

# Ecological time versus standard clock time: the asymmetry of phenologies and the life history strategies of some soil arthropods from Mediterranean ecosystems

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A model is formulated aiming to describe census data for populations changing non-symmetrically with time. The model is based on the concept of ecological time, conceived as an environmental gradient. A method of changing time scales, by using a periodic equation relating ecological to standard clock time unit, is presented.

The model has been applied to simulate phenological curves of population abundance for oribatid mites and *Collembola* from a Mediterranean ecosystem. The concept of "phase difference continuum" is introduced and the life history strategies of oribatids and *Collembola* are discussed.

Asymmetries as well as synchronizations in population development, annual periodicity and inter-annual stability, are common features for almost all populations studied, summer drought being the adverse period for the majority of them. Precocity, iteroparity and high rate of juvenile development into successive stages during the favourable period, hold for all phenological patterns. Adults' demographic parameters and the animals' ability for altering their physiological status are the characteristics discriminating between various strategies. Most *Collembola* display left-skewed phenology, while most oribatids display a right-skewed one.

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The temporal distribution of a population and the shape of its phenological pattern depend on the timing of a species' life cycle development, as well as on its activity. Phenology reflects, to an extent, the dynamics of a population in the field and, consequently, its demography. Furthermore, activity phenomena such as immobilization, vertical migration or aggregational behaviour, are of great importance for phenology, especially in the case of soil microarthropods. Therefore, phenology reflects also the physiological response of organisms to the fluctuations of the environmental variables. Thus, the description and interpretation of census data is a complex enterprise, involving the consideration of demographic as well as physiological adaptations.

The study of an arthropod's life cycle in strongly

seasonal environments, such as the mediterranean, involves the description of the synchronizations of their life cycle development with the oscillations of the environment. To some extent, this also holds for arthropods from moderately fluctuating environments.

The great number of available phenological data on soil arthropods from several ecosystems constitutes the starting point for further ecological surveys and studies. Many authors have tried to categorize arthropod phenologies into qualitative classification systems (e.g. Lebrun 1971, Wolda 1988). Unfortunately, little has been done with respect to the formulation of analytical models for the description and interpretation of their phenologies. In order to describe the timing of oribatid mites' life cycle in the field, Stamou (1986) proposed a

simple phenological model, which belongs to the Lotka-Volterra type of deterministic models. It yields bell-type symmetric curves and the description of the life cycle development is based upon the values of its parameters. This model was successfully fitted to census data concerning oribatid mites (Asikidis 1989, Stamou and Sgardelis 1989, Asikidis and Stamou 1992), sampled in regions with transitional climate between mediterranean and temperate. Due to asymmetries and discontinuities displayed by the phenologies, the model failed to fit census data for oribatids and collembolans from a dry Mediterranean ecosystem in Attiki (Sgardelis and Margaritis 1983), where sharp seasonal fluctuations of environmental variables were recorded. Non-symmetric phenograms are given also by other authors (e.g. Block 1966, Luxton 1981a), for soil microarthropods from temperate regions. Besides, most of Lebrun's (1971) phenogram types are also non-symmetric.

Non-symmetric phenograms can be simulated by changing the time scale. In fact, it is possible to delete graphically the asymmetry of phenograms by adjusting the scales of the time-axis whenever sharp density changes are recorded and vice versa. Changing time scales results in the definition of a new variable, termed ecological time, which is a function of the standard clock time. In this paper a method of changing time scales is presented and applied to non-symmetric census data for oribatid mites and collembolans. This technique also provides a methodology for a more or less objective analysis of phenological patterns, with respect to the synchronization of life cycle development.

## Ecological time

A known technique for changing time scales is by using physiological time (e.g. degree-day) instead of standard time (Cancela da Fonseca 1958, Mitchell 1977). By this method, initially equal intervals on the time axis become unequal. The technique takes into account the dependence of population development on environmental variables, particularly temperature and/or humidity. More elaborated versions of this method were suggested by Lebrun and Van Ruymbeke (1971) and Van Straalen (1985). Nevertheless, the use of physiological time demands a large research effort, since it involves equations relating the rate of population development to environmental variables, thus combining both field and laboratory data, which in general are not available when exploring only census data.

Our approach for changing time scales is based upon the following considerations: 1) the timing of a population in the field is determined by the sequence of demographic events, and 2) the rate of the demographic events depends on the fluctuations of environmental variables.

