

POPULATION DYNAMICS OF THE TWO-SPOTTED SPIDER MITE: AN AGE-STRUCTURED MODELA. Astudillo Fernandez¹, T. Hance², G. Van Impe² and J.L. Dencubourg¹¹ Unit of Social Ecology, Université Libre de Bruxelles CP231. bvd. du Triomphe, 1050 Bruxelles, Belgium² Unité d'Ecologie et de Biogéographie, Université Catholique de Louvain. Croix du Sud, 4-5 (Carnoy) 1348 Louvain-La-Neuve, Belgium**Abstract**

It is well known that the age structure of a founding population of spider mites can highly influence the subsequent growth of the colony. In order to study this topic, a mathematical model for the population growth of *Tetranychus urticae* is presented. Existing age-structured models are based on life tables, which are heavy to use. Our aim is to synthesize the information contained in life tables, in order to make it more suitable for theoretical research. The experimental data used to parameterize the model was obtained from 214 mites, living on bean plants at 24°C. Age-specific mortality and fertility rates were fitted to curves. This allowed them to be incorporated into the model as mathematical functions of age, instead of tabulated values. Computation of the model gives an insight on the effect that initial conditions have on population growth. Furthermore, the simplicity of the model makes it an appropriate theoretical tool to study the consequences of phenomena affecting age-structure such as migration or the Allee effect.

Key wordsexponential growth, *Tetranychus urticae*, mathematical modelling, fertility, mortality**Introduction**

Since the use of insecticides and fungicides became a common practice in agricultural systems, cultivators have had to deal with ravaging outbreaks of spider mites (Acari: Tetranychidae). These phytophagous mites that feed by sucking out the content of leaf cells, can destroy vast cultures in just one summer (Walter and Proctor 1999). Their success is mainly due to their varied and efficient dispersal behaviours (Hussey and Parr 1963) and to their outstanding population growth potential (Sabelis, 1981). In this paper, the latter is studied through the approach of mathematical modelling. The species chosen for this study is *Tetranychus urticae*, the two-spotted spider mite,

as it is among the most economically important and documented spider mite pests.

At the beginning of a ravaging process, quantity of food can be seen as unlimited and the population can be considered to grow exponentially. The well-known model for exponential growth (Turchin 2003) includes a constant growth rate r , defined as the intrinsic rate of natural increase (Birch 1948).

$$\frac{dN}{dt} = rN$$

In a population composed of individuals of different ages (hence, of different fertility and mortality potentials), the intrinsic rate of natural increase can only be constant over time if the age

structure of the population is also constant over time (Birch 1948). This stable age distribution (hereafter referred to as SAD) can be calculated from the life tables. In spider mite species the stable age distributions are quite similar and roughly average 66% of eggs, 26% immature and 8% adult (Carey 1982).

In the particular case of *Tetranychus urticae* during an outbreak, the assumption of stable age distribution is hardly ever verified. Besides the fact that founding colonies are too small to have a SAD, their composition is determined by processes that affect age-classes differently. The large part of individuals alive in early summer is wintering individuals (diapause). Diapause is only induced on adult females (Veerman 1985), particularly at very young age (Raworth 2007). Founding mites can also be migrants and it has been shown that preovipositing females have a more pronounced tendency to migrate than other stages (Hussey and Parr 1963, Yano 2008). Such founding populations, mostly composed of adult females, are thus far from the SAD.

Over time, any population eventually converges to its stable age structure. However, at local population level, this situation is never encountered because spider mite populations grow so rapidly that the host plant is killed before SAD can be reached (Hance and Van Impe 1999). Furthermore, age-structure is constantly altered by events that affect only certain age-classes (Carey 1983). A typical example is natural acarine predator *Phytoseiulus persimilis* that shows a clear preference for eggs (Blackwood et al. 2001).

The exponential growth model is therefore not sufficient to describe population growth of *Tetranychus urticae* under the conditions that concern us, and age-structure must be taken into account.

Our major objective is to formulate a mathematical model that describes the evolution of an age-structured population in time, starting from a given age distribution, so as to give basic output like the intrinsic growth rate, the SAD, or the amount of time needed to reach it. Moreover, it should give insight into less trivial questions such as what are necessary initial conditions to ensure growth or to quantify the effects of different founding age-structures. Finally, we intend to complete the understanding of population dynamics of *Tetranychus urticae*, as it is fundamental to study topics such as collective choices and Allee effect.

Experimental data

Data used to parameterise the model was gathered from Van Impe's previous work (1985), where a more detailed description of the methods can be found. Experiments were carried out under constant temperature (24°C) and constant relative humidity (85%).

