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The local dynamics of acarine predator-prey (*Cheyletus eruditus*-*Dermanyssus gallinae*) populations: identification of a lumped parameter model

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A simple lumped parameter model representing trophic interactions in terms of biomass, has been constructed for the analysis of population interactions between the chicken mite *Dermanyssus gallinae* and the predatory mite *Cheyletus eruditus*. The model is identified by parameters derived from stage-structured models built for both unlimiting and limited food conditions. Procedures are proposed for estimating the following parameters: the specific growth rate of the prey population, the maximum food consumption (demand) corrected for preference, food exploitation for the predator population, the search rate and the search efficiency coefficient in the functional response model, and the loss of biomass due to respiration and, in the case of the predators, food shortage. The comparison between the estimates obtained by different estimation procedures indicates that the logical structure of the model is coherent. Furthermore, the estimates are in agreement with data reported in the literature. Theoretical and numerical studies of the lumped model appear in BUFFONI *et al.* (1995).

Keywords: *Dermanyssus gallinae*, *Cheyletus eruditus*, population model, parameter estimation, predator-prey interactions, metabolic pool

INTRODUCTION

The chicken mite *Dermanyssus gallinae* (DE GEER, 1778) is a wide-spread pest of laying hens as well as of other domestic and wild birds (LANCASTER & MEISCH, 1986). In a survey carried out in Switzerland, chicken mites were found in 33 out of 39 poultry houses (MAURER *et al.*, 1993b). *D. gallinae* is a temporary ectoparasite which attacks the resting host preferentially at night, and, after a short intake of blood, retires into shelters in the surroundings of the host's resting places. These shelters consist, for example, of crevices in the perch occupied by resting hens.

D. gallinae can cause anaemia in chicken (KIRKWOOD, 1967) and lead to a highly significant decrease in the egg production of laying hens (JUNGSMANN *et al.*, 1970). However, this effect is not always distinct: in an experimental poultry house mite populations were allowed to increase to such high densities that the carrying capacity of the poultry house was assumed to be reached. Nevertheless, there was no difference in egg production and physiological blood parameters in comparison to a control poultry house. Once the mite population started to increase, however, the hens changed their behaviour and avoided the perch as a resting place. This change is very undesirable from a poultry house management standpoint, and con-

trol measures are considered justified (MAURER, 1993). Since a sustainable control system was sought, chemical control measures were dismissed and biological control was taken into consideration (MAURER *et al.*, 1993a).

In a survey, MAURER *et al.* (1993b) observed the predatory mite *Cheyletus eruditus* (SCHRANK, 1781) in Swiss poultry houses. Some preliminary experiments confirmed the observations made in the literature that the predator was a potential biological control agent of *D. gallinae* (FROLOV, 1971). Therefore, experiments were undertaken to study the qualities of the predator which, based primarily on empirical evidence, are considered to be desirable attributes of natural enemies (see for example, MESSENGER *et al.*, 1976). Again, the predator kept its promises as a biological control agent (MAURER, 1993). On the basis of these results we proceed to an analysis of predator-prey population interactions.

The complexities inherent in interactions between predator and prey life stages and the limited information available for the two species under study precluded us from constructing a comprehensive population system model. We argue that the identification of a simple lumped parameter model representing the local biomass transfer between two trophic levels is adequate to obtain sufficient insight into the predation process for an evaluation of the efficiency of the predator *C. eruditus*.

The model is described in terms of biomass production and elimination as well as in terms of food demand and search/capture parameters, which, in general, are not directly observable. To estimate these parameters we use detailed developmental stage-structured population models designed for specific conditions: prey populations with unlimited food developing in absence of predators; predator populations with unlimited food at the beginning of an observation period and no food in the subsequent phase. The model requires stage-specific parameters, i.e. developmental times, survival and fecundity rates, weight, and sex ratios, which have been obtained from poultry house and/or laboratory experiments (MAURER, 1993).

The purpose of this paper is the estimation of the parameters for a simple lumped parameter model.

PREY DYNAMICS

Model description

The prey population is assumed to develop at a constant temperature of 25°C. Without loss of generality in this work we consider a simplified system model with three developmental stages. The extension to more stages is straightforward. *D. gallinae* pass through 4 stages before reaching the adult stage: from the egg hatches a larva which moults to a protonymph without feeding. The protonymph feeds on a bird and moults to a deutonymph which feeds again before becoming an adult male or female. The juvenile development of the prey is reduced to two stages: the non-feeding life-stages (egg and larva) are summarised to the «egg» stage and the feeding juveniles (proto- and deutonymph) form the «nymph» stage; male and female adults are combined to the «adult» stage. The following demographic parameters for the *D. gallinae* (x) stages «egg» ($i = 1$), «nymph» ($i = 2$) and «adult» ($i = 3$) are used:

T_{xi}	= duration of the stage (days);
S_{xi}	= stage-specific survival;
M_{xi}	= specific mortality rate (day^{-1});
F_x	= fecundity (eggs/female);

W_{xi} = dry weight (g) per individual.