Thus, in equal time intervals, during different time

periods, different rates of demographic events may be recorded. The time interval during which a defined and constant number of demographic events (i.e. births plus deaths) occurs, is the unit of a new time scale, termed ecological time. Immigrations or specimens entering the active phase of their development are included in births, while emigrations or specimens entering the inactive phase of their development are included in deaths. In general, this new time scale is a curvilinear function of the standard clock time and should be considered as a complex environmental gradient. Thus, the concept of ecological time is more widely applicable, although abstractly defined, than that of physiological time, involving only temperature or/and humidity oscillations.

## Changing time scales

The model presented in this paper is based upon two assumptions: 1) population development with respect to ecological time, considered as an environmental gradient, can be described by a symmetric bell-type curve, and 2) the ecological time unit is a periodic function of the standard time one.

We should note that the first assumption of the model holds only in the case where the rate of change in the number of births and/or deaths, with respect to ecological time, is constant or bell-shaped, and consequently  $r$  (i.e. births minus deaths) displays a linear or sigmoid decline. Otherwise, population curves in ecological time are non-symmetric since the sum of births plus deaths, occurring in the ecological unit, is constant by definition. Nevertheless, this assumption was considered necessary for the sake of simplicity although exploration of different situations will be done in papers to follow. Besides, there is some evidence giving support to the above two hypotheses. As regards the first one, the response of organisms to environmental gradients is in general bell-shaped (Whittaker 1956), although other curve shapes are also possible. Lebrun and Van Ruymbeke (1971) also described a bell-shaped response of the acarid *Damaeus onustus* to changes in physiological time. As regards the second hypothesis, a bell-type relationship between the units of two time scales' is also assumed by Van Straalen (1985) who established successfully the relationship between standard clock time and physiological time for two collembolan populations.

Based on the above considerations, a model aiming to describe skewed phenologies can be implemented as follows:

Firstly, an equation relating the ecological time to standard time is established:

$$t_{ei} = f(t_i) \quad (1)$$

where  $t_{ei}$  = ecological time and  $t_i$  = standard time.

Concerning the form of Eq. (1), it was assumed that

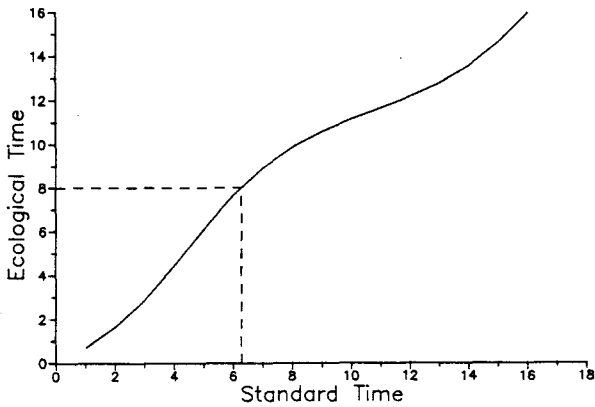


Fig. 1. S-type relationship of ecological to standard time yielded by a model producing right skewed asymmetric phenologies.

in seasonal environments a periodic equation may describe the relationship of the two time scale units:

$$f'(t_i) = \Delta t_c / \Delta t_i = \exp\{a_c + b_c \cos(2\pi(t_i - \varphi_c) / T_c)\} \quad (2)$$

where  $\Delta t_c$  = the ecological time unit with respect to the standard time one,  $\varphi_c$  = phase defining the maximum number of ecological time units, corresponding to the standard time one,  $T_c$  = period, and  $a_c$  and  $b_c$  constants. The ratio  $b_c/a_c$  defines the sharpness of the curve, while  $\varphi_c$  defines the time point where the length of the ecological time unit is minimum and, consequently, the rate of occurrence of the demographic events is maximum. According to the above definition, the ecological time unit appears to vibrate in relation to the standard clock time. Integration of Eq. (2) defines an S-type relationship of ecological to standard time (Fig. 1), the form of which depends on the ratio  $b_c/a_c$  and is equivalent to the empirical relationship of physiological to standard clock time found by Van Straalen (1985).

Secondly, a periodic function, which is the deterministic component of the model proposed by Stamou (1986), is fitted to the data; the formulation of the model was based upon considerations, relevant to Lotka-Volterra model building:

$$N(t_c) = \exp\{a + b \cos(2\pi(t_{ci} - \varphi) / T)\} \quad (3)$$

where  $N$  = population density,  $\varphi$  = phase determining the position of the population density peak with respect to ecological time,  $T$  = period,  $a$  and  $b$  constants (the ratio  $b/a$  defines the sharpness of the curve). By substituting  $t_{ci}$  from Eq. (2) to (3), a phenological model relating population size to standard time is obtained.

