Ber. nat.-med. Verein Innsbruck	Suppl. 10	S. 177 – 182	Innsbruck, April 1992

8th International Congress of Myriapodology, Innsbruck, Austria, July 15 - 20, 1990

Modeling the Phenology of *Glomeris balcanica*

(Diplopoda, Glomeridae)

by

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Abstract: A method of phenological data exploitation is suggested and applied to census data regarding a population of *Glomeris balcanica* (VERHOEFF) from an evergreen sclerophyllous formation in Northern Greece. A phenological model was formulated, based on the concept of "ecological time", the unity of which is an exponential trigonometric function of standard clock time. The results of this analysis show that periodicity and asymmetry are the main characteristics of the phenology of *G. balcanica* population. Juveniles display a 3.5 year temporal pattern, while adults display seasonal pattern. In consequence, only the latter have to cope with the seasonality of the mediterranean climate. With respect to their phenological characteristics, stadia I and II, stadia III and IV as well as pseudomatures and adults can be assigned to three distinct groups. The life history strategies of *G. balcanica* were discussed.

1. Introduction:

Mediterranean climate is characterized by a mild winter coupled with a summer drought period. The environmental variables, particularly temperature and humidity display strong annual fluctuations. For instance, an annual temperature range of 40° C is not exceptional in mediterranean regions. It was demonstrated in many cases (STAMOU & SGARDELIS 1989, IATROU & STAMOU 1990, ASIKIDIS & STAMOU 1990), that population dynamics of mediterranean soil arthropods is governed by the regular oscillations of the temperature-humidity complex.

In Greece, apart from the work of KARAMAOUNA (1987), only fragmentary information exists on the ecology of diplopods, appearing as a by-product of studies with other objectives (SGARDELIS & MARGARIS 1983, STAMOU et al. 1984, PANTIS et al. 1988, SGARDELIS 1988, STAMOU & SGARDELIS 1989). The life cycle of the diplopod *Glomeris balcanica* (VERHOEFF 1906) was studied in a *Quercus coccifera* L. formation near Thessaloniki (IATROU & STAMOU 1991). In this paper we applied a method for analysis of phenological data proposed by STAMOU & SGARDELIS (submitted) to census data of *G. balcanica*. Our aim was the integrated description of the demographic traits of this population.

2. Methods:

The phenograms of soil arthropods from mediterranean type ecosystems very often appear asymmetric, due to the fact that, regarding population development, time is not a homogenous variable. During certain periods the demographic events occur extremely frequent, so that phenograms display discontinuities. These discontinuities are linked to discontinuities in the environmental variables complex. Thus, the problem of population dynamics is reduced to the problem of the response of population density to the environmental gradient. Since seasonality characterizes mediterranean climate, trigonometric equations can be fitted to data concerning the fluctuations of the environmental variables. As a result, the environmental gradient is symmetric with respect to standard clock time.

STAMOU & SGARDELIS defined the unity of "ecological time" as the standard clock time interval during which a constant number of demographic events occurs. Thus, ecological time is demographically defined and is considered equivalent to the environmental gradient depicted in relation to standard clock time. The relationship of ecological time to standard clock time is the integral of the function relating the units of these two time scales:

$$t_{ecol} = \int_0^t \exp\{a_1 + b_1 \cos[2\pi(t - \Phi_1)/T_1]\}\,dt \qquad (1)$$

Where a1 and b_1 are constants, Φ_1 = phase and T_1 = period. The response of population density to the environmental gradient, that is to ecological time, was also considered an exponential trigonometric function of the latter (STAMOU 1986):

$$N_{tecol} = \exp\{a + b\cos[2\pi(t_{ecol} - \Phi)/T]\} \qquad (2)$$

(a, b constants, Φ = phase, T = period). Inserting equation 1 into equation 2 a model describing population dynamics with respect to standard time is obtained.

The model has eight parameters. They can be estimated by using numerical techniques (a relevant program is available on request). To describe phenology, parameters Φ and Φ_1 are of particular interest. The former defines the exact time the population density peaks and the latter defines the exact time the rate of occurence of the demographic events is highest. Consequently, their difference $\Delta\Phi = \Phi - \Phi_1$ defines the exact time the demographic events appear strongly condensed, in relation to the population density peak. For $\Delta\Phi > 0$ the highest rate of demographic event coincides with the period of increasing population density, resulting in right skewed asymmetric phenograms. The inverse happens for $\Delta\Phi < 0$, resulting in left skewed asymmetric phenograms, while for $\Delta\Phi \cong 0$ flat graphs are yielded. The ratio of the constants a/b is a measure of the population size at its peak in relation to its overall mean density. Thus, this ratio, actually measuring occurence-dominance, could be used for comparative purposes, describing the numerical importance of populations. The ratio of the constants b_1/a_1 describes the flatness fo the graph of ecological time plotted against standard time. It is a measure of the time, during which the numbers remain constant. Finally, the coefficient $R_t = dN_t/N_t$ stands for the rate of density change in time. Between successive higher and lower values of R_t numbers change drastically.

