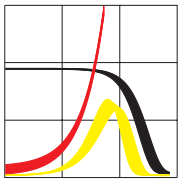

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Individual fecundity dynamically predicts remaining life expectancy in medflies

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Individual fecundity dynamically predicts remaining life expectancy in Medflies.

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Abstract

We analyze relationships existing between reproduction-related traits and longevity in Medfly individuals. We show that dynamic prediction of remaining life expectancy is available basing on a parameterized individual fecundity pattern. We describe individual fecundity as a three-stage pattern with a number of reproduction-related traits and use this description to classify individual fecundity patterns in the 1000-fly female population of Medflies by the rate of fecundity decrease. Using a 100-flies learning sample we estimate correlation between remaining time to live and the coefficient describing that rate. We use this technique at 20th, 25th and 30th day to predict deaths, which will follow during 10-day interval after the prediction day. About 41-62% of the individuals predicted to die within this interval really die (in comparison with only 18-38% of dying flies predicted not to die). These results are statistically significant. We test this finding and discuss the meaning of the results.

Key words: individual fecundity pattern, parameterization, prediction, longevity, remaining life expectancy, Medflies, mathematical model.

Introduction

The prediction of different events is a very interesting issue in demography as well as in medicine. For example, important policy decisions are made basing on forecasting of the elderly population far into the future (Lee, Miller 2001, Li et al. 2004). In medicine, in many studies the main result under assessment is the time to some clinical outcome.

During the last years, when the surprisingly many genes were found to be common in humans and animals, a number of papers arose devoted to prediction of life in different animals with relation to humans. These studies create a wide front which includes different species from mice to humans (Altman, Royston 2000, Harperr et al. 2004, Cargill et al. 2003, Clark et al. 2003, Miller 2001, Piantanelli 2001, Stevens et al. 2000, Watari et al. 2002). In these papers different biomarkers of aging, i.e. the parameters of an organism predicting mortality risk at some late age, were used. For example, Miller (2001) shown that longevity in mice may be predicted by the measures of CD4 memory T-cells in peripheral blood. It was found that 'variation among mice in T-cell subset accounts for only a small, though significant, proportion of the variance among mice in longevity' (ibid, p. B183). Piantanelli et al. (2001) suggests the body weight as a main life span predictor in mice, although the earlier findings of Smith et al. (1991) contradict it. Cargill et al. (2003) have studied weather age of ovary determines remaining life expectancy in mice.

Strong associations of reproduction-related traits with longevity were found in individual medflies (Carey et al. 1998, Muller et al. 2001, Papadopoulos et al. 2002, 2004). Papadopoulos et al. (2002) found that medflies exhibit supine behavior starting 16.1 days prior to their death. They used this behavior as a trait to predict time to death in individuals. A unit increase in supine level increased mortality by 26.3%. This work continues the earlier studies on relationship between physical activity and life span in flies (Trout and Kaplan 1970, Sohal and Buchan 1981, Sohal 1986). In particular, in *Musca domestica*, 'correlations between life span and walking was -0.338 and between life span and flying was –0.418' (Sohal and Buchan 1981, p. 160). Trout and Kaplan (1970) found that a number of 'buzzes' diminish with age in Shaker mutants of *Drosophila*. Advanced-aged flies some days before death can not fly and thus these flies can be simply detected in an aging population (Sohal 1986, p.39). Papadopoulos et al. (2004) have studied high signaling rates that predict extended life span in male medflies.

On-line prediction of life expectancy was shown to be possible (Muller et al. 2001). These authors studied a Medfly population consisting of 1000 flies. The statistical properties of this population were thoroughly studied by Carey et al. (1997, 1998, 1999, 2000). Muller et al. reveal that in individual Medfly the rate of decline in egg laying with age predicts subsequent mortality. "The larger the remaining reproductive potential, the lower the subsequent mortality", they said (Muller et al. 2001, p.445). They found an increased mortality risk in flies for which egg production declined rapidly early on, irrespective to the level of egg production.

Nonetheless, some estimates, needed for the prediction, can be evaluated only given the fecundity scores until individual death. Indeed, Muller's exponential approximation for an individual egg count, $f(x) = \beta_0 \cdot \exp(-\beta_1(x-\theta))$, has three parameters to be estimated. These are the peak of fecundity, β_0, the age at the peak, θ, and the rate of decline, β_1. These three parameters can be estimated only a-posteriori, when the essential part of the entire lifetime is passed. For example, in (Muller et al. 2001) the three parameters are random ($\beta_0 = 57.25 \pm 16.70$, $\beta_1 = 0.090 \pm 0.093$, $\theta = 11.09 \pm 3.55$).