Thus, this method aims at establishing a relationship between ecological and standard time, fitting a symmetric curve in ecological time to the raw data and plotting the results against standard clock time. This may result in the appearance of non-symmetric graphs,

the form of which depends on the parameters in Eq. (1). In the case we report here, the form of the graphs depends on the phase difference  $\varphi - \varphi_c$ , given that  $b_c > 0$ .

The model contains eight parameters. Parameters  $\varphi$  and  $T$  are estimated in terms of ecological time, and parameters  $\varphi_c$  and  $T_c$  in terms of standard clock time. In order to refer to a unique time scale, namely standard clock time, parameters  $\varphi$  and  $T$  should be expressed with respect to this time scale. The graphical solution of this problem involves graphs relating ecological to standard time (e.g. in Fig. 1, 8 ecological time units correspond to 6.28 standard time units). The algebraic solution can be reached by using numerical techniques (see below).

In order to describe phenology, parameters  $\varphi$  and  $\varphi_c$  are of particular interest. The former defines the exact time at which the population density peaks and the latter defines the exact time at which the rate of occurrence of the demographic events is highest. Consequently, their difference,  $\Delta\varphi = \varphi - \varphi_c$ , defines the position of the time interval where demographic events are most strongly condensed with respect to the population density peak. For  $\Delta\varphi > 0$ , the highest rate of demographic events coincides with the period of increasing population density, resulting in right skewed asymmetric phenograms, while for  $\Delta\varphi < 0$ , the highest rate of demographic events coincides with the period of decreasing population density, resulting in left skewed asymmetric phenograms. Finally for  $\Delta\varphi = 0$ , symmetric graphs, either sharp or flat, are produced.

The difference between parameters  $T$  and  $T_c$  is also of interest, since in relation to the magnitude of this difference, successive cycles of population development may exhibit considerable differences in skewness. Further parameters, facilitating the description of life cycle development, are also estimated:  $R_{11}$ ,  $R_{12}$  = are interpreted as the phenograms' inflection points, that is the time points where the rate of population change either speeds up or slows down and the first derivative of Eq. (3) is maximum.  $M_{11}$ ,  $M_{12}$  = are interpreted as the time points between which population size is above the overall mean density ( $M = M_{12} - M_{11}$  is the time period during which the population size is above the overall mean density). SK% is equal to  $(\varphi - M_{11}) / (M_{12} - M_{11})$ . This latter parameter defines the skewness of the graph and varies in the range 0–100%. For SK% < 50 the graph displays right skewed asymmetry, for SK% > 50 it is left asymmetric, while for SK% = 50 the graph is symmetric.

The model was fitted to data and parameters were estimated by using numerical techniques. For  $t_{ci} = f(t_i)$ , where  $i = 1, 2, \dots, n$ , given as a time vector and for a given set of  $T$  and  $\varphi$ , the parameters  $a$  and  $b$  were estimated by least-square regression (log-transformed data). Further parameters were also numerically estimated. Finally, the goodness-of-model fit was tested by using Analysis of Variance techniques (a computer program for parameter estimation and model fitting test is available upon request).

Table 1. The parameters of the phenological model fitted to 7 oribatid mite and 10 collembolan species from a Mediterranean ecosystem (for definition of parameters see text).