3. Results:

The model was separately fitted to census data regarding anamorphic immature stadia I to IV, epimorphic pseudomature and epimorphic mature stadia. Before model fitting, raw data were smoothed by using the filter:

$$Y_t = \sum_{t-1}^{t+1} X_t/3$$

(STAMOU & SGARDELIS 1989). The estimated parameters are given in Table 1.

Table 1: The parameters of the model fitted to smoothed census data of *Glomeris balcanica*. Ratios of certain parameters are also given.

	T	T_1	ϕ	$\phi-\phi_1$	b/a	b_1/a_1
Stadium I	32,00	31,74	0,1	-0,58	0,80	-1,90
Stadium II	31,10	30,90	2,9	0,88	1,19	-2,41
Stadium III	36,10	33,44	10,3	-1,10	1,06	-2,90
Stadium IV	30.20	26,57	10,2	1,28	1,07	-3,69
Pseudomatures	29,40	24,92	25,3	-0,72	1,14	-1,95
Matures	11,60	11,56	3,5	-2,12	0,22	-2,91

Data for juveniles show periodicity in the range of 29.4 - 36.1 months, while those for adults display annual periodicity. Moreover, in all life stages, but in pseudomatures discrepancies in the values of parameters T and T_1 were not recorded. Thus, with the exception of the latter no distinct phases in the development of numbers can de distinguished in immatures and adults.

The density peak for stadium I occured in November ($\Phi = 32.01$). Stadium I was sampled in high numbers during a short period. The most remarkable changes in density occured from September to late April/early May, so that the graph of Rt displays a sharp oscillation during this period (Fig. 1c). The relative importance of this life stage is high ($b/a = 0.80$), since it occurred in the field during the whole sampling period. Nevertheless it showed low density from August 1984 until August 1986. During this period density remained constant and the graph of ecological time is flat (Fig. 1b). The phenogram displays slight left skewed asymmetry ($\Delta\Phi = -0.58$). It indicates that specimens in stadium I develop more rapidly into stadium II than do eggs into stadium I.

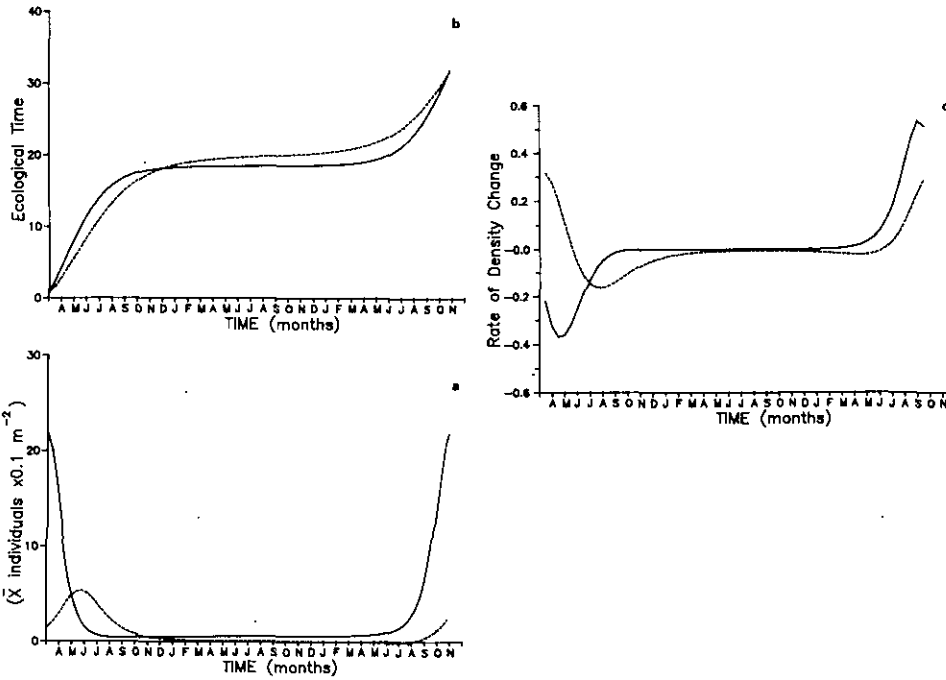

Fig. 1a - c: a) The phenological model applied to data concerning stadia I (solid line) and II (dashed line). b) Ecological time plotted against standard clock time for stadia I (solid line) and II (dashed line). c) Rate of density change for stadia I (solid line) and II (dashed line).