The natural mortalities M_{xi} , at low densities, are related to T_{xi} and S_{xi} by

$$\begin{aligned} M_{xi} &= 1/T_{xi} \log(1/S_{xi}) & \text{for } i = 1, 2, \text{ and} \\ M_{xi} &= 1/T_{xi} & \text{for } i = 3 \end{aligned} \quad [1].$$

Let $X_i(t)$ be the number of prey specimens in stage i at time t and let $x_i(t)$ and $x(t)$ be the average biomass in stage i and the average total biomass, respectively:

$$x_i(t) = W_{xi} X_i(t), \quad x(t) = x_1(t) + x_2(t) + x_3(t) \quad [2].$$

In absence of predators the dynamics of the prey can be described by a system of ordinary differential equations:

$$\begin{aligned} dX_1/dt &= -(1/T_{x1} + M_{x1})X_1 + F'_x X_3 \\ dX_2/dt &= 1/T_{x1} X_1 - (1/T_{x2} + M_{x2} + G \cdot x) X_2 \\ dX_3/dt &= 1/T_{x2} X_2 - (M_{x3} + G \cdot x) X_3 \end{aligned} \quad [3],$$

in which the production rate F'_x is calculated from

$$F'_x = 0.5 F_x/T_{x3} \text{ (eggs/adult day}^{-1}\text{)} \quad [4],$$

0.5 being the sex-ratio of *D. gallinae*. We have introduced a feedback term $G \cdot x$ in the equations for the «nymph» and «adult» stage to take into account the increase of mortality at high population densities. Here, G ($\text{g}^{-1} \text{ day}^{-1}$) is a measurement of the strength of the feedback. System [3] may be written in matrix form as

$$d\mathbf{X}/dt = \mathbf{A}_x \mathbf{X} - G \cdot x (0, X_2, X_3)^T \quad [3'],$$

where

$$\mathbf{X} = (X_1, X_2, X_3)^T, \quad \mathbf{A}_x = \begin{bmatrix} -(1/T_{x1} + M_{x1}) & 0 & F'_x \\ 1/T_{x1} & -(1/T_{x2} + M_{x2}) & 0 \\ 0 & 1/T_{x2} & -M_{x3} \end{bmatrix}$$

Parameter estimation

The demographic parameters (T_{xi} , S_{xi} , F_x , W_{xi}) are estimated as described by MAURER & BAUMGÄRTNER (1992). Briefly, the behaviour of *D. gallinae* has been investigated, and life table studies have been carried out.

The duration and stage-specific survival of the «egg» stage was observed at 25 °C and 65–75 % relative humidity under long day conditions on 60 individuals kept singly in culture cells as described by ATHIAS-BINCHE & HABERSAAT (1988). The development of «nymphs» was observed on a cohort of mites (starting with 1900 eggs) feeding on young chicks in an experimental cage. A regression model after MANLY (1987) allowed the estimation of the stage-specific survival and the duration of the nymphal stage. The survival and egg production of adult females were observed on a cohort of 120 young females which were followed during their adult life.

The biomass of the life-stages of *D. gallinae* was determined on a micro balance with accuracy $\pm 0.1 \mu\text{g}$ after drying the mites at 60 °C for 3 days (5 groups of approximately 100 individuals were weighed per stage). The demographic parameters and the dry weight of *D. gallinae* are presented in Tab. 1. The production rate

Tab. 1: Demographic parameters of the chicken mite *Dermanyssus gallinae* and its predator *Cheyletus eruditus*. (25 °C; 65–75 % RH).

Species Stage	Duration [days]	Stage-specific survival rate	Mortality [/day]	Fecundity [eggs/female]	Dry weight [mg/100 ind.]
<i>Dermanyssus gallinae</i> (prey)					
“egg”	2.5	0.537	0.249	54	0.2985
“nymph”	5.3	0.817	0.038		0.7647
“adult”	18.0	0	0.056		2.8766
<i>Cheyletus eruditus</i> (predator)					
“egg”	10.5	1.0	0	117	0.057
“nymph”	10.8	1.0	0		0.095
“adult”	34.6	0	0.03		0.256

F'_x , as defined in [4], is equal to 1.35 eggs/adult day⁻¹. The sex-ratio of *D. gallinae* is 0.5 (OLIVER, 1965).

Additional studies showed that blood parameters of the hens remained rather constant (MAURER, 1993) and, from a demographic standpoint, the food quality did not affect *D. gallinae* life table statistics. Furthermore, in the present study, hosts were always present, and consequently the food for *D. gallinae* was unlimited and of constant quality.

Model results

System [3] has a unique positive steady state solution $X_i^* = \delta_i/G$, ($i = 1, 2, 3$) and $x^* = \delta_0/G$, where the parameters δ_i ($i = 0, 1, 2, 3, 4$) depend on T_{xi} , M_{xi} , and F'_x , thus the ratios x_i^*/x_j^* are independent of G ; x_i^* and x^* are the average steady state biomass in stage i and the average total biomass, respectively