	T	T <sub>c</sub>	φ	φ <sub>c</sub>	Δφ	b/a	b <sub>c</sub> /a <sub>c</sub>	R <sub>0</sub>	R <sub>11</sub> , R <sub>12</sub>	M <sub>11</sub> , M <sub>12</sub>	M	SK%
<b>Oribatidae</b>												
<i>Micropoppia minus</i>	6.3	4.6	0.9 7.1 13.4	0.7 5.3 9.9	0.2 1.8 3.5	0.66	-5.4	0.39	-3.0 5.4-8.8 12.2-	-2.7 5.7-8.7 12.4-	- 3.0 -	- 47 -
<i>Multioppia</i> sp.	10.9	10.8	2.4 13.3	1.9 12.7	0.5 0.6	0.42	-1.88	0.62	1.1-4.1 12.0-	1.3-3.7 12.2-	2.4 -	46 -
<i>Hermaniella granulata</i>	10.4	14.9	2.8 13.2	-0.6 3.4	3.4	0.70	-15.30	0.74	1.0-6.7 11.7-	1.2-6.3 11.8-	5.1 -	31 -
<i>Eupelops</i> cf. <i>halophilus</i>	9.1	9.5	2.8 11.9	2.4 11.9	0.4 0	0.73	-2.13	0.59	1.5-4.1 11.0-13.5	1.7-4.0 11.1-13.4	2.3 2.3	48 35
<i>Oribatula</i> sp.	13.1	11.4	2.3 13.1	3.6 13.1	-1.3 0	0.74	-2.18	0.51	-0.5-3.3 12.3-	-0.2-3.2 12.5-	3.4 -	74 -
<i>Tectocephus velatus</i>	10.3	11.0	3.3 13.6	4.0 15.0	-0.7 -1.4	0.43	-4.02	0.60	1.3-4.4 10.6-	1.4-4.3 11.1-	2.9 -	66 -
<i>Licnodamaeus pulcherrimus</i>	10.1	10.1	3.0 13.1	3.0 13.1	0 0	0.42	-1.35	0.78	2.2-3.8 12.2-	2.4-3.6 12.3-	1.2 -	50 -
<b>Collembola</b>												
<i>Sphaeridia pumilis</i>	6.2	6.2	5.9 12.1	6.7 12.9	-0.8 -0.8	0.82	-8.79	0.44	4.6-7.0 11.2-13.5	5.1-6.6 11.3-12.8	1.5 1.5	53 53
<i>Cryptopygus bipunctatus</i>	11.7	10.9	12.1	13.0	-0.9	1.22	-2.01	0.83	8.2-12.9	11.0-12.8	1.8	61
<i>Xenylla</i> sp.	10.9	9.6	4.7	7.0	-2.3	0.82	-14.07	0.61	0.8-6.9 13.5-	1.6-6.5 14-	4.9 -	63 -
<i>Metaphorura bipartita</i>	14.7	9.4	12.1	13.4	-1.3	1.29	-2.98	0.65	4.9-13.8	5.6-13.3	7.7	84
<i>Ceratophysella engandinensis</i>	11.6	11.3	9.8	11.0	-1.2	1.00	-24.35	0.85	7.2-11.8	7.7-11.5	3.8	55
<i>Folsomia quadrioculata</i>	13.0	11.2	10.8	11.1	-0.3	1.12	-3.28	0.86	5.4-13.4	7.3-12.6	5.3	66
<i>Parisetoma notabilis</i>	12.9	12.6	10.8	10.9	-0.1	1.09	-3.84	0.62	6.5-13.6	7.6-12.2	5.6	57
<i>Isotomurus palustris</i>	13.0	12.6	11.1	13.0	-1.9	1.14	-3.88	0.70	6.8-13.0	8.6-12.5	3.9	64
<i>Onychiurus meridiatus</i>	12.0	13.1	7.1	4.7	2.4	1.15	-3.64	0.61	4.9-13.1	5.1-11.6	6.5	31
<i>Orchesella irregularilineata</i>	10.9	9.9	2.7 13.6	2.7 12.6	0.0 1.0	0.69	-3.83	0.40	0.7-4.7 11.7-16.6	1.0-4.5 12.1-16.2	3.5 4.1	49 37

## Case studies

The model was applied to simulate non-symmetric census data, concerning eight oribatid and eleven collembolan species, sampled at monthly intervals in a Medi-

terranean ecosystem (Hortiatis, Northern Greece). For the description of the study area and the sampling design, see Asikidis and Stamou (1991). Population dynamics of three other oribatid species from the same community have been given elsewhere (Asikidis and

Table 2. The demographic characteristics of populations displaying right-skewed, left-skewed and symmetric phenologies.

Left skewed phenology	Right skewed phenology	Symmetric phenology
Precocity	Precocity	Precocity
Iteroparity	Iteroparity	Iteroparity
High rate of juvenile development into next stadia during the favourable period	High rate of juvenile development into next stadia during the favourable period	High rate of juvenile development into next stadia during the favourable period
Small number of eggs overcoming adversity	Large number of eggs overcoming adversity	Either small or large number of eggs overcoming adversity
Evenly distributed reproductive effort during adulthood	Unevenly distributed reproductive effort during adulthood	Evenly distributed reproductive effort during adulthood or confined in short time periods
Right convex adult survivorship curve	Left convex or linear adult survivorship curve	Right convex or S-type adult survivorship curve