Also specimens in stadium II occurred for a short period and considerable changes in numbers took place from April to August. The density peak lays in May/June ($\Phi = 2.9$). The relative importance if this stadium is the lowest ($b/a = 1.19$) and it was not recorded in the field from January 1985 until August 1986. Lesser changes in numbers took place for a longer period and the graph of ecological time appears less flat than that of stadium I ($b_1/a_1 = -2.41$). The phenogram is right skewed ($\Delta\Phi = 0.88$), indicating a delay in the development of specimens into stadium III.

Concerning numbers, stadia III and IV share common traits. The most important changes occurred from October to April and the density peak lays in December/ January ($\Phi = 10.3$), that is 7.4 months later than the density peak of stadium II. Density development was continuous and the graphs of ecological time do not display a plateau. Finally, their relative importance is comparable.

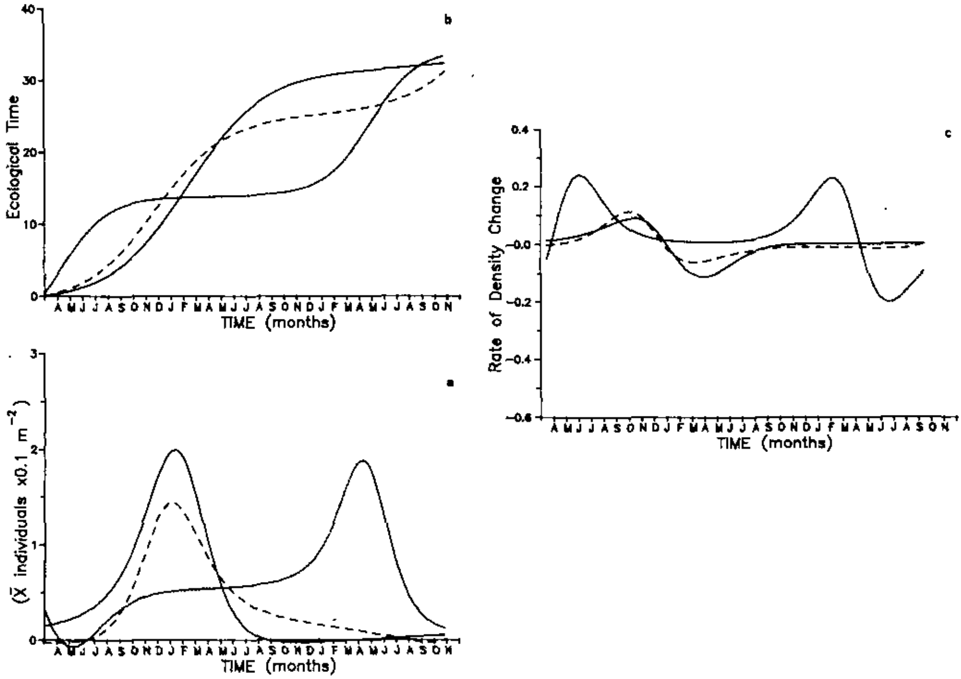

Fig. 2a - c: a) The phenological model applied to data concerning stadia III (solid line), IV (large dash) and pseudomatures (short dash). b) Ecological time plotted against standard clock time for stadia III (solid line), IV (large dash) and pseudomatures (short dash). c) Rate of density change for stadia III (solid line), IV (large dash) and pseudomatures (short dash).

The phenogram of stadium III is left skewed ($\Delta\Phi = -1.1$), while that of stadium IV is right skewed ($\Delta\Phi = 1.28$).

Two distinct phases can be distinguished in the development of population density of pseudomatures. Changes in numbers occurred during the period April to June 1984, followed by a period of constant density. Notable density changes occurred again from February 1986 until June 1986, with the density peak laying in April/May 1986 ($\Phi = 25.3$). In accordance, the graph of ecological time is flat ($b_1/a_1 = -1.95$) and the phenogram appears strongly skewed on the left ($\Delta\Phi = -0.72$). Finally, the relatice importance of this life stage is low ($b/a = 1.14$).

Adult density displays seasonality and numbers change rapidly during the moulting period from July to October (IATROU & STAMOU 1991). Lesser changes in adult density occurred during November/February and again during March/June probably linked to the low winter temperatures. The peak of density occurred in June/July ($\Phi = 3.5$). In any case the development of adult numbers is continuous and the graph of ecological time does not display a plateau ($b_1/a_1 = -2.91$), while the phenogram displays left skewed asymmetry ($\Delta\Phi = -2.12$). Adults were sampled in relatively high numbers during the whole sampling period, so that their relative importance is the highest ($b/a = 0.22$).