Two hundred fourteen female deutonymphs of same age (± 4 hours) were placed individually on bean leaf discs (4 cm²). The following day, they entered their final quiescent stage (theleiochrysalis) and 4 males were placed on each disc in order to ensure mating at eclosion. One day after, all female adults had emerged and it is considered day one of the experiment. From this point onwards, every day at the same time, each living female was transferred to a new leaf disc. Eggs on the old disc were counted. The offspring of 101 females (a total of 5760 larvae) was kept for further observations on immature development.

Longevity, oviposition period and daily number of eggs were collected for each female. Offspring observations provided data on immature survival and age-specific sex ratios.

Formulation of the model

Few simplifications are made. First of all, only the female population is modelled. In terms of birth rate, the number of males can be ignored if we consider that all females are fertilised (Hance and Van Impe 1998). Indeed, although females usually outnumber males (Krainer and Carey 1991), occurrence of virgin females is very low (Potter, 1978). Secondly, only three events of life history are taken into account: birth, oviposition, and death.

The first step was to find the mathematical expressions that best described fertility and mortality as functions of age. Experimental data was fitted to its corresponding curve with the least squares non-linear method (MATLAB). Mortality rates at late ages were calculated on a small number of individuals and can present aberrant values. We avoided that problem by fitting the survival curve rather than the mortality curve. Statistics of the fits are summarised in Table 1. Mortality $m(a)$ was deduced from survival $s(a)$ according to the following relation (Gross & Clarke 1976), with a = age.

$$\frac{ds}{da} = m(a)s(a)$$

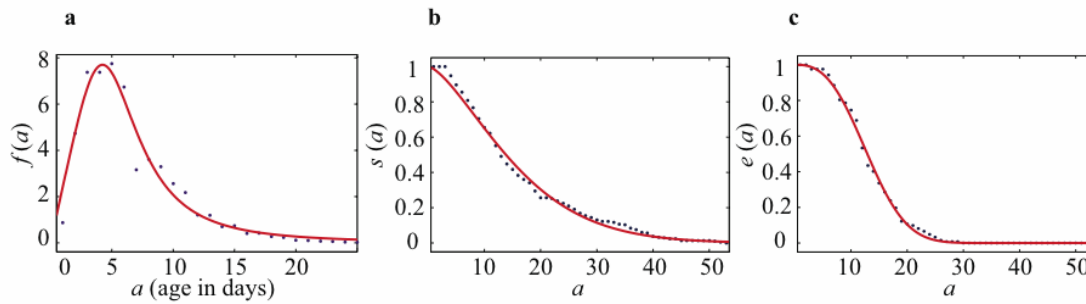


Figure 1. Experimental data (blue dots) and fitted curves (red) for the 3 life events considered. (a) f is Daily number of female eggs per female as a function of adult age a (in days). (b) s is the proportion of individuals reaching adult age a . (c) e is the proportion on females still ovipositing at adult age a .

Table 1. Summary of the curve fits.

| Fertility (a) | Survival (b) | Oviposition (c) |
|--|--|--|
| $f(a) = \frac{\alpha \cdot a}{\beta + a^\sigma}$ | $s(a) = \exp(-\gamma \cdot a^\mu)$ (survival) $m(a) = \gamma \cdot \mu \cdot a^{(\mu-1)}$ (mortality) | $e(a) = \exp(-\lambda \cdot a^\theta)$ $o(a) = \lambda \cdot \vartheta \cdot a^{(\vartheta-1)}$ |
| Parameters (with 95% confidence intervals) | | |
| = 2591 (426.1, 4755) = 1075 (106.8, 2043) = 4.057 (3.659, 4.455) | = 0.0145 (0.0115, 0.0175) = 1.471 (1.401, 1.541) | = $6.984 \cdot 10^4$ (9.149, 4.819) $\cdot 10^4$ = 2.697 (2.582, 2.813) |
| Statistics | | |
| SSE = 7.281 Adjusted R^2 = 0.9668 | SSE = 0.03638 Adjusted R^2 = 0.9929 | SSE = 0.016 Adjusted R^2 = 0.9976 |

One way to model age-structured populations is with partial differential equations defining the evolution of the number of individuals of continuous ages in continuous time (McKendrick 1926). It is an elegant formulation because with just one equation (equ. 1) and the set of initial conditions (equ. 2), it can account for complex dynamics of an age-structured population.

$$\frac{\partial N(t,a)}{\partial t} = -m(a)N(t,a) - \frac{\partial N(t,a)}{\partial a} \quad (1)$$

with $N(t,a)$ = number of individuals of age a at time t , and $m(a)$ = mortality function. The initial population structure is $N(0,a)$, and the number of births is given by

$$N(t,0) = \int_1^{a_{\max}} f(a)N(t,a) \quad (2)$$

However, this formulation entails technical difficulties surrounding partial differential equations such as i.e. heavy numerical resolutions or existence and uniqueness of solutions (Cushing1998). Therefore we will use the corresponding discrete equation (eqs.3 and 4).