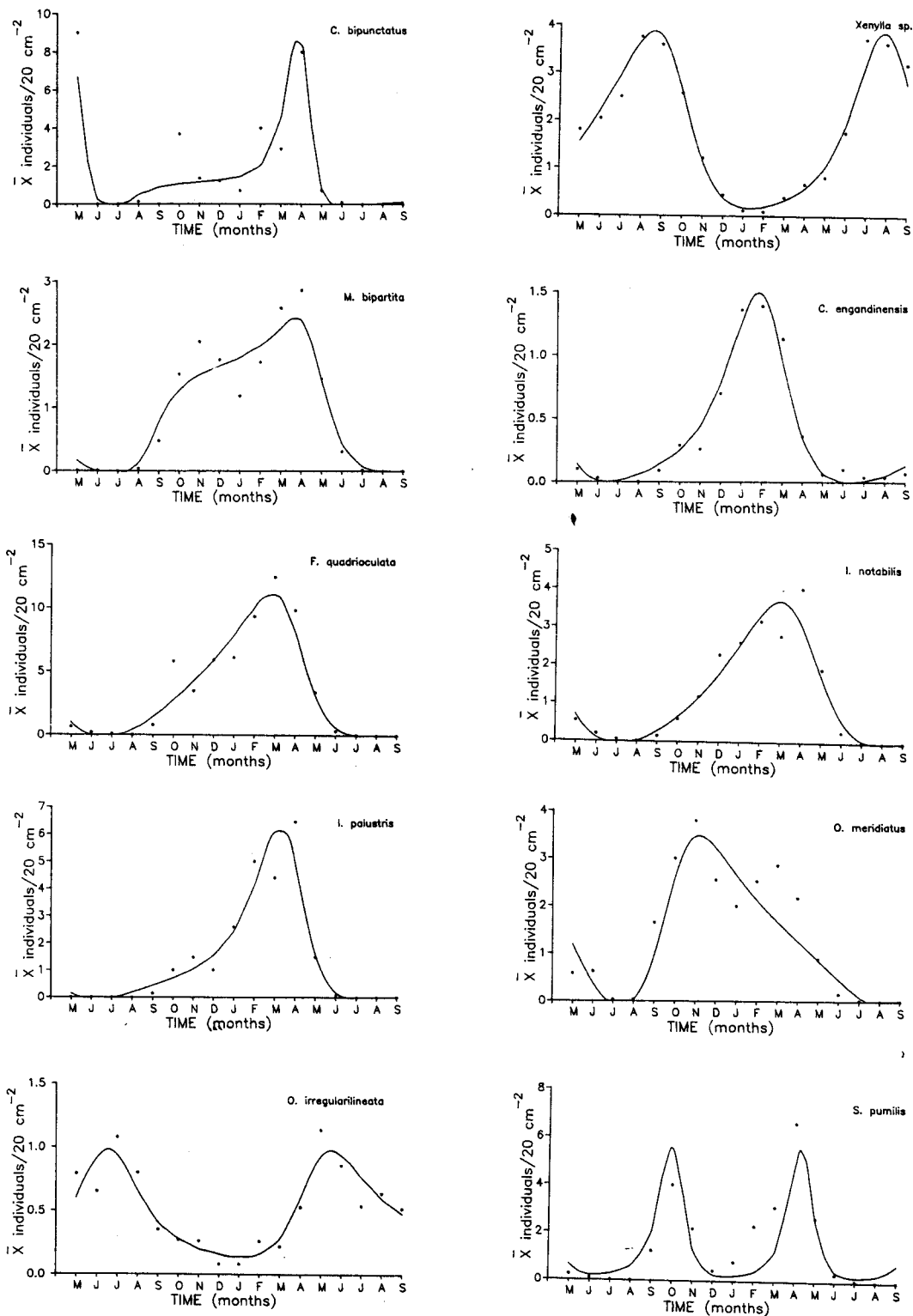


Fig. 2. The fitting of the model to census data for collembolan populations from a Mediterranean ecosystem.