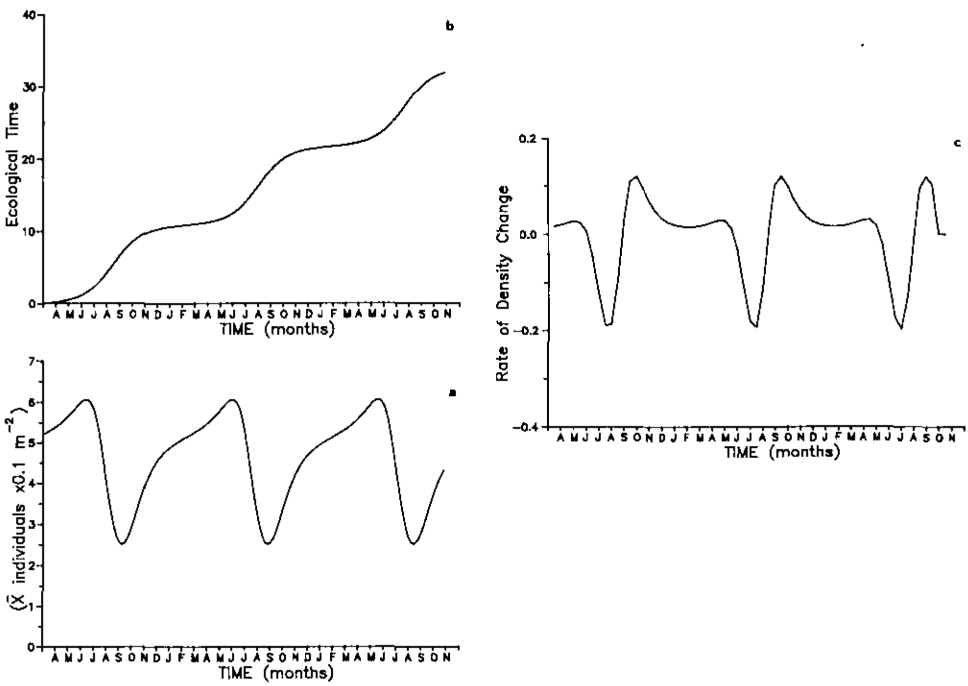

Fig. 3a - c: a) The phenological model applied to data concerning adults. b) Ecological time plotted against standard clock time for adults. c) Rate of density change for adults.

4. Discussion:

The main conclusions drawn from the above presentation are the following: The model applied enables the consideration of life cycle traits in an integrated way. The ecologically meaningful parameters and ratios can be used to compare the demographic characteristics of the life stages. The results of the analysis show that periodicity is a fundamental feature of *G. balcanica* population dynamics. Juveniles display an about 3,5 year temporal pattern which parallels the local interannual temperature-humidity cycle (IATROU & STAMOU 1991). This cycle is important for the population development of a long lived millipede such as *G. balcanica.* Adults display annual temporal pattern. Thus, only matures appear susceptible to the seasonality of the mediterranean climate. They are able to respond rapidly to summer drought, moulting, while their density recovers gradually from autumn through winter to peak in early summer. The low temperature environmental stress in winter does not seem to affect numbers of any life stage, but adults.

Apart from periodicity, asymmetry is also an important characteristic of the development of the life stages of *G. balcanica.* Three life stage groups can be distinguished, with respect to their rate of development: stadia I and II, stadia III and IV, pseudomatures and adults. This distinction can to some extent be compared to discontinuities in biometric features (IATROU & STAMOU 1988). Stadia I, III and pseudomatures develop rapidly into next life stages. On the contrary, the development of eggs and of specimens in stadia II and IV is considerably delayed.

The use of the parameters Φ and Φ_l as well as their difference $\Delta\Phi$, allows for the formulation of a general hypothesis regarding the problem of the synchronization of population dynamics with the periodicity of the mediterranean climate. Indeed, instead of the r-K continuum inadequate for mediterranean arthropods it is possible to utilize the ΔΦ continuum and to oppose the negative or right skewed, the positive or left skewed and the zero or flat strategists to the r-, K- and even A strategists. Positive selected or right skewed strategists are those which are able to encounter environmental stress usually by depositing eggs. They recover rapidly. Negative selected or left skewed strategists are those which respond rapidly to stress and withstand it usually activating special physiological processes like quiescence, diapause etc. According to these comments adult *G. balcanica* should be considered as negative selected or left skewed strategist.

5. Literature:

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