Muller et al. divided the arbitrary chosen sample of 531 flies from a 1000-flies population in three groups (low-, medium- and high-risk groups) at 25th day. To do this they were basing on the estimated rate of fecundity fading for previous days. Then they found that in these groups the really observed deaths at days 26-30 was 14 out of 177, 26 out of 177 and 61 out of 177. Thus they demonstrated the possibility of creating the risk groups for Medflies basing on analysis of fecundity.

In spite of these findings the problem of life prediction continues to need additional studies. The problem of prediction of the remaining time to live could not be thought as solved. It is unclear how to spread the projection technique to the rest of the population or how to process the total population to create the groups.

The search of biomarkers that can predict life in animals is lasting. 'Ideally, the rate of change in a biomarker of aging should be predictive of lifespan' (Ingram et al. 2001, p. 1025). Fecundity is one of such biomarkers. In this study we turn once more to fecundity to project an individual life expectance in a total 1000-fly population of Medflies. Parameterization of fecundity patterns made by us earlier (Novoseltsev et al. 2003) opens a possibility to predict longevity in flies given their individual egg laying scores.

Demographic prediction of life expectancy.

It is simple to evaluate "demographic" life expectancy for a fly at age x given survival data for a medfly population. At age 0, it is equal to the mean-population life span (that is the value of survival pattern at the 50% survival level). The predicted value is the same for all the flies, and the prediction error for an i-th individual is $\Delta_i(0) = LS_i - \text{mean}LS_0$. Here mean$LS_0$ is the mean-population life span.

For a part of a population still alive at age X, the mean life span becomes greater, but again it is the same for all members of the population as before, meanLS_X. Then the prediction error for i-th individual is $\Delta_i(X) = \text{LS}_i - \text{mean}LS_X$. Fig. 1a represents the mean life expectancy for the overall population of Mexico medflies, and for three sub-populations of older flies, which constitute 75, 50 and 25% of the initial volume of population. The errors for these groups are presented in Fig. 1b. The mean error for the prediction for the 1000-flies population is 16.487.

Correlations between Reproduction and Longevity

In agreement with the parameterization idea (Novoseltsev et al. 2003), an adult individual fecundity pattern has three stages, maturation, maturity and senescence. The first stage (maturation) is defined as a period between eclosion and the first egg laid. It is described by a single parameter, t_{onset}. The maturity stage is described by two parameters, a duration T and 'reproductive capacity' RC. This capacity is represented by the height of the plateau of egg laying. The final part of the pattern is an exponential decay of egg laying and it is described by the time constant of the exponent, τ_{tail}. A life span, LS, completed the list of the parameters.

The main feature that differentiates such a description from usually used mean-population one is the absence of a maximum in individual fecundity pattern. The maximums that are observed in the experimental populations are artifacts related to averaging (Novoseltsev et al., 2003a, 2003b).

A prediction of longevity is based on the correlation between individual LS and the parameters of approximation of the fecundity pattern. The correlation coefficients between the five parameters for a 1000-fly population of Medflies are presented in Table 1.

Basing on fecundity parameters, in fact we can predict the longevity only in flies, which already enters the senescence-caused fecundity tail. We can not tell anything about (i) flies with no egg laid, and (ii) flies, which live too short to overlive the fecundity plateau period. Thus 64 zero-egg flies from 1000-fly population escape a procedure of dynamic longevity projection. Demographic prediction is used for these flies instead.

The high degree of correlation, which exists between the remaining part of life δ_i and τ_{itail} guarantees us the good prediction of δ_i given τ_{itail}. This means that a fecundity pattern contains enough information for a dynamic projection of individual longevity. For example, if one will choose 100 flies from a1000-flies population as a learning sample, this correlation will be as shown in Fig. 3.

To estimate δ_i we define the regression function

$$\delta^* = a \cdot \tau_{tail} + b, \quad (1)$$

where δ^* is estimation of δ, and the coefficients a = 0.97, b=9.709. When no tail is detected in the prediction, we will use the value of mathematical expectation in the learning sample as a prediction of the remaining time to live. When the 20th day is used for prediction, LS^* = 39.0 (days).