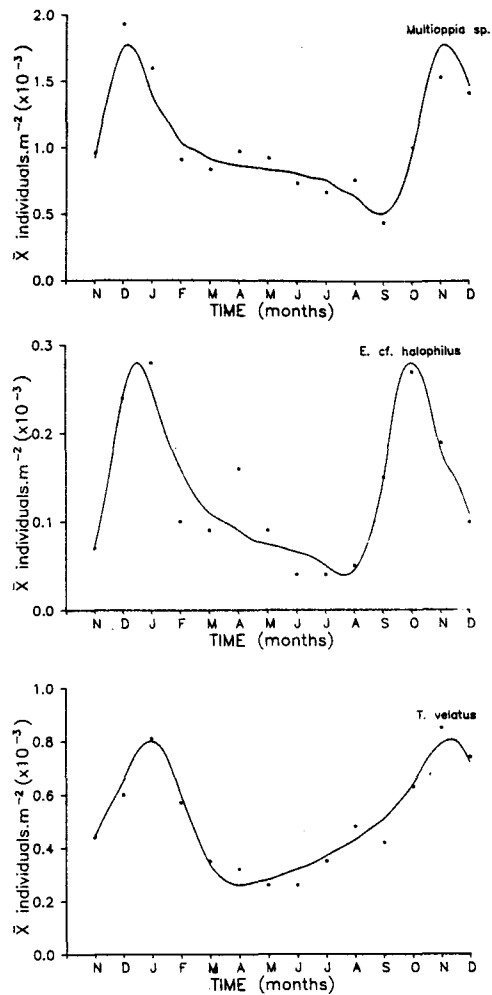
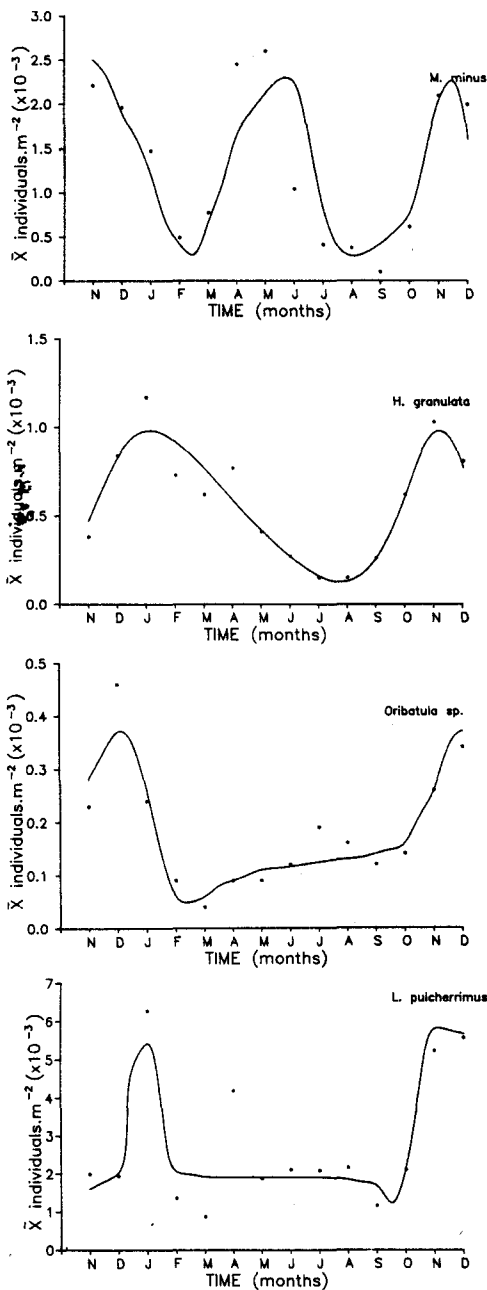


Fig. 3. The fitting of the model to census data for oribatid populations from a Mediterranean ecosystem.

Stamou 1992). As regards the remaining collembolan and oribatid species of the community, which are not presented here, it was difficult to model their phenology due to their small numbers as well as to their discontinuous appearance in samples. The results of the simulation are given in Table 1 and Figs 2 and 3. Coefficients of determination  $R_0$ , measuring the goodness of fit of the model, are also given.

### Collembola

No extensive discrepancies between the parameters  $T$  and  $T_c$  were determined. Thus, phenograms appeared relatively stable with respect to time. All collembolan species but one (*Sphaeridia pumilis*) displayed annual periodicity and can be classified into one of three phenological types. Most species with annual periodicity, *Cryptopygus bipunctatus*, *Xenylla* sp., *Metaphorura bipartita*, *Ceratophysella engandinesis*, *Folsomia qua-*

*drioculata*, *Parisotoma notabilis* and *Isotomurus palustris*, displayed left-skewed phenology. *Onychiurus meridius* and *Orchesella irregularilineata* displayed right-skewed phenology, whereas *Pseudocoinella albida* was the only representative of the flat-type phenology. Since in the latter case the model did not fit significantly, the results of this simulation are not given here. Finally, *Sphaeridia pumilis* with six-month periodicity, displayed also left-skewed asymmetric phenology.