$$x_i^* = W_{xi} \cdot X_i^*, \quad x^* = x_1^* + x_2^* + x_3^* \quad [5].$$

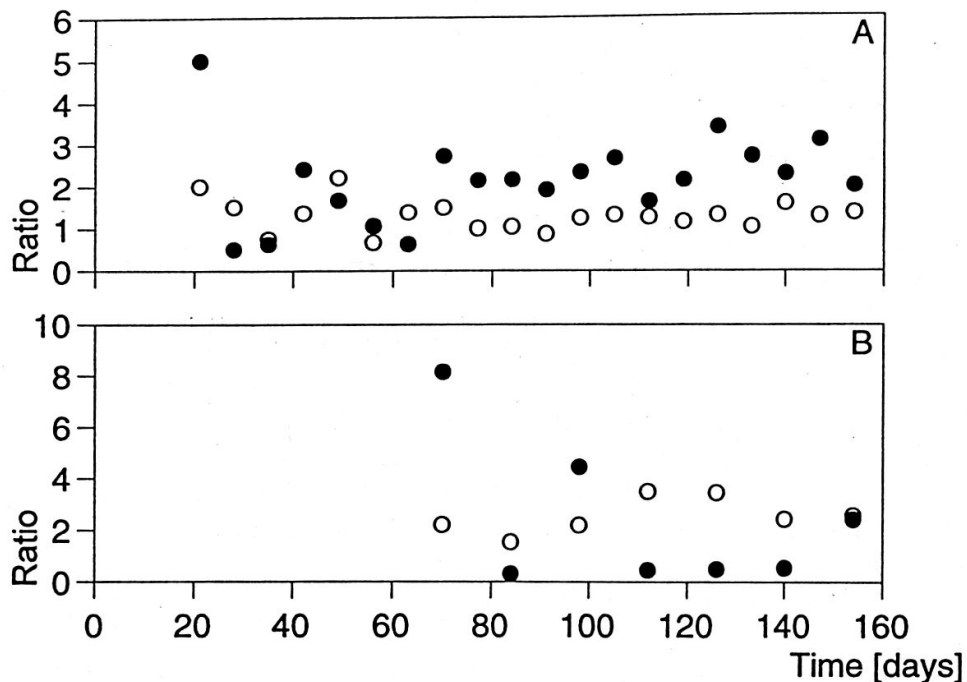


Fig. 1: Time evolution of the mite *Dermanyssus gallinae*: observed ratio “eggs”/“adults” (closed circles), observed ratio “nymphs”/“adults” (open circles).

A: poultry holding “Marti” (initial conditions 100 % “nymphs”).

B: poultry holding “Strickhof, compartment II”.

Tab. 2: Average ratios “eggs”/“adults” and “nymphs”/“adults” of *Dermanyssus gallinae* after a population development of 10 weeks. Computed steady state ratios and observed values.

	“eggs”/“adults”	“nymphs”/“adults”
observed		
Strickhof, Compartment II	2.39	1.23
Marti	2.41	2.56
computed	2.09	1.70

If we assume $G = \delta_0 (= 0.264)$, then the solution to [3] is normalised so that $x^* = 1$, and the computed values of X_i^* and x_i^* are

$$X_1^* = 0.13, \quad X_2^* = 0.105, \quad X_3^* = 0.062; \quad [6.1]$$

$$x_1^* = 0.13 e, \quad x_2^* = 0.27 e, \quad x_3^* = 0.60 e, \quad [6.2]$$

where e is the biomass of a *D. gallinae* egg. The analysis of the variational matrix of system [3] shows that the steady state solution of systems [3] is asymptotically stable.

The evolution of the population of the mite *D. gallinae* has been observed in the experimental poultry holding «Strickhof, compartment II» (MAURER, 1993) and in the poultry holding «Marti» (unpublished data). The experiments started with a population of 100% «nymphs» in the poultry holding «Marti» and with 46% «eggs», 31 % «nymphs», and 23 % «adults» at «Strickhof, compartment II». The time evolution of the observed and computed ratios «eggs»/«adults» and «nymphs»/

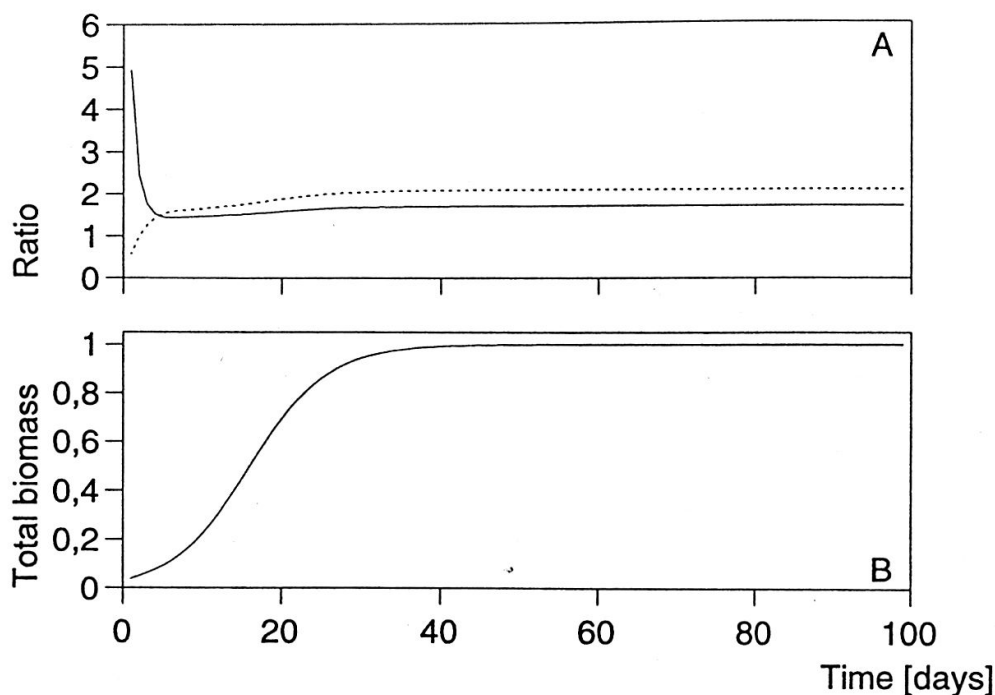


Fig. 2: Calculated time evolution of the mite *Dermanyssus gallinae*, in absence of its predator, with initial conditions of 100 % “nymphs” and $x(0) \ll 1$.