$N_{t,a}$ is the number of individuals of adult age a at time t . It is given by the number of individuals of age $a-1$, at time $t-1$ minus those that died.

$$N_{t,a} = N_{t-1,a-1} \cdot (1 - m(a-1)) \quad (3)$$

The number of individuals of age 1 (births), is given by

$$N_{t,1} = \sum_i N_{t-1,i} \cdot f(i) \quad (4)$$

Before adulthood (the first 10 days), mortality and fertility are considered null. Survival of immature stages is implicit in fertility rates as fertility rates represent female offspring that actually reached adulthood. From age 11 onwards, mortality and fertility are given in table 1.

The total population at time t is given by equation (5).

$$N_t = \sum_a N_{t,a} \quad (5)$$

Most females (57%) stopped laying eggs because they entered senescence, and not because they died. We test to what extent senescence affects the population dynamics by incorporating it into the model. We fitted the proportion of females still able to lay eggs as a function of age ($e(a)$, Table 1). The number of births in this model becomes:

$$N_{t,1} = \sum_i N_{t-1,i} \cdot e(i) \cdot f(i) \quad (6)$$

Finally, a Monte-Carlo simulation of the model is

computed. At every time step, each individual of the population has a probability of dying given by the mortality function. Offspring is given by the value of the fertility function rounded up to the nearest integer. We make stochasticity intervene only in deaths, and use mean values for fertility. The reason for this is that our experimental data did not reveal a clear pattern of deviation from the mean, it was impossible to make an objective choice on what distribution to chose.

Results

Regardless of initials conditions, population structure undergoes damped oscillations for a certain amount of time (Fig. 2). It exponentially converges to stable age distribution. It is impossible to tell at which point it reaches SAD, because in theory the oscillations continue indefinitely, and their perception only depends on the scale of the observations. It is very clear nevertheless that if a population is founded by one female (as in Fig. 2), the population remains far from SAD for at least the first 50 days. This is true whether we incorporate senescence into the model or not.

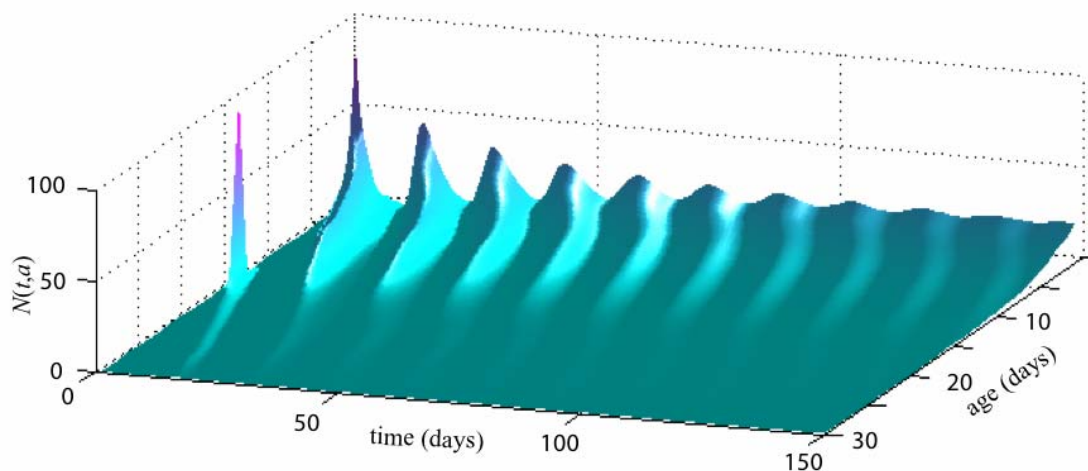


Figure 2. Evolution of the age-structure of a population with time. In this case, the founding female is 14 day old.

Stable age distribution is usually given in percentage of eggs, immatures and adults. In the case without senescence, it is 61.7 % of eggs, 29.9 % of immatures and 8.4 % of adults (Table 2). The rate of increase of the population also oscillates as it converges to the intrinsic rate of natural increase, here $r = 0.265$.