Results: risk-groups in a 1000-flies population of Medflies

Now we form a risk-and non-risk groups as it is shown in Fig. 6. The risk group consists of the individuals who are predicted to die during 10 days after the prediction. All other flies are included into non-risk group. After the prediction we compare the predicted result with real data (Fig. 7).

Then we twice repeat the total projection procedure, for day 25th and day 30th, producing for three projection days (including day 20th) the data presented in Fig. 8. The results are statistically meaningful. To demonstrate this, we randomly form the reference group (e.g., 276 flies from 900, at the prediction day 20) and control how many flies die in the group during 10 days after the prediction (days 20-30 in our example).

Repeating this procedure 10 000 times, we construct a histogram showing the percentage of flies really dying during this interval (Fig.9, the upper left plate). Comparison of this result with the percent of flies really dying in the risk-group (shown by the vertical line at the point 41%, relating to the prediction result) demonstrates that the probability of arising of this number, $P < 0.0001$. The same test repeated for non-risk group (90 flies, arbitrary chosen from 506) shows that the really observed mortality in the group has never been observed in the random samples. The corresponding pattern is presented down in the left.

We repeat this procedure for two other days of prediction, 25 and 30. The results are the same - $P < 0.0001$.

The other way to analyze the prediction is to use histograms of ages-at-deaths in risk- and non-risk groups (Fig. 10). Survival patterns for these groups are presented in Fig. 11, showing the mean values of deaths in risk- and non-risk groups. The confidence intervals for the mean values are given in Table 3.

The flies having no eggs as well as the flies, which were estimated as living at the fecundity plateau at the moment of prediction, were provided with demographic predictions. Such flies are rather numerous in the populations under prediction. At the first prediction at day 20^{th}, they were 351 flies. Later on, the number of such flies diminishes, but at the 30^{th} day they were still 263 flies.

Thus we demonstrate various techniques to test if the results of prediction of remaining life expectancy in Medflies. All they tell us that the prediction is statistically significant.

Discussion

Normally, an analysis of life expectancy refers to demographical problems, but similar problems arise in food industry when they are to predict shelf life of different foods (McDonald and Sun 1999, Carlsen et al 2001). There also exist extensive areas in which one must predict life span in in-patient therapy. Modeling approach is used, for example, in prediction of life expectance after various examinations in breast cancer patients (routine follow-up, Jakobs et al. 2001, adjuvant therapy, Ravdin et al. 2001). Mathematical modeling is used in management of a waiting list for the liver

transplant (Vanness 2002) and in predicting the performance of the heart valve replacement (de Kruyk et al. 1998). It is also used in case of cystic fibrosis (Aurora et al. 2000), cirrhosis with ascites (Fernandes-Esparrach et al. 2001) or type II diabetes (Stevens et al. 2000).

A few models were developed for human fecundity and fecundability with special attention to behavioral, social, and physiological factors (Wood 1989, Weinstein 1990). Natural fertility, particularly in traditional populations, was also studied (Larsen and Vaupel 1993, Larsen and Yan 2000). Life expectancy prediction is essential part of modern biodemography (Carey 2005) and medicine, especially for patients diagnosed with terminal diseases (Henderson et al., 2001). Usually in medical application they use median survival time, i. e. the duration that 50% of the subjects can survive (Motulsky 1995).

Till now the most popular among the models used for prediction of survival time is the Cox proportional hazards model (Haverkamp et al. 1995). This model uses the scores of sporadic amyotrophic lateral sclerosis and provides 'highly accurate' prediction for the 80% of patients. However, even for such a successful model, 'the evaluation of the survival of an individual patient is of doubtful value' (Preux et al. 1996, p.153). The latest studies confirm these doubts (Turner et al. 2002, Magnus et al. 2002).

The 'criteria assessing an accurate prediction of life expectancy ... has been difficulty to establish' (Okada et al. 1999, p.12). That is why the studies of life expectancy prediction are continued on animals.

The only attempt to predict the mortality in flies basing on egg laying scores was made by Muller et al. (2001), although their evaluations were not too successful. Muller and co-workers model the declining part of the age-related fecundity in medflies *Ceratitis Capitata* by an exponential function, which starts at some age with a 'peak egg laying,' but they neglected the early pattern of fecundity.