A: ratio “eggs”/“adults” (dotted line), ratio “nymphs”/“adults” (solid line).

B: total biomass.

«adults» is shown in Fig. 1A, B, and in Fig. 2A, respectively. The average ratios «eggs»/«adults» and «nymphs»/«adults» after 10 weeks, together with the computed steady state ratios X_1^*/X_3^* and X_2^*/X_3^* , are shown in Tab. 2. The agreement of the predictions (Fig. 2A, Tab. 2) with the observed proportions (Fig. 1A, B, Tab. 2) confirms the consistency of the estimated parameters.

Let $X_i(t)$ be the solutions to [3] with initial conditions $X_i(0)$, so that $x(0) \ll 1$; then, the trend of the biomass $x(t)$ given by [2], is a sigma-like type of growth (Fig. 2B) and it is well fitted by a logistic curve. The specific growth rate of the prey is represented by $r_x g(x)$, where

$$g(x) = (1 - x) \quad [7],$$

and $r_x = 0.2 \text{ day}^{-1}$. The intrinsic growth rate r_x is the unique positive real eigenvalue of the matrix A_x of the coefficients of the linear terms in [3']. This parameter represents the intrinsic growth rate of a population with stable age structure. The carrying capacity of the system is relative to prey biomass. The steady state is approached in about 40 days.

PREDATOR DYNAMICS

Model description

The predator population is assumed to develop at a constant temperature of 25 °C. Let the parameters T_{yi} , S_{yi} , M_{yi} , F_y , and W_{yi} for the predator *C. eruditus* (y) be defined as in the previous section on the dynamics of the prey *D. gallinae*. Moreover, let $Y_i(t)$ be the number of predator specimens in stage i at time t and let $y_i(t)$ and $y(t)$ be the average biomass of stage i and the average total biomass, respectively

$$y_i(t) = W_{yi} \cdot Y_i(t), \quad y(t) = y_1(t) + y_2(t) + y_3(t) \quad [8].$$

The predator dynamics can be described by the following system of ordinary differential equations:

$$\begin{aligned} dY_1/dt &= -1/T_{y1} \cdot Y_1 + F'_y \cdot Y_3 \\ dY_2/dt &= 1/T_{y1} \cdot Y_1 - (1/T'_{y2} + M'_{y2}) \cdot Y_2 \\ dY_3/dt &= 1/T'_{y2} \cdot Y_2 - M'_{y3} \cdot Y_3 \end{aligned} \quad [9].$$

For the case of unlimited food supply, the production F'_y , the duration T'_{y2} , and the mortalities M'_{y2} and M'_{y3} are calculated from

$$F'_y = 1 \cdot F_y/T_{y3} \text{ (eggs/adult day}^{-1}\text{)}, \quad [10]$$

1 being the sex-ratio of the predator (see below), and

$$T'_{y2} = T_{y2}, \quad M'_{y2} = M_{y2}, \quad M'_{y3} = M_{y3} \quad [11].$$

M_{y2} and M_{y3} are estimated as explained in the subsequent section. When no food is available, the duration of the nymphal stage is lengthened, and nymphal mortality increases. Adult mortality rate decreases lengthening the adult life span, and no reproduction occurs (MAURER, 1993). The parameters F'_y , T'_{y2} , M'_{y2} , and M'_{y3} are calculated from

$$F'_y = 0; \quad T'_{y2} = 2 T_{y2}; \quad M'_{y2} = M_{y2} + 1/2 T_{y2}; \quad M'_{y3} = 1/2 M_{y3} \quad [12].$$

System [9] may be written in matrix form as

$$dY/dt = A_Y Y \quad [9'],$$

where

$$Y = (Y_1, Y_2, Y_3)^T, \quad A_Y = \begin{bmatrix} -1/T_{Y1} & 0 & F'_{Y3} \\ 1/T_{Y1} & -(1/T'_{Y2} + M'_{Y2}) & 0 \\ 0 & 1/T'_{Y2} & -M'_{Y3} \end{bmatrix}$$