When it is far from SAD, population grows in pulses

corresponding to peaks of oscillations in the growth rate. The evolution of population size greatly depends on initial conditions of age structure. We compared the growth of populations founded by one single female of different ages (Fig. 2). It appears that there is an optimal age to start a population, but it depends on the day when the size of the population is measured. For example, the largest size on day 13 is reached by a 11 day-

old founding female. On day 15 however, the largest size is obtained by a 14 day-old founder. From there onwards, the largest population is always the one founded by a 14 year old.

Table 2. Comparison of the SAD and the intrinsic rate of natural increase obtained with the general model, and the senescence model.

| General model | | With senescence | |
|---------------|-------|-----------------|-------|
| $r = 0.265$ | | $r = 0.261$ | |
| SAD | | SAD | |
| eggs | 61.69 | eggs | 61.27 |
| immatures | 29.88 | immatures | 30.07 |
| adults | 8.43 | adults | 8.66 |

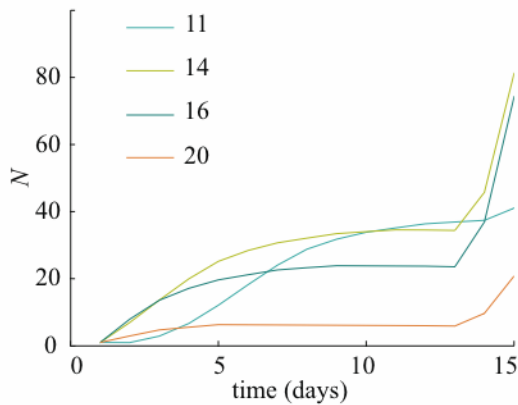


Figure 3. Sizes of populations founded by one female over time. Different colours correspond to different ages of the founders.

Growth by pulses is faster than the exponential growth of SAD populations. Figure 3(a) shows that the population size of a colony founded by 14 days old females is always larger than the size of a population founded by the same number of females, distributed according to SAD. Fig 3b shows that the size of the population growing by pulses can be up to ten times higher than the population with an exponential growth.

If we consider senescence in the model, the value of r slightly decreases and the composition of SAD weakly changes (Table 2). Consequently, colony size reaches lower numbers when senescence is integrated in the model. The greater the age of the founders, the bigger the difference between the results of the two models. Nonetheless, in the first 30 days, the ratio between the two is never higher than 1.25 (Fig. 5).

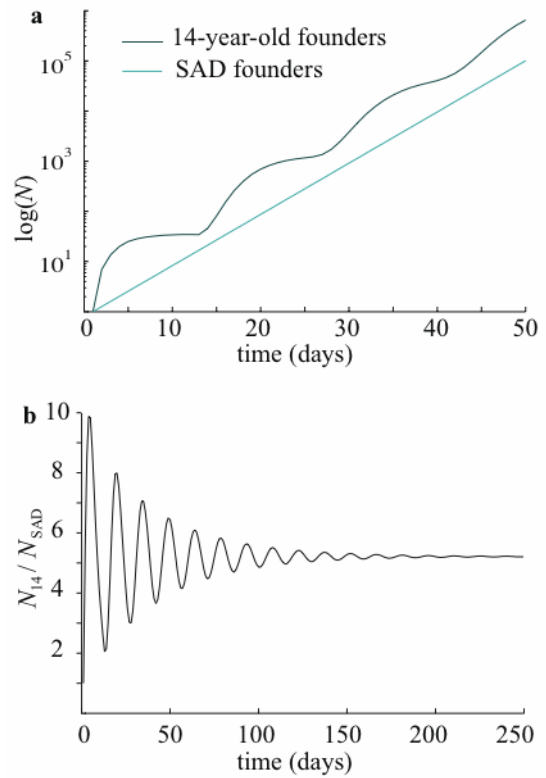


Figure 4. Comparison of populations founded by a stable-age-distributed colony and by 14 day-old. (a) Population size of the two populations (in logarithmic scale) (b) The ratio between the two populations.