The model revealed synchronization of the life cycle development of most species. Indeed, for most species the development of the life cycle starts in October–November and comes to an end in August–September. For six out of seven species, with left asymmetry and annual periodicity, the model revealed a density peak in late winter – early spring. Density of *O. meridius* peaks in autumn, while that of *S. pumilis* peaks twice a year, in autumn and in spring. *Xenylla* sp. and *O. irregularilineata* are summer-dwelling species, the first peaking at the end of the drought period, while the latter peaks earlier in the season. Besides density peaks, density inflection points also coincide.

There is a clear synchronization in the occurrence of demographic events. For most species, the higher density of the demographic events coincides with the beginning of the drought period, leading to a rapid reduction of the population size. Exceptions are *O. meridius*, where the high density of demographic events at the end of the drought period leads to a rapid recovery of the population, and the two summer species *O. irregularilineata* and *Xenylla* sp., with condensed ecological time at the beginning and end of the drought season, respectively. For *S. pumilis*, the rate of occurrence of demographic events peaks twice a year, at the end of the favourable seasons, e.g. in autumn and in spring.

Differences within the phenological patterns mainly refer to the duration of population activity in the field. *M. bipartita*, whose density remains above the annual arithmetic mean for 7.7 months and *C. bipunctatus*, whose density exceeds the annual arithmetic mean for only 1.8 months, were the extreme cases.

## Oribatids

In general, no extensive discrepancies in parameters  $T$  and  $T_c$  have been recorded and the phenograms appeared relatively stable with respect to time. All oribatid species but one (*Micropoppia minus*), displayed annual periodicity. They can be classified into three phenological types. Four species, *M. minus*, *Multioppia* sp., *Hermaniella granulata*, and *Eupelops* cf. *halophilus*, displayed right-skewed phenology. *Oribatula* sp. and *Tectocephus velatus* have left-skewed asymmetric dynamics, while *Licnodamaeus pulcherrimus* displayed an acute symmetric phenogram. Finally, *Sphaerochthonius splendidus* displayed hazardous oscillations and the model failed to fit to the data.

The model revealed synchronization in the life cycle of most species. Indeed, the density peak of all species with annual life cycles occurs in late autumn – early winter. For most species, condensed ecological time, i.e. high rate of demographic events, is recorded in autumn resulting in a rapid increase of the population size and a right asymmetry, while a high density of demographic events occurring later in winter, leads to a rapid reduction of the left asymmetric populations.

Population size of all species exceeded the overall mean annual density for a shorter period than that of the collembolan populations (from 1 to 1.4 months).

## Discussion

The goal of this paper was to formulate a general model for interpreting non-symmetric census data. Population dynamics can be described by using either clock time (standard time) or the timing of demographic events (ecological time). The relationship between these two time scales depends on the demographic as well as the physiological response of each species to the environmental variables. Thus, the dynamics of each population are characterized by a specific ecological time scale.

Beyond describing the asymmetry of census data, the method provides empirical equations relating ecological to standard time, and thereby allows the identification of the time gradient. In the case we report here, bell-shaped models, relating the time units, showed a good fit to census data. Towards the middle of the bell-shaped curves, ecological time is more dense than standard time, while the opposite happens towards the edges of the curve.

The consideration of the time gradient has direct methodological implications. In ordinary phenograms interpretations are drawn either from the mere inspection of the peaks of the phenograms (Mitchell 1977, Luxton 1981a), or from the examination of graphs of smoothed raw data (Block 1966), or even from the consideration of the parameters of phenological models (Stamou and Sgardelis 1989). In the new graphs the interpretations are based on the relationship of the two time scales. Consequently, biological interpretation is possible on the basis of a univocally defined variable  $t_{ei} = f(t_i)$  and the parameters of the equation relating these two time scales. This enables the consideration of the life cycle in a more integrative way, whereas the demographically meaningful parameters and ratios can be used to compare the characteristics of different populations.

The consideration of the phenograms of some soil arthropods from mediterranean areas may illustrate our point of view. In Mediterranean type ecosystems population dynamics and activity are controlled by strongly oscillating humidity and temperature conditions. Many authors (Sgardelis and Margaritis 1983, Pantis et al. 1988,

Sgardelis 1988, Asikidis 1989, Iatrou 1989, Asikidis and Stamou 1991) attributed the observed discontinuities in population development during the transition from the favourable to the unfavourable seasons and vice versa to environmental thresholds. In this paper, a continuous function describes the relationship between ecological and standard time. This means that discontinuities are attributed to a strongly condensed period of ecological time in relation to standard time, that is, to differences in time scales.