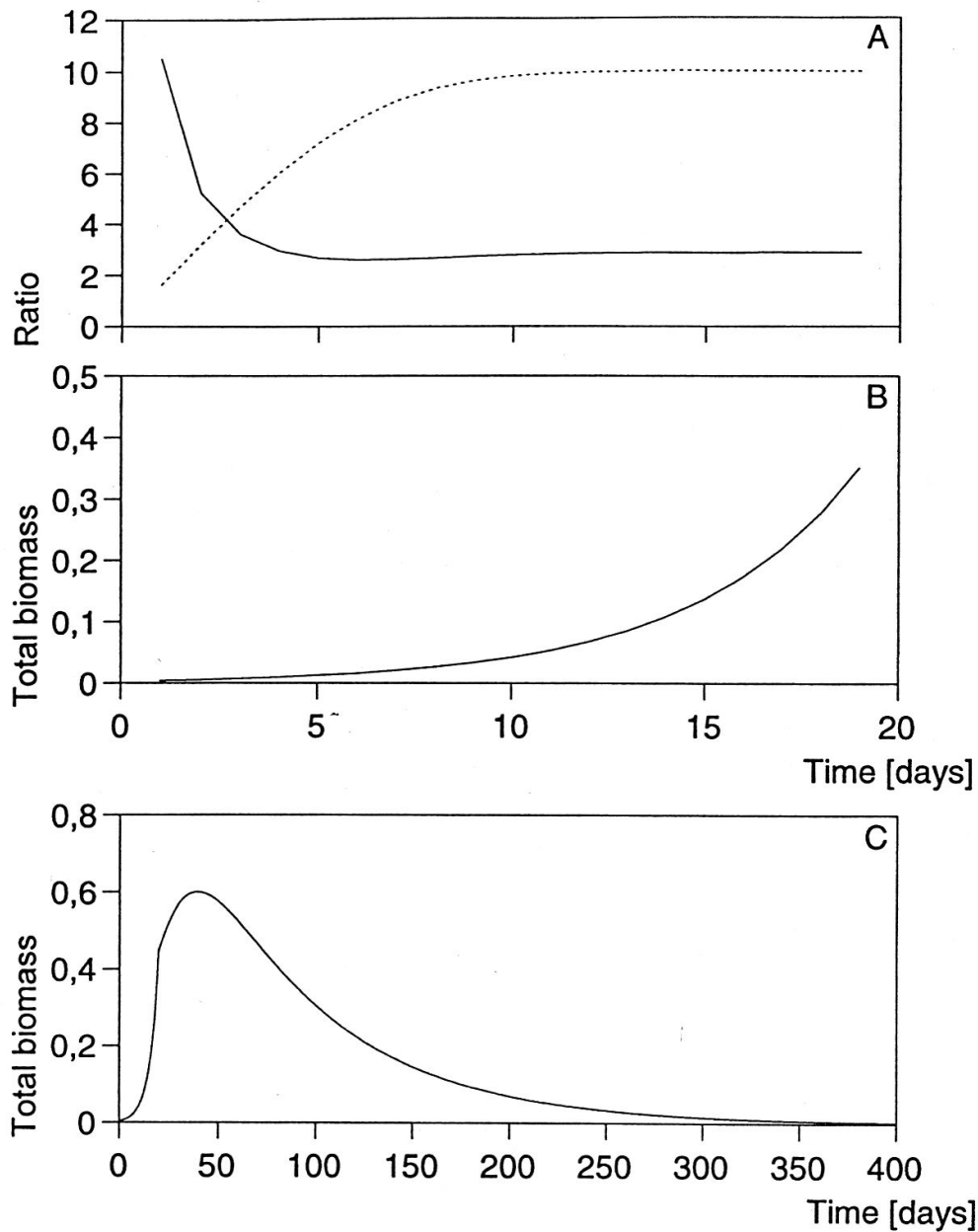


Fig. 3: Calculated time evolution of the mite *Cheyletus eruditus* with initial conditions of 100 % "nymphs" and $x(0) \ll 1$.

A: ratio "eggs"/"adults" (dotted line), ratio "nymphs"/"adults" (solid line).

B: total biomass, if a surplus of prey is available.

C: total biomass, if a surplus of prey is available ($t < 20$ days), and in absence of prey ($t > 20$ days).

Parameter estimation

The predatory mite *C. eruditus* was found in the same habitat as *D. gallinae* during a survey of the chicken mite occurrence in Switzerland (MAURER *et al.*, 1993b). The juveniles develop through 4 stages and, as for *D. gallinae*, the juvenile development is reduced to 2 stages in this work. With rare exceptions, *C. eruditus* develops parthenogenetically (VOLGIN, 1989). Since no males have ever been found during the experiments, the sex ratio is assumed to be 1.

The development of *C. eruditus* was observed at 25 °C and 65–75 % relative humidity in culture cells (ATHIAS-BINCHE & HABERSAAT, 1988). Eaten prey was replaced every day. As a standard, 20 «eggs» of *D. gallinae* were offered to each predator. The data were used to calculate the developmental time, stage-specific survival, and oviposition at abundance of prey «eggs» given in Tab. 1. The production rate, as defined in [10], is equal to 3.29 eggs/adult day⁻¹.

Model results

Let $Y_i(0)$ be such that $y(0) \ll 1$; for the case of unlimited food supply (eqs. [10], [11]), the asymptotic behaviour of $Y_i(t)$ versus t is of exponential type. As t increases, the ratios $Y_i(t)/Y_j(t)$ approach constant values in about 10 days. In particular, as t increases, we obtain that

$$[Y_1(t), Y_2(t), Y_3(t)]/y(t) \rightarrow [2.71, 0.78, 0.27]/e \quad [13],$$

where e is the biomass of a *D. gallinae* egg.

The evolution of the computed ratios $Y_1(t)/Y_3(t)$, $Y_2(t)/Y_3(t)$, and $y(t)$ is shown in Fig. 3A and 3B, respectively. The asymptotic behaviour of $y(t)$ is $\equiv \exp(r_y t)$, where $r_y = 0.24 \text{ day}^{-1}$ is the unique real positive eigenvalue of the matrix A_y [9'] under the assumption of abundance of prey.

