

Leslie model for predatory gall-midge population

Vlastimil Křivan *, Jan Havelka

Institute of Entomology, Academy of Sciences, Branišovská 31, 370 05 České Budějovice, Czech Republic

Accepted 16 August 1999

Abstract

A Leslie matrix model for predatory gall-midge is constructed. From the model we estimate the stable age distribution which is important when the gall-midge is used in biological control. We compare the two common parametrizations of Leslie matrix., i.e. the flow-birth and the pulse-birth projections. We show that both parametrizations lead for the given data set to practically the same results. Then we study the optimal gall-midge introduction scheme which leads quicker to the stable age distribution if only certain instars can effectively be introduced. This is also important, because in biological control we need to minimize the time that a population needs to reach the stable age distribution. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: *Aphidoletes aphidimyza*; Biological control of aphids; Inoculative method of introduction; Leslie matrix; Stable age distribution

1. Introduction

The basic population growth law says that a population which is not limited, grows exponentially. However, the exponential growth law assumes homogeneous and non-structured populations. For age-structured populations (which are typical for insects with various developmental stages and instars) demographic effects will lead to some additional fluctuations unless the population is in a stable age distribution. Thus, when dealing with structured populations we have either to take into account that the

population growth may not be exponential, or we have to assume that the population has already reached a stable age distribution because then it grows exponentially. Structured populations can be modelled either by discrete models, i.e. Leslie matrices (Roughgarden, 1979; Caswell, 1989a,b, 1996; Selhorst et al., 1991), or by continuous models, i.e. Gurtin–MacCamy model (Roughgarden, 1979). In this paper we will use the discrete approach based on Leslie matrices which are constructed from life tables. There exist several possible parametrizations of the model with different predictions. Caswell (1989b) defines two main types of model parametrization: birth-flow and birth-pulse models. The birth-flow model assumes that animals reproduce continuously in each age class, while the birth-pulse model assumes that

* Corresponding author. Tel.: +420-38-7775365; fax: +420-38-43765.

E-mail address: krivan@entu.cas.cz (V. Křivan)

reproduction occurs at certain fixed times only. Since gall-midges reproduce continuously in nights, and they do not reproduce during the day, neither of the two parametrizations match exactly this situation. For this reason we will use both parametrizations to see possible differences.

Since the beginning of the 1970s, the predatory midge *Aphidoletes aphidimyza* has been used for biological aphid control in greenhouses. For successful biological pest control based on the method ‘pest-in-first’ it is important to know whether midge populations reach naturally stable age distributions, how long does it take to reach stable age distributions, and what is the stable age distribution. Knowing that gall-midge population tends naturally to a stable age distribution may still not be enough from a practical point of view, especially if the time to reach the stable age distribution is too long. In this case we may ask how the bioagent should be introduced into the environment in such a way which reduces the time necessary for reaching approximately stable age distribution. Of course, if we can introduce a predator population which has already stable age distribution, then this time would be zero and this introduction pattern would be optimal. However, from practical point of view this cannot be done, because technically only certain age classes can effectively be introduced. Therefore, we ask: how can we optimize introduction of predators in order to approach stable age distribution as closely as possible in a given time? In this paper we propose one possible schedule for gall-midge population which is based on the assumption that only pupae in the cocoons will be introduced. However, the proposed scheme, which is based on quadratic optimization, can also be used for different age classes and populations.

2. Parametrization of the model

We will consider four insect developmental stages: egg, larvae, pupae and adult. Each of these four stages lasts for $d_i (i = 1, 2, 3, 4)$ days. The age of each individual is measured in days since the egg was laid. The census for gall-midge population was made at midday. Gall-midges reproduce

during nights only and we will assume that they reproduce between 8 p.m. and 4 a.m. Age class i , ($i = 1, \dots, s$) contains all individuals whose age is between $i - 1$ and i . For adults the probability of surviving till age a is $\ell(a)$ ($\ell(0) = 1$), and m_i is the expected number of female offsprings for a female in age class i .

Following Caswell (1989b) we have the following estimates for the probability that an individual in age class i will survive from time t to $t + 1$:

$$P_i^f = \frac{\ell(i) + \ell(i+1)}{\ell(i-1) + \ell(i)}, \quad P_i^p = \frac{\ell(i+0.5)}{\ell(i-1+0.5)},$$

$$i = 1, \dots, s.$$

Here the superindex f refers to the birth-flow model while p refers to the birth-pulse model. We note that $\ell(a)$ is approximated from the available data by a piecewise linear approximation.