In fact, Muller divide the sample of arbitrary chosen 531 flies (from 789 flies that were living at day 25) into three groups basing on the predicted mortality. The first group was named low-risk group, in which the "reproductive potential" was highest. In our terms, reproductive potential corresponds to value of τ_{tail}. Since reproductive potentials and values of τ_{tail} differ in these groups,

the observed death rates also vary. During the 5-day period, following day 25, the number of deaths in low-, medium- and high-risk groups was 14 out of 177 flies, 26 out of 177, and 61 out of 177.

However, this solution has to be well improved. It was not clear how to expand the Muller's technique for the rest of population, 258 flies. These flies could not to be processed by Muller et al. technique as for they either do not lay eggs or they laid too small quantity of eggs. It is possible that they have two equal maxima in eggs scores.

Finally, Muller et al. took an initial point to calculate the coefficient of the fecundity decrease too early. Calculation of the coefficient in their study started at day θ=11.09±3.55 (days). In our study the calculation was fulfilled under least square approximation technique of the three-stage fecundity pattern, and usually started much later.

A parameterization of individual fecundity pattern allows us for a prediction of remaining time to live in all flies that overlive 25 days basing exclusively at the information on their fecundity prior the day of prediction. In this paper we divide 900 flies into two groups, risk- and non-risk and show that the prediction is statistically significant.

The random character of the egg scores essentially confuses the prediction. Indeed, the errors of individual prediction of the life spans are comparable with the errors of demographic prediction. For example, in the first prediction at the day 20, the mean-square error of individual prediction was σ = 14.02 whereas the error of demographic prediction, 13.39. Later on the numbers were similar. For example, at day 30 it was 12.14 vs. 12.06.

We believe that the results will stimulate interest of the researchers in life expectancy prediction, which is based at fecundity scores. Such an approach will result in understanding of how to predict longevity and mortality in various species as well as in humans.

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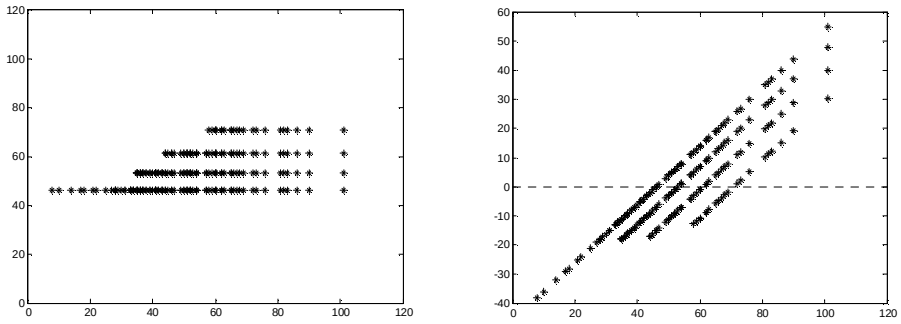


a b

Fig. 1.

Demographic life projection in a 1000-fly Mexico population. (a). Values of projected expected life time or a population in general, and for 75, 50 and 25% of its initial quantity (from below). (b) The related errors for data in Fig. 1a.

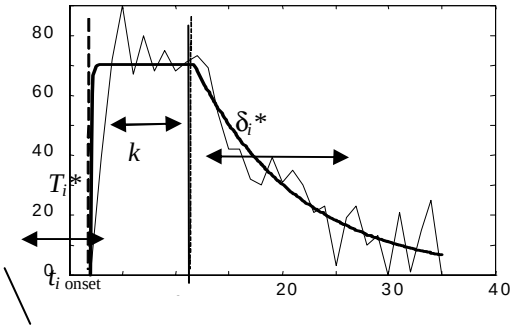


Fig. 2.

Prediction of remaining longevity in a fly female. Age at prediction of longevity equals to ($t_{ionset} + T_i + k$). Two values are essential at this age, the remaining time to live δ_i, and its estimation, δ_i^*. The estimation is based on the of τ_{itail} . To estimate τ_{itail}, k daily scores of egg laying are used.