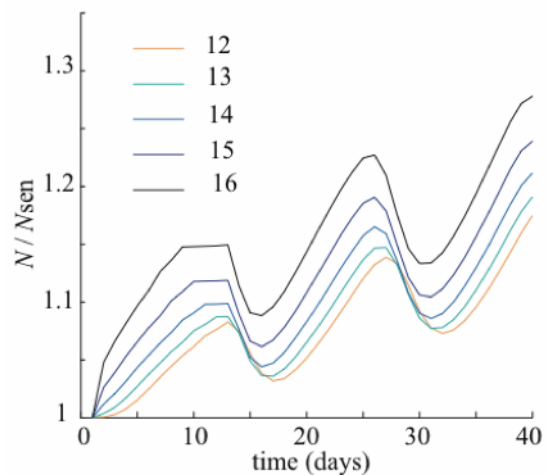


Figure 5. Ratio between the population size calculated with the general model and the population size calculated with the senescence model. Different colours represent different ages of the female founder.

Monte-Carlo simulations show that as long as there is an ovipositing female among the founders of a colony, it will almost inevitably grow. It is easy to understand from a probabilistic point of view.

Even the oldest ovipositing female (24 days old) has a probability of dying of $P=0.074$. The condition for extinction is that she dies before laying an egg. Otherwise, the condition is that the egg dies during preoviposition ($P=0.021$). As the number of conditions for extinction increases, the probability decreases. Therefore, even the most likely scenario for extinction has a very low probability ($P=0.074$).

Discussion

We present mathematical functions that describe the pattern of age-specific mortality and fertility rates of *T. urticae*. However, the relevance of the model is not restricted to *Tetranychus urticae* under our experimental conditions. We tested the goodness of fit of these functions on other spider mite life tables (Gutierrez & Chazeau 1972, Hamilton *et al* 1986, Laing 1969) and obtained very good results (R^2 always above 0.9). Moreover, our equations fit well ($R^2 > 0.9$) to life tables of other taxa, like the plant louse *Aphis fabae* (Hance 1990). Life tables represent a key tool in pest control. Synthesising the information they contain by modelling the fertility and survival data could improve and facilitate their use in pest management.

This study confirms that the outbreak potential of *Tetranychus urticae* can be explained by its population dynamics. First of all, the composition of founding populations (in the field as in greenhouses) is mostly composed of young females (Parr and Hussey 1966, Yano 2008). Our model corroborates that females in their first days of oviposition are precisely optimal founders, in terms of ensuring rapid growth. As a consequence of the initial composition of populations, these populations remain far from SAD (Carey 1983). We showed that even in conditions where nothing interferes with age-structure besides deaths and births, SAD is not reached in the first two months. This deviation from SAD allows populations to increase by pulses, which guarantees faster growth than with the classical exponential law. Finally, we pointed out that the stochastic aspect of death is not sufficient to cause extinction of a founding population.

Age-structure and its dynamics have been included in various growth models. Lewis (1942) and Leslie (1945) formulated a discrete matrix model that set the grounds for theoretical and applied research on a large number of species (Cushing 1998, Dennis 1991).

$$N_{t+1} = T \cdot N_t$$

N is the vector containing the number of

individuals in each age class, and T the transformation matrix derived from life tables. The first row and the diagonal components of T are respectively the age-specific fertility and mortality rates.

Such models have been used on *Tetranychus urticae* to study predator-prey dynamics (Hance and Van Impe 1999, Selhorst *et al* 1991), or for calculation of stable age distributions and their corresponding intrinsic rate of natural increase (Laing 1969, Carey and Bradley 1982). The results of our model are in line with those found in previous studies in terms of SAD and r (for a review see Carey 1982).

Matrix models are fairly simple to formulate and to compute. However, their disadvantage lies in the fact that they are based on life tables, which are heavy to use: they contain as many parameters as entries on the table, which makes them inflexible and unsuitable for theoretical research.

Another way to incorporate variations of age-structure into a colonizing population model was proposed by Hance (1990). The model is based on Lotka's equation. Growth rate r is replaced by a damped sinusoidal function of time. This function imitates the damped oscillations of growth rate as the population converges to SAD. The conclusion of his study agrees with ours in that growth by pulses is faster than exponential growth.

The model that we present here can be defined as a combination of discrete and continuous modelling techniques. On one hand, it is discrete in time age, which avoids the complications of partial differential equations. On the other hand, age-specific mortality and fertility are defined as continuous functions of age, like in continuous models. This major difference with the matrix models, allows us to reduce the number of parameters to only 5. This makes it an adequate starting point for theoretical research.

More particularly, it would be interesting to study the role of growth rate oscillations in collective choices. Collective migration of spider mites, for instance, can result from the amplification of trail following (Yano 2008). Oscillations in population size typically play a role in the triggering of such amplifications by provoking the exceedance of thresholds. It also seems that spider mites are subject to Allee effects (Van Impe 1985). Such positive feedback loops can stabilise the oscillations and prevent them from converging into their stationary values.

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