparently the main factor is the age. Thus, the infection rate in herds of juvenile and adult animals compared indicates (Breev and Minář 1976a, b, 1978a, b, 1979, Minář and Breev 1977) that in juveniles the infection rate is higher, dispersion greater and correspondence of the empiric distribution of parasite numbers with the negative binomial distribution lower. This may be explained by the unstability of immune responses in juvenile animals, in which the scale of immunity to infection m is not a distinctly expressed variable. Therefore, as an estimate of the parameter q_0 it is natural to select that minimal value of probability of larval survival which is observed in the herd of young animals, where the distribution of larval numbers does not agree with the negative binomial.

Apart from the upper immunity threshold q_0 examined, there is also a low limit for the values of parameter q, if the regulatory system is stable. This is due to the fact that the inner resources of the host's organism which it must expend for the maintenance of stable regulations are not limitless. If the value of the upper threshold q_0 in the stable regulatory system is fixed, then the stable regulations may occur with different values of the scale parameter m. The greater the value m, the smaller the value of the parameter $q = q_0^m$, i.e. the lower the level of infection rate in the herd which can be maintained by the natural regulatory system. However, the increase of the intensity scale of defensive responses is connected with the rapid increase of the intensity of immune processes (involved are orders of variables) and apparently with qualitative changes in the mechanism of immunity. Therefore, there is a maximum value m_1 of the parameter m, above which the organism is not able to raise the intensity of defensive responses. It is this maximum scale m_1 which determines the low limit $q_1 = q_0^m$ for the possible values of the parameter q in the stable regulatory system. q_1 was indicated as the low immunity threshold to infection (Bart and Zagretdinov 1976).

If the infection rate of herd is lower than the threshold q, the natural regulatory system is unable to maintain such a low infection rate by own means. Hence it follows that it is unable by its own means to fully eliminate the parasite population. This conclusion expresses the essence of interrelationships in parasitism and the reality of the existence of the "host-parasite" system.

The situation with an infection which is too low for the chances of regulatory system may also arise in the process of control, resulting in contradictory effects for the control purposes. Let us examine two real examples. Table 1 presents the data of the infection rate in cattle herds (adult animals) kept at the school farm "Vartemyaki" in the Leningrad Region of the USSR (after Breev 1968a). Here $[x]^-$ is the whole part of the number x. For instance, $[3.5]^- = 3$; $[3.3]^- = 3$. Selected here is $q_0 = 0.858$ the probability value of parasite survival for the herd of juveniles in 1964. The Table shows that in 1965 there was a very low infection rate,

Table 1. Studies on the infestation of adult cattle with warble fly larvae of the farm "Vartemyaki", Leningrad Region, USSR

Year	Number of animals	Incidence of infestation %	Mean M	k	$q = \frac{M}{k+M}$	$m = \frac{\lg q}{\lg q_0}$
1963	186	13.98	0.312	0.110	0.731	1
1964	224	16.07	0.406	0.120	0.772	1
1965	266	12.03	0.158	0.286	0.356	6
1966	139	51.08	1.777	0.427	0.806	1

and that it abruptly rose the following year. This may be explained by the fact that in 1964 the control measures taken against the warble flies coincided with unfavourable climatic conditions (wet summer). Consequently the infection rate decreased to the level which could be maintained provided that the intensity of defensive response ($m = 6$) increased abruptly. However, the regulatory system did not cope with it and the infection rate rose abruptly.

Table 2 presents data on the infection rate in herds of adult animals at the farm "Važec" in Czechoslovakia.

Table 2. Studies on the infestation of adult cattle with warble fly larvae at the farm "Važec", Central Slovakia, ČSSR

Year	Number of animals	Incidence of infestation %	Mean M	k	$q = \frac{M}{k+M}$	$m = \left[\frac{\lg q}{\lg q_0}\right]$
1973	443	19.9	0.591	0.131	0.8185	1
1974	390	9.7	0.074	0.056	0.5683	4
1975	543	13.8	—	—	—	—
1976	513	19.1	0.6179	0.1172	0.8405	1
1977	240	8.3	0.3208	0.0395	0.8584	1

Here $q_0 = 0.8828$ is selected according to the estimate relevant to the herd of juveniles in 1977. The infection rate in 1974 decreased abruptly, while in 1976 it was restored due to the fact that the successful treatment of cattle in 1975 was impeded by the epidemic of foot-and-mouth disease, and the natural regulatory system was unable to maintain such a low infection rate ($m = 4$).

6. Practical conslusions and data on the control results obtained

Let us examine the conclusions which may be drawn from the mentioned theory for the application in the control of *H. bovis*.

First, in the strategy of the control measures two phases should be outlined. In the first phase we direct our attention at the assistance to the natural regulatory system. A gradual decrease of infection rate occurs until the level which corresponds to the low threshold of immunity q. The continuity of treatment is essential and the climatic conditions favourable to control measures must be considered. The second phase corresponds to the low infection rate in the herd ($q < q_1$). The control measures undertaken are directed at a complete eradication regardless of any support to the natural regulatory system. This phase requires greater efforts in the organization of control.

The application of such a strategy led, for example, to a complete elimination of *H. bovis* in the Leningrad Region of the USSR where the method of complete eradication of cattle warble flies, developed by K. A. Breev, was used over a large territory under conditions of low numbers of parasites. The method consists in the change of the system of monitoring the foci of infection, necessary because the effect of the above negative reactions of the regulatory system is most manifest while the incidence of infection is low and therefore an increased attention to the problems of control is required.

The second conclusion consists in the fact that the strategy in which the control of the infection in herds of young animals is undertaken, proves to be more effective. While treating the young animals we decrease the upper threshold q_0 for the adult animals. As the variable m of the maximum intensity scale of defensive reactions is essentially stable for the fixed herd, the value of the lower threshold $q_1 = q_0{}^m$ decreases along with decreasing value of the upper threshold q_0 and thus a great effect is achieved during the control measures at the first stage where less organisational efforts are necessary. It is this method of control that was used in Czechoslovakia.

ОСНОВНЫЕ РЕГУЛЯТОРНЫЕ ПАРАМЕТРЫ СИСТЕМЫ „ХОЗЯИН—ПАРАЗИТ" ДЛЯ ОВОДОВ СЕЛЬСКОХОЗЯЙСТВЕННЫХ ЖИВОТНЫХ НА ПРИМЕРЕ *HYPODERMA BOVIS*

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Резюме. При изучении закономерностей взаимосвязи ,,хозяин—паразит" на примере подкожных оводов у крупного рогатого скота была выявлена жесткая внутренняя система регуляции численности паразитов на хозяине, выраженная на уровне популяций. Эта регуляторная система подчиняется математическо-статистическим закономерностям и поэтому ее можно моделировать и отдельные ее особенности выражать математическим способом. Распределение паразитов в популяции хозяина согласуется с негативным биомиальным законом. В работе проанализированы главные математические формулировки регуляторной системи (параметры) и защитных реакций хозяина на инвазию паразитов. Из выше упомянутых закономерностей вытекают важные заключения для борьбы с гиподерматозом крупного рогатого скота на практике. Математическая модель объясняет два этапа борьбы — первый этап, согласуясь с естественной регуляторной системой, приводит к выраженному снижению степени нападания, а второй имеет целью ликвидацию болезни. Из выше указанного следует, что борьба с гиподерматозом выгодна прежде всего у молодняка, как показали результаты борьбы, проводимой в ЧССР.

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