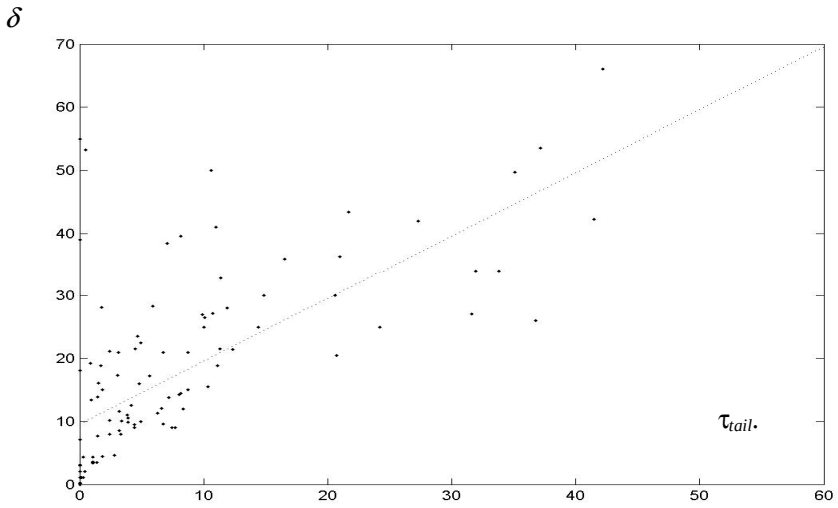
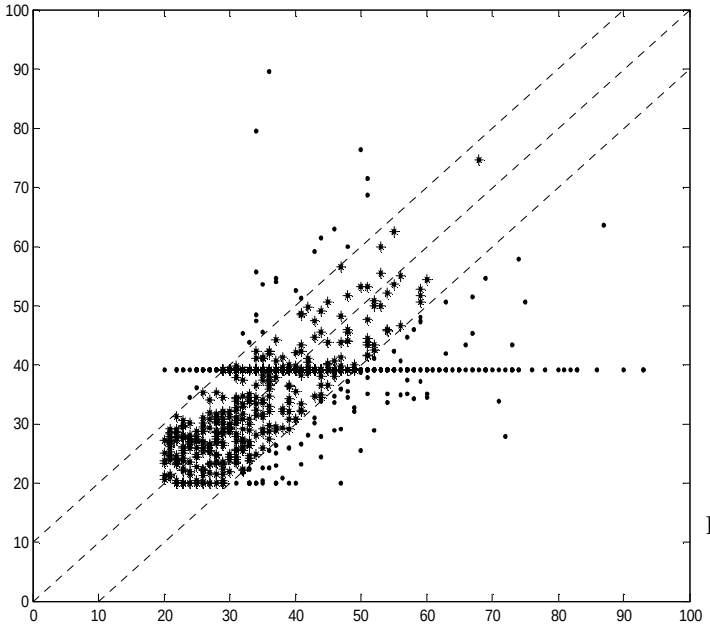


Fig. 3.

Correlation between δ and τ_{tail}; $r = 0.69$

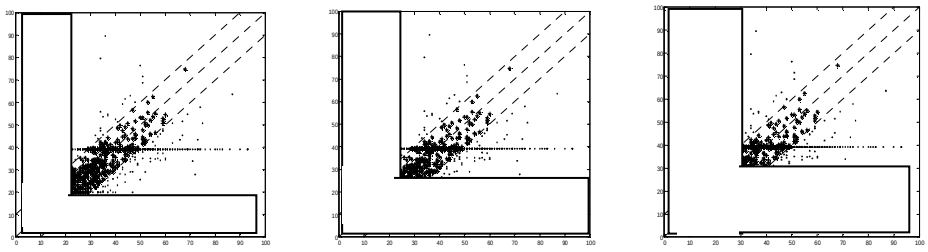
Predicted life time



Real life time

Fig. 4.

Predicted life time vs. real life time for 900 flies when projection is made at day 20. The main part of the points is located in the area “Predicted life time ±10 days”.



A B C

Fig. 5.

Dynamic usage of information when predicting remaining time to live. (A – C). 20 to 30th day. The white area in each plate shows the volume of known information. It arises with time going.

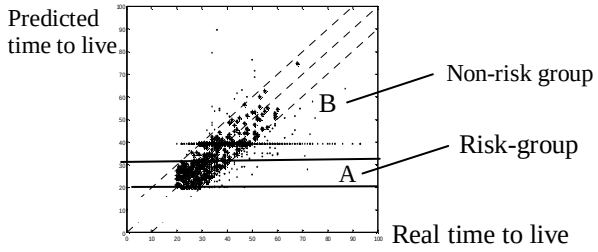


Fig.6.