From the life tables a Leslie matrix which describes the growth of structured populations is constructed in the following way. Let $N_i(t)$ denote the abundance of individuals at time t (measured in days) which are in the age class i and let $N(t) = (N_1(t), \dots, N_s(t))$ denote the composition of the population. Fecundity of females in the age class i is estimated by (Caswell, 1989b)

$$F_i^f = \ell(0.5) \frac{m_i + P_i m_{i+1}}{2}, \quad F_i^p = \ell(0.5) (P_i^p)^{0.5} m_i.$$

Then the Leslie matrix which corresponds to the change of the population structure in one day has the following form:

$$L = \begin{pmatrix} F_1 & F_2 & F_3 & F_4 & \dots & F_s \\ P_1 & 0 & 0 & 0 & \dots & 0 \\ 0 & P_2 & 0 & 0 & \dots & 0 \\ 0 & 0 & P_3 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & P_{s-1} & 0 \end{pmatrix}, \quad (1)$$

where we dropped the superindex. The population dynamics is described by

$$N(t+1) = LN(t)$$

with $L = L^f$ or $L = L^p$ depending on which parametrization we choose. The stable age distri-

bution exists if the largest real eigenvalue of the Leslie matrix is larger than is the absolute magnitude of other eigenvalues (Caswell, 1989b). As test data we took life tables for the Sankt Petersburg gall-midge population (Havelka and Zemek, 1999), see Table 1. The condition for reaching stable age distribution was satisfied for this set of data. The stable age distribution is given by the eigenvector of the Leslie matrix which corresponds to the largest real eigenvalue λ of L . When

the population reaches stable age distribution, it will grow exponentially with the intrinsic growth rate parameter r which is given by

$$r = \ln \lambda.$$

For the Sankt Petersburg population the stable age distributions corresponding to the two model parametrizations are given in Table 1. The corresponding growth rates are $r^f = 1.23774$ and $r^p = 1.22915$. We see that the differences between the

Table 1
Stable age distributions^a

Instar	Age class	Age (days)	Natality	Survival	Stable ^f	Stable ^p
Eggs	1	0–1	0	1	0.208596	0.203113
	2	1–2	0	0.92	0.161651	0.158502
Larvae	3	2–3	0		0.127568	0.125957
	4	3–4	0		0.102652	0.102064
	5	4–5	0		0.08260	0.0827024
	6	5–6	0		0.066466	0.0670125
	7	6–7	0	0.916	0.053482	0.0542983
Pupae	8	7–8	0		0.042623	0.0435758
	9	8–9	0		0.03363	0.0346226
	10	9–10	0		0.02652	0.0274932
	11	10–11	0		0.0209	0.0218187
	12	11–12	0		0.016461	0.0173044
	13	12–13	0		0.012956	0.013715
	14	13–14	0		0.01019	0.0108625
	15	14–15	0	0.7348	0.0080087	0.00859689
	Adults	16	15–16	0	0.65	0.0060118
17		16–17	6.76	0.65	0.0045596	0.00496317
18		17–18	16.34	0.61	0.0036838	0.00403789
19		18–19	17.16	0.6	0.0028847	0.00318404
20		19–20	13.92	0.56	0.0022381	0.00248765
21		20–21	11.82	0.5	0.0017335	0.00194025
22		21–22	13.3	0.45	0.0012798	0.00144245
23		22–23	12.91	0.43	0.00092669	0.00105175
24		23–24	8.39	0.38	0.00069353	0.000792628
25		24–25	6.82	0.35	0.00051575	0.000593564
26		25–26	5.97	0.32	0.00037553	0.000435213
27		26–27	5.23	0.25	0.00027847	0.000324974
28		27–28	3.6	0.23	0.0001914	0.000224929
29		28–29	1.75	0.18	0.00013022	0.000154102
30		29–30	2.36	0.13	0.000089866	0.000107089
31		30–31	1.62	0.1	0.000054896	0.0000658749
32		31–32	1.68	0.03	0.000032906	0.0000397632
33		32–33	0.72	0.02	0.000015027	0.0000182849
34	33–34	0	0	0	0	

^a Life tables for a gall-midge population and stable age distributions corresponding to two different parametrizations of the Leslie matrix

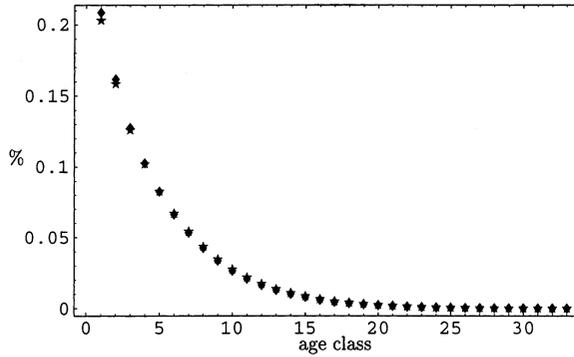


Fig. 1. Stable age distributions for the Sankt Petersburg gall-midge population computed by using flow-birth projection (\diamond) and pulse-birth projection (\star).

two parametrizations of the Leslie model are from any practical point of view negligible for this particular data set. The stable age distribution gives the proportion of every age class in the total population, see Fig. 1. We see that differences resulting from the two parametrizations of the Leslie matrix have only negligible effect on the stable age distribution.