In this case of abundant prey, $M_{y1} = 0$, and $M'_{y2} = 0$; thus, only the mortality of adults contributes to the elimination of biomass. The specific rate m_1 is calculated from

$$m_1 = M_{y3} \cdot W_{y3} \cdot Y_3 / y = 0.007 \text{ day}^{-1} \quad [14.1].$$

In absence of prey (eq. [12]), the decrease of $y(t)$ as $t \rightarrow \infty$ (Fig. 3C) behaves as

$$\exp(-m_0 \cdot t) \quad [14.2],$$

where $m_0 = 0.014 \text{ day}^{-1}$ is the minimum modulus of the eigenvalues of the matrix A_y in [9'] under the assumption of prey absence (in this case A_y is lower triangular with non positive diagonal entries).

PREDATOR-PREY DYNAMICS

Model description

The mathematical model of the predator-prey dynamics is described by the following system of o.d.e.:

$$\begin{aligned} dx/dt &= r_x x g(x) - y b f(x, y) \\ dy/dt &= y [c b f(x, y) - v - m(x, y)] \end{aligned} \quad [15],$$

where $x(t)$ and $y(t)$ are the biomasses of prey and predator at time t , respectively. r_x is the specific growth rate of the prey, b is the specific demand rate of predators for prey biomass, c is the proportion of biomass captured and available to the predators, and v is the specific respiration rate of the predators. Predator-prey interactions are modelled on the basis of ratio-dependent functional response theory (GUTIERREZ, 1992, 1996), and on the basis of the metabolic pool representing resource acquisition and allocation (GUTIERREZ & BAUMGÄRTNER, 1984).

The local dynamics of the predator-prey interaction is specified by the following assumptions for the functions $g(x)$, $f(x, y)$, and $m(x, y)$:

a) In absence of predation, the prey is limited only by environmental conditions, and population development is self-limiting (eq. [7]).

b) The predators are limited only by food-supply. The functional response of predators to prey supply is similar to a model proposed by GUTIERREZ *et al.* (1988a, 1988b), the exception being the formulation of the probability of prey finding

$$f(x, y) = 1 - \exp[-xS(y)/by] \quad \text{with } S(y) = s[1 - \exp(-ay)] \quad [16];$$

$S(y)$ is the search/capture rate, s and a are the maximum rate and efficiency coefficient of the search/capture process in a specified environment and are considered as control parameters (when $x/y \gg 1$ we obtain $f = 1$). By assuming $a \ll 1$ we obtain $S(y) = s$ and the functional response numerically becomes equal to IVLEV's (1961). When put into a physiological context the demand driven functional response of GUTIERREZ *et al.* (1981) is obtained.

c) The influence of energy shortage on the developmental times of the juvenile and on the life span of adult predators is taken into account by assuming that the specific mortality rate depends linearly on f , thus $m(x, y)$ is given by

$$m(x, y) = m_0 + (m_1 - m_0) f(x, y) \quad [17],$$

where m_0 and m_1 are positive constants. m_0 is the specific mortality rate in absence of prey ($f \equiv 0$), and m_1 is the specific mortality rate in the case of abundant prey ($f \equiv 1$); the parameter $m(x, y)$ can be modified to account for migration processes.

At last, we have the o.d.e. system for the two trophic level population dynamics

$$\begin{aligned} dx/dt &= r_x x(1-x) - ybf(x, y) \\ dy/dt &= y[-u + b'f(x, y)] \end{aligned} \quad [18],$$

where x and y are dimensionless, and $u = v + m_0$, $b' = cb + m_0 - m_1$. Steady state solutions of system [18] and local stability analysis are reported in a recent paper by BUFFONI *et al.* (1995).

Parameter estimation

The parameters introduced in the model [18] are the following: the specific rates (day^{-1}) r_x , b , b' , u , and the control parameters relative to the prey capture process s (day^{-1}) and a (dimensionless). These parameters are estimated as follows.

The specific rate r_x could be obtained from cohort life tables which account for biomass. In this study, r_x is estimated by the positive real eigenvalue of the matrix A_x .

The specific rate b can be estimated from population experiments. Provided a stable age distribution for both the prey and the predator population, and accessible unlimited food, the approximation

$$b = -1/y(t) [(x(t + \Delta t) - x(t))/\Delta t] \quad [19]$$

can be used. Thereby, the time interval Δt should be small enough so that the growth processes are negligible.

Since such an experiment is difficult to carry out, b has been estimated from

Tab. 3: Daily predation rates of the predator *Cheyletus eruditus* on different life-stages of the prey *Dermanyssus gallinae*. (25°C; 65–75% RH).

Stage of the predator <i>C. eruditus</i>	Stage of the prey <i>D. gallinae</i>		
	“egg”	“nymph”	“adult”
“egg”	0	0	0
“nymph”	1.14	1.0	0
“adult”	3.6	3.2	1.4

standard experiments, in which the biomass of a particular prey life stage is offered to a particular predator life stage. Subsequently, we need to make some assumptions on the preference of the predators for the prey stages. Empirical evidence (MAURER, 1993) has suggested that the predators prefer eggs over nymphs and nymphs over adult prey. We assume that the predators prefer prey stages with a high energy content relative to the cost of conversion and handling. The daily predation rates of *C. eruditus* on individuals of different life-stages of *D. gallinae* are given in Tab. 3. The biomass of *C. eruditus* (Tab. 1) was calculated from the body length given by VOLGIN (1989) as described by EDWARDS (1967, cited in PERSSON & LOHM, 1977) for Prostigmata.