Risk-group for 20th day. Group A – flies predicted to die during 10 days after prediction (risk group), group B – flies predicted not to die during 10 days after prediction (non-risk group).

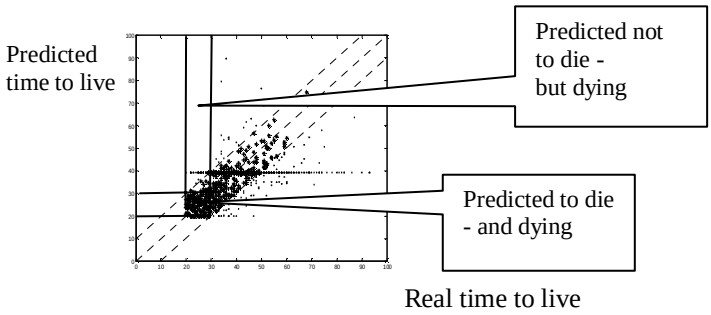


Fig. 7.

Comparison the predicted and the real results.

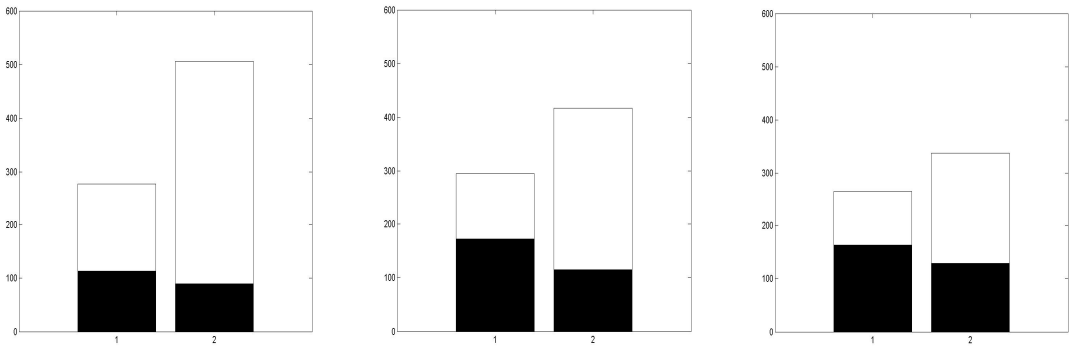


Fig. 8.

Results of prediction of remaining life time for 900 flies from a 1000-flies population of Medflies. At each day, A – the size of the risk-group and the number of flies, which really dies during 10-days interval after the prediction (black colour), B – the same for non-risk groups. The data are presented in Table 2.

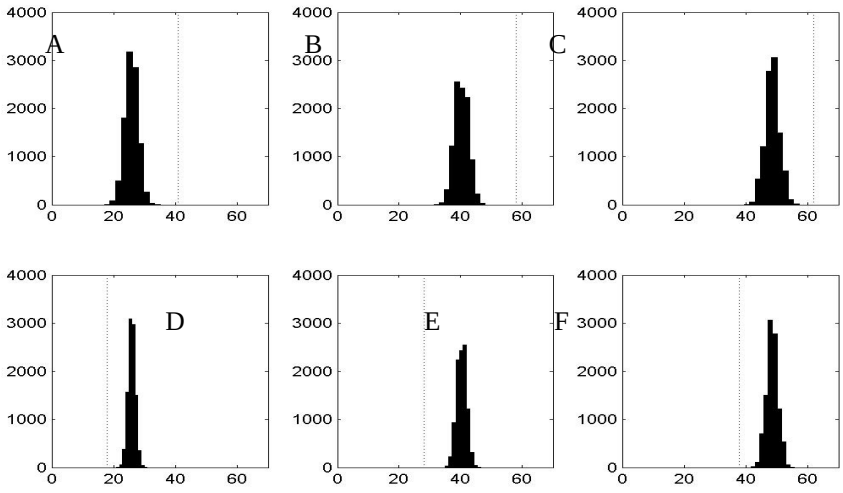


Fig. 9.

Percentage of dying flies in a randomly chosen group: (A) 276 flies from 900, (B) 295 flies from 900, (C) 264 flies from 900, (D) 506 flies from 900, (E) 417 flies from 900, and (F) 338 flies from 900. N = 10 000, $P < 0.0001$.