The three types of phenological curves can be related to the principal adaptations of Acari and Collembola in Mediterranean ecosystems, and the discussion of their life history strategies can be based on the consideration of the phase difference continuum  $\Delta\phi$ , instead of the  $r, K$  continuum. The consideration of soil microarthropods' life history strategies are as yet fragmentary (Mitchell 1977, Kaneko 1988). In our opinion, this is due to the fact that the demographic characteristics of oribatids and collembolans hardly fall on the plane of  $r, K$  and  $A$  strategies defined by Greenslade (1983). Most authors make efforts to describe the synchronizations of microarthropods' life cycles with oscillating environmental variables, by searching for the triggering factors controlling life cycle development (e.g. Luxton 1981a,b). The consideration of the phase difference continuum is part of this attempt.

Regarding the demographic characteristics of soil arthropod populations corresponding to the three phenological curves, we suggest the following:

Right-skewed phenology refers to species adapted to recover rapidly after an adverse period. For these species, ecological time is more dense than standard time during the increase of population size. Thus, the rapid recovery of the population could be a result of eggs hatching which have been deposited in high numbers at the beginning of the adverse period, as well as the high rate of juvenile development into adult stadia, which in turn give birth to new offspring. The even decline in population size after the density peak indicates a reduced reproductive effort of later adult stadia, as well as a left-convex or linear adult survivorship curve.

Left-skewed phenology refers to species adapted to respond rapidly to adversity and recover slowly after it. Ecological time is condensed during the decreasing phase of population size. The even increase in population density indicates a small number of eggs overcoming adversity, a high rate of juvenile development into adult stadia and an evenly distributed reproductive effort through adulthood. A right-convex adult survivorship curve accounts for the rapid decline in population size, during the transition from the favourable to the adverse period.

A rapid development of juveniles into adult stadia, coupled with a right-convex or S-type adult survivorship curve, results in a symmetric phenology. The reproductive effort could either be confined to short periods (sharp phenograms), or evenly distributed through

adulthood (flat phenograms). Respectively, the number of eggs, hatching after the end of the adverse period, could be either low or high. Thus, precocity, iteroparity and high rate of juvenile development into adult stadia during the favourable period, are common characteristics for the three phenological types, while the characteristics discriminating strategies refer to the adults' demographic parameters, namely the number of eggs deposited at the beginning of the adverse period, the distribution of reproductive effort over time and the survivorship curves. Our experimental data (Asikidis 1989, Argyropoulou unpubl.) are in agreement with the above suggestions.

Besides adult demographic characteristics, the animals' ability to alter their physiological status, like quiescence in oribatids (Stamou 1989) and anhydrobiosis in Collembola (Poinot-Balaguer and Barra 1978), could be of considerable importance, especially in the flat-type phenology. Furthermore, other population features such as a broad habitat selection, that is, the ability for vertical and horizontal movements towards protected microsites, e.g. beneath stones (Sgardelis 1988), coupled with food specialization (Cancela Da Fonseca and Poinot-Balaguer 1983, Stamou and Asikidis 1992), are also important for microarthropod life cycle synchronization with environmental imperatives.

Comparing the phenologies of Collembola and oribatids in Mt Hortiatitis, it is possible to conclude that asymmetries characterize their life cycle development. Most collembolan species peak in late winter – early spring and display left-skewed phenology, while most oribatid species peak in late autumn – early winter, displaying right-skewed phenology. Seasonality and predictability, which are typical characteristics of the Mediterranean ecosystems, result in synchronization, as well as in inter-annual stability, of population and life cycle development for both collembolan and oribatid species. Annual periodicity is also a common feature for almost all the populations studied (fifteen out of seventeen). Summer drought is the most important environmental stress for the majority of the species, while winter is the adverse period for a few of them. The relatively low rate of immature development of oribatids, compared with collembolans, and the capacity of their earlier life stages to develop slowly, even during the adverse period (Asikidis and Stamou 1991), results in an age structured cohort overcoming adversity, whereas this is not the case with Collembola. In the case of the latter, the cohort consists either of eggs deposited at the beginning of the adverse period or of animals which have entered the state of anhydrobiosis. Thus, the density of oribatids peaks soon after the summer drought, while the density peak for most Collembola occurs later in the year. It seems likely that in oribatids, the energy consuming distribution over life stages of their adaptive capacity against adversity is compensated by lower mortality rates of these stages, while the inverse happens in Collembola.



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