Let i, j denote the three stages: «egg» ($i, j = 1$), «nymph» ($i, j = 2$) and «adult» ($i, j = 3$). The average biomasses W_{xi} and W_{yi} of *D. gallinae* and *C. eruditus* spec-

Tab. 4: Average biomasses of the stages of *Dermanyssus gallinae* (W_{xi}) and *Cheyletus eruditus* (W_{yi}), and average daily predation rates of the stages of *C. eruditus* on the stages of *D. gallinae* (B_{ij}) expressed in units of *D. gallinae* “eggs”. Preference factors (P_{ij}), and probabilities of the *D. gallinae* stages of being captured by *C. eruditus* stages (Q_{ij}) as explained in the text [eq. (22), (23)].

Parameter	Stage of <i>C. eruditus</i>	Stage of the prey <i>D. gallinae</i>		
		“egg”	“nymph”	“adult”
W_{xi}		1.00 e	2.56 e	9.64 e
W_{yi}	“egg”	0.19 e		
	“nymph”	0.32 e		
	“adult”	0.86 e		
B_{ij}	“egg”	0	0	0
	“nymph”	1.14 e	2.56 e	0
	“adult”	3.6 e	8.19 e	13.5 e
P_{ij}	“egg”	0	0	0
	“nymph”	1	0.45	0
	“adult”	1	0.44	0.27
Q_{ij}	“egg”	0	0	0
	“nymph”	0.73	0.27	0
	“adult”	0.67	0.24	0.09

imens, respectively, and the average daily predation rates B_{ij} of *C. eruditus* stages on different stages of *D. gallinae* in terms of biomass, assuming the biomass e of *D. gallinae* egg as a unit, are obtained from data in Tab. 1, and are shown in Tab. 4. Accordingly, we assume that 100 % of the egg biomass is ingested. A revision of this percentage would require the modification of all parameters listed below. We further assume that, independent of the stage of the prey, the quantity of *D. gallinae* biomass effectively ingested by a *C. eruditus* nymph and by a *C. eruditus* adult be equal to B_{21} and B_{31} respectively. We define the preference factor P_{ij} of a *C. eruditus* stage i for a *D. gallinae* stage j by

$$\begin{aligned} P_{2j} &= B_{21}/B_{2j} & \text{for } j=1, 2, \text{ and} \\ P_{3j} &= B_{31}/B_{3j} & \text{for } j=1, 2, 3 \end{aligned} \quad [20].$$

P_{ij} represent the ratios (biomass ingested)/(biomass killed) and is used as a measure of preference.

Let X_i^* be the *D. gallinae* steady state stage distribution in absence of *C. eruditus* and let the *D. gallinae* stages be captured by the *C. eruditus* stages proportionally to the ratios

$$\begin{aligned} Q_{2j} &= P_{2j}X_j^*/(P_{21}X_1^* + P_{22}X_2^*) & \text{for } j=1, 2, \text{ and} \\ Q_{3j} &= P_{3j}X_j^*/(P_{31}X_1^* + P_{32}X_2^* + P_{33}X_3^*) & \text{for } j=1, 2, 3 \end{aligned} \quad [21].$$

The computed stage distribution X_j^* is given in [6.1]; the matrices $[P_{ij}]$ and $[Q_{ij}]$ are reported in Tab. 4. Thus, the rate b (corrected for preference) is given by

$$b = (B_{21}Q_{21} + B_{22}Q_{22})R_2 + (B_{31}Q_{31} + B_{32}Q_{32} + B_{33}Q_{33})R_3 \quad [22],$$

where R_2 and R_3 are the ratios

$$R_2 = Y_2/y, \quad R_3 = Y_3/y \quad [23].$$

Y_i is the *C. eruditus* stage distribution when enough prey is available, which is non-stationary but in a dynamic equilibrium, i.e. the ratios Y_i/y are time-independent and given in eq. [13]. According to this method $b = 2.67$ (day⁻¹).

The specific rate

$$u = v + m_0 \quad [24]$$

represents the loss of predator biomass due to maintenance respiration (v) and specific natural mortality (m_0) in absence of prey. m_0 has been defined as the minimum modulus of the eigenvalues of matrix A_j ; v can be obtained from measurements on population maintenance respiration rates. Alternatively, the maintenance respiration can be measured on individuals and expressed for the population by

$$v = v_2 \cdot R_2 + v_3 \cdot R_3 \quad [25].$$

The maintenance respiration v_2 and v_3 of *C. eruditus* «nymphs» and females was calculated, assuming that the metabolic rate per μg life weight was the same as the one of another prostigmatid mite, the spider mite *Tetranychus cinnabarinus* BOISD. (THURLING, 1980). In a micro-respirometer at 25 °C, the metabolic rate of starved *T. cinnabarinus* females was 1 nl O₂ μg^{-1} live weight h⁻¹. The maintenance respiration of an individual per day was calculated (1 nl O₂/h corresponding to 20.2 μJ ; BRODY, 1945, cited in HABERSAAT 1991) and expressed as a percentage of a *D. gallinae* «egg» (energy content of Gamasina: 23000 $\mu\text{J}/\mu\text{g}$ dry weight; WALLWORK, 1974). Accordingly, the maintenance respiration of a *C. eruditus* female is 4.5 % of a *D. gallinae* «egg», and for a *C. eruditus* «nymph» it is 1.7 % of a *D. gal-*

linae «egg» per day so that $v = 0.025$, and $u = 0.04$. The maintenance respiration is expected to be higher as the prey becomes scarce since *C. eruditus* is more actively searching for prey.