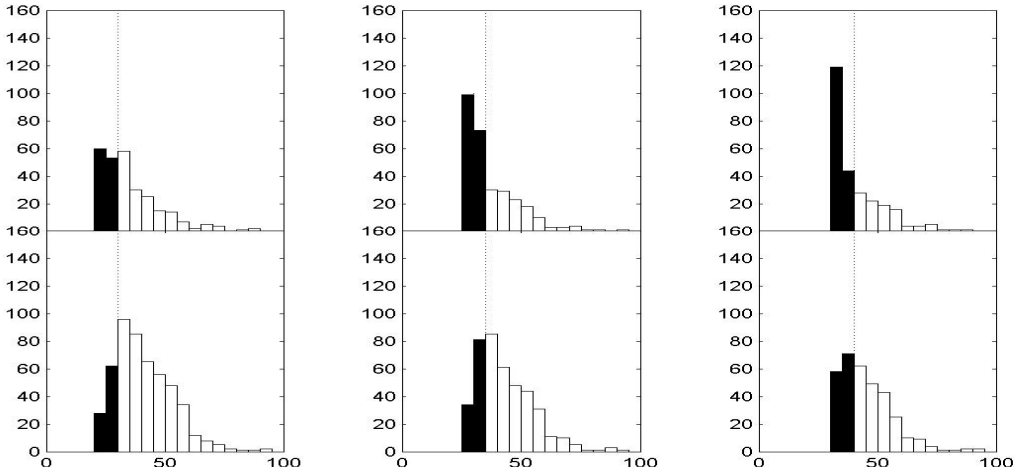


Fig. 10.

Histograms of ages-at-death in risk- (above) and non-risk (below) groups. First ten days are shown with black color.

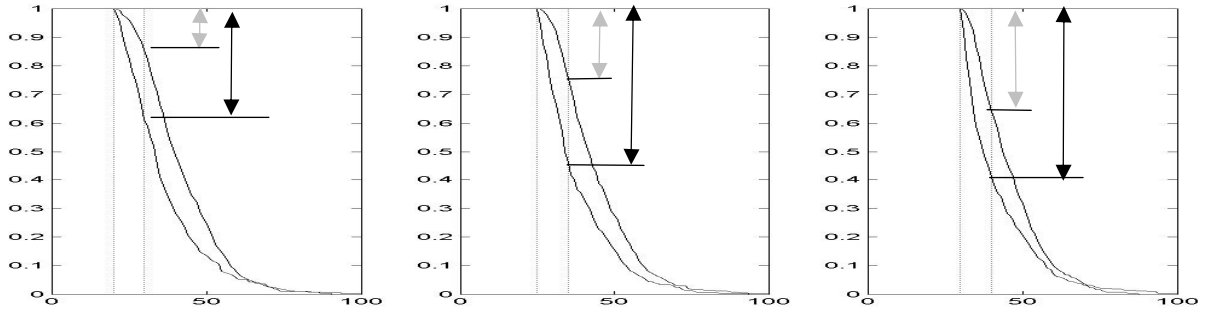


Fig. 11.

Survival patterns for risk- and non-risk groups for different days of prediction. Light arrows demonstrate mean-population mortality in non-risk groups whereas black ones, in risk-groups. The confidence intervals for the mean values are presented in Table 3.

Table 1

Correlation coefficients in a 1000-fly population of Medflies

		1	2	3	4	5
1	*RC*	-	- 0.217	- 0.336	0.285	- 0.080
2	*T*		-	- 0.006	- 0.267	0.474
3	t_{onset}			-	- 0.137	0.240
4	τ_{tail}				-	0.423
5	*LS*					-

Table 2.

Risk- and Non-risk groups in a 1000-fly population of Medflies

	Prediction at day 20	Prediction at day 25	Prediction at day 30
Risk-group %	113 from 276 41%	172 from 295 58%	163 from 264 62%
Non-risk %	90 from 506 18 %	115 from 417 28%	129 from 338 38%
Total	203 from 782 26 %	287 from 712 40%	292 from 602 49%

Table 3.

Confidence intervals in a 1000-fly population of Medflies

Day 20 mean LS	Day 25 mean LS	Day 30 mean LS
35.7 (34.1 – 37.2) 41.5 (40.4 – 42.6) *P*<0.0001	37.5 (36.2 – 38.8) 43.7 (42.5 – 44.8) *P*<0.0001	40.9 (39.6 – 42.3) 45.8 (44.6 – 47.0) *P*<0.0001