3. Optimal predator introduction

Demographic fluctuations which are due to age structure may cause deviations from the exponential growth rate after the predator population is introduced. These fluctuations could be eliminated by introducing population which has already stable age distribution, but this can be technically impossible. For example, in the case of gall-midge population, pupae in the cocoons are technically easily introduced into greenhouses. Therefore, it will take same time before the population will reach stable age distribution. In Fig. 2 the heavy line corresponds to the case where all age classes of pupae (i.e. age classes 8–15) are introduced in the same numbers into the environment. We see, that this schedule leads to long term oscillations in population numbers. Since the time to reach approximately stable age distribution may be quite long, we may try to speed up reaching the stable distribution. Our strategy will be to introduce animals of only certain age classes

but during maximum k days. Let u be a vector which consists only of zeros and ones. If $u_i = 1$ then it means that the animals of age class i are suitable for introduction while $u_i = 0$ means that animals of this age class are not introduced. Every day we will introduce a certain (yet unknown) amount of animals and we want to do this for maximum of k days. Using the Leslie model which now becomes

$$N(j+1) = LN(j) + a_j u, \quad j = 0, \dots, k-1,$$

we get that after k days the composition of the population will be

$$N(k) = a_0 L^k u + a_1 L^{k-1} u + \dots + a_k u.$$

Here coefficient $a_j > 0$ denotes the number of individuals released at day j . In general we cannot find these coefficients so that $N(k)$ has stable age distribution but we may estimate these coefficients in such a way that the quadratic difference of $N(k)$ from the stable age distribution is minimized, i.e.

$$\sum_{i=1}^s (N_i(k) - S_i)^2 \rightarrow \min,$$

where (S_1, \dots, S_s) denotes the stable age distribution. For example, assuming that we want to introduce only cocoons (i.e. individuals of age class 8–15 for Sankt Petersburg population) for

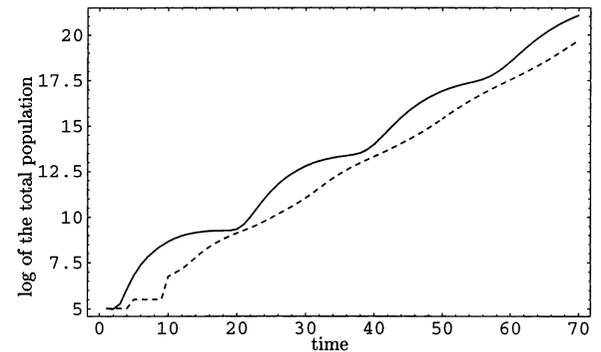


Fig. 2. In this figure the logarithm of the total population is shown. The heavy line describes the growth of a typical population which shows fluctuations due to demographic effects. After some time these fluctuations are vanishing and population grows exponentially. The dashed line shows the population growth when the population is introduced into environment in the optimal way as described in the paper.

maximum of 10 days we found using MATLAB procedure for quadratic optimization with state constraints the following optimal introduction schedule: 1st day introduce 20 cocoons, 5th day introduce two cocoons, and 10th day introduce two cocoons. It is clear from Fig. 2 that using this procedure we reduce fluctuations in gall-midge population densities and we speed up the convergence to the stable age distribution.

4. Conclusions

In this paper we derived a discrete-time model for description of a gall-midge population growth. Leslie matrix population models depend on their parametrization. The two mainly used parametrizations are so called birth-flow, and birth-pulse parametrizations (Caswell, 1989b). The birth-flow model assumes that birth occurs continuously over the time interval, while birth-pulse models assume that reproduction is concentrated in short breeding periods. Since gall-midge as many other insect populations reproduce continuously in nights, neither of the two parametrizations applies. For this reason we compared predictions obtained from the two models by using a gall-midge life history data. The stable age distributions based on the two models are practically identical, see Fig. 1. The difference in the intrinsic growth rate parameters is also very small. Thus we may conclude that for the gall-midge population under the study the differences between the two parametrizations of the Leslie matrix are negligible. Since the aim in biological control is to introduce predator population which

will grow exponentially, we also studied how the gall-midge should be introduced in an optimal way. Optimality here means that after the introduction the gall-midge population will have approximately stable age distribution. Using quadratic optimization we showed that this goal can be achieved by consecutive introduction of certain age classes in a relatively short time, see Fig. 2.

Acknowledgements

This work was a part of the project supported by grants GA CR (201/98/0227, 513/95/0322) and MŠMT (VS96086).

References

- Caswell, H., 1989a. The analysis of life table response experiments I. Decomposition of treatment effects on population growth rate. *Ecol. Model.* 46, 221–237.
- Caswell, H., 1989b. *Matrix Population Models, Construction, Analysis, and Interpretation*. Sinauer, Sunderland, MA.
- Caswell, H., 1996. Analysis of life table response experiments II. Alternative parametrizations for size- and stage-structured models. *Ecol. Model.* 88, 73–82.
- Havelka, J., Zemek, R., 1999. Life table parameters and oviposition dynamics of various populations of the predaceous gall-midge *Aphidoletes aphidimyza*. *Entomol. Exp. Appl.* 91, 481–484.
- Roughgarden, J., 1979. *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. Macmillan, New York.
- Selhorst, T., Söndgerath, D., Weigand, S., 1991. A model describing the predator-prey interaction between *Scolothrips longicornis* and *Tetranychus cinnabarinus* based on the Leslie theory. *Ecol. Model.* 59, 123–138.