The specific predator biomass accumulation rate b' can be expressed as

$$b' = r_y + u \quad [26],$$

where r_y is the intrinsic growth rate of the predator population when offered a surplus of prey, and u is the biomass loss according to [24]. The intrinsic growth rate r_y can be obtained from cohort life tables which account for biomass. In this study r_y has been estimated by the positive real eigenvalue of A_y and $b' = 0.28$ has been obtained.

Alternatively, b' can be expressed by means of

$$b' = c b + m_0 - m_1 \quad [27],$$

where

$$c = \alpha(1-\beta) \cdot (1-\delta) \quad [28],$$

also known as a component of the metabolic pool equation (GUTIERREZ & WANG, 1976; BAUMGÄRTNER *et al.*, 1987; GUTIERREZ, 1996). α is the ratio of biomass ingested to biomass killed

$$\alpha = (B_{21} R_2 + B_{31} R_3)/b \quad [29]$$

with R_2 and R_3 defined in eq. [23].

The parameters β (egestion ratio) and δ (conversion ratio) can be estimated from metabolic experiments (see BAUMGÄRTNER *et al.*, 1987, for details). Accordingly, $(1-\beta)(1-\delta) = 0.19$ (MAURER, 1993).

In summary, we obtain $\alpha = 0.7$, $c = 0.13$, and $b' = 0.34$. This corresponds to the results of FERAGUT *et al.* (1992) and to the values reported by HELLE & SABELIS

Tab. 5: Main parameters used in the demographic analysis of the trophic interactions of *Dermanyssus gallinae* and *Cheyletus eruditus*.

Parameter	Value	Unit	Equation (No.)
r_x	0.2	day ⁻¹	
r_y	0.24	day ⁻¹	
b	2.67	day ⁻¹	(22)
n	0.025	day ⁻¹	(25)
m_0	0.014	day ⁻¹	(14.2)
m_1	0.007	day ⁻¹	(14.1)
u	0.04	day ⁻¹	(24)
b'	0.28	day ⁻¹	(26)
a	0.7		(28)
c	0.13		(29)

(1985). Note that the estimation of b' via metabolic rates yields a higher value than the one obtained via eq. [26].

The parameters s , a are difficult to estimate; direct observations on predator-

prey populations under specified conditions could be used for this purpose, i.e. by solving an inverse problem. BUFFONI *et al.* (1995) considered them as control parameters and, by varying them as well as initial conditions, carried out numerical simulations.

The estimates of the parameters appear in Tab. 5.

CONCLUDING REMARKS

A simple lumped parameter model representing trophic population interactions in terms of biomass is found adequate to obtain insight into the dynamics of an acarine predator-prey system. It provides a solid ground for addressing poultry house management problems and evaluating a biological control agent (BUFFONI *et al.*, 1995).

A procedure is described which identifies the model by estimating the relevant parameters. This procedure uses developmental stage-structured models (eqs. [3], [9]) under both unlimiting and limiting trophic conditions, and incorporates demographic and physiological data originating mainly from controlled experiments or observations in poultry houses (MAURER, 1993). The predictions made by the stage-structured prey model [3] favourably compare to the dynamics observed in two poultry houses. In these models three developmental stages have been considered but the structure could easily be modified to account for more stages as well as parameter distributed models (MAURER & BAUMGÄRTNER, 1994).

Different methods have been used for parameter estimation; they provided consistent estimates, which indicates a coherent logical structure of the simple lumped parameter model. Furthermore, the estimates correspond to data reported in the literature (HELLE & SABELIS, 1985; FERAGUT *et al.*, 1992). The existence and uniqueness of positive steady state solutions of system [18] have been shown, and local stability analysis has been performed as function of ecological (r, b, b', u) and behavioural (s, a) parameters; these studies confirm the feasibility for a biological control of the prey (BUFFONI *et al.*, 1995).

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ZUSAMMENFASSUNG

Auf der Grundlage von Biomasse wurde ein einfaches Modell mit zusammengefassten Parametern für trophische Wechselwirkungen entwickelt. Mit diesem Modell werden die Interaktionen zwischen Populationen der Vogelmilbe *Dermanyssus gallinae* und der Raubmilbe *Cheyletus eruditus* analysiert. Das Modell wird mit Parametern identifiziert, welche von stadienspezifischen Modellen hergeleitet wurden. Diese Modelle wurden für Bedingungen ohne Nahrung oder mit unlimitierender Nahrung entwickelt. Es werden Verfahren für die Schätzung der folgenden Parameter vorgeschlagen: Die spezifische Wachstumsrate der Beutepopulation, der unter Berücksichtigung der Präferenz erhaltene maximale Beuteverzehr (Nachfrage) und die Ausnützung der Beute durch die Räuberpopulation, die Suchrate und der Koeffizient des Wirkungsgrades der Suche im Modell der funktionellen Reaktion, der durch die Atmung verursachte Biomasseverlust, sowie die Folge von Nahrungsmangel im Falle der Räuberpopulation. Der Vergleich zwischen Parameterschätzungen, welche mit verschiedenen Verfahren vorgenommen wurden, weist darauf hin, dass eine kohärente logische Modellstruktur vorliegt. Darüber hinaus stimmen die Schätzungen mit Literaturdaten überein. Das Modell mit den zusammengefassten Parametern wurde von BUFFONI *et al.* (1995) in theoretischen und numerischen Studien untersucht.

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