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The impact of diet switching on resource allocation to reproduction and longevity in Mediterranean fruitflies

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Understanding the factors that determine the allocation and utilization of organism resources may provide an insight into the mechanisms of adaptation, ageing and reproduction. Resource allocation, which is regarded as a method of adaptation, increases fitness and is genetically controlled. Experiments with variable diet feeding of female Mediterranean fruitflies (*Ceratitis capitata*) demonstrated that the feeding regime dramatically influences lifespan, mortality and the reproduction of flies. An analysis of experimental data and numerical experiments reveals that resource allocation could explain lifespan increase when females are switched from a sugar-only to a protein-containing diet. The heterogeneity of the initial female cohort in terms of the total amount of resources and its allocation to the processes of maintenance and reproduction plays a significant role in this.

Keywords: lifespan; adaptation; trade-off; fertility; mortality; *Ceratitis capitata*

1. INTRODUCTION

The allocation of a limited amount of resources to different traits is one of the common accepted models of physiological adaptation (Sibly & Calow 1986; Novoseltsev *et al.* 2002). It is discussed as one of the possible reasons of observed trade-offs (Roff 1992; Stearns 1992).

Discovery of the factors that govern the allocation and utilization of organism resources is of major theoretical and practical importance as this information may allow us to influence the fundamental physiological processes such as adaptation, regeneration, ageing and reproduction. Many experimental works investigated the impact of resource allocation on lifespan in different species and in various conditions. However, the results of these experiments are contradictory and therefore not easy to interpret: the correlation between lifespan and fertility (e.g. the number of eggs laid by insects) was found to be positive, negative or insignificant in different experiments (Bell 1984). Van Noordwijk & de Jong (1986) suggested that individual differences exist in the proportion of resources allocated to alternative traits (this leads to a negative correlation) and also in the amount of total resource itself. If the variation in the resource level is high and the variation in the proportion of allocation is low, then the traits will be positively correlated.

The resource allocation is controlled by activating genetic programmes that provide better fitness to environmental factors. The characteristics of the environment and of the individual change with time, and a solution that was once optimal may become non-optimal. Obviously, an ability to reallocate resources, especially on a principal level such as reproduction and maintenance, should increase individual fitness dramatically. Hence, it is natural to expect such ability to be implemented as a method of adaptation and its consequences to be observed in fieldwork and in experiments.

The aim of this work is the quantitative analysis and modelling of processes regulating changes in the longevity and fertility of female *Ceratitis capitata* fruitflies, using data from experiments made by Carey *et al.* (1998), who studied the effect of dietary changes.

2. MATERIAL AND METHODS

We used the data of the experiments with Mediterranean fruitflies (*C. capitata*) described by Carey *et al.* (1992, 1998). A pool of male and female flies from a large-scale rearing facility was kept in single-pair cages on sugar and water (diet *s*). At 30, 60 and 90 days, subgroups of 100 pairs (denoted P_{30}, P_{60} and P_{90}) were provided with a full diet *ad libitum* (diet *p* containing yeast hydrolysate). Their reproduction and survival were monitored until the last female died. Lifetime reproduction and survival were also monitored from eclosion for two 100-pair control cohorts—one kept on a sugar-only (control *S*) and the other on a full diet (control *P*).

An average fly of cohort *P* laid 27 times more eggs than a fly of cohort *S* but lived 7 days less (table 1). The mortality of flies that were given the full diet dropped and egg laying intensified. In cohorts *P*, P_{30}, P_{60} and P_{90}, the laying period lasted 25–30 days (27 days on average). After that, the mortality rate rose rapidly and all flies died within 3–5 days. The survival patterns in the cohorts are shown in figure 1.

The main conclusions drawn in Carey *et al.* (1998) are as follows.

(i) The life history of Mediterranean fruitflies is characterized by two physiological modes with different demographic schedules of fertility and survival: a *waiting* mode in which both mortality and reproduction are low, and a *reproductive* mode in which mortality is very low at the onset of egg laying but accelerates as eggs are laid.

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Table 1. Mean lifespan, $\overline{X}$ (days), mean lifetime reproduction, $\overline{F}$ (eggs), and correlation between individual values, r_{XF}, for flies in experimental and model cohorts.

(Data for experiments P, P_{30}, P_{60} and P_{90} are presented after switching from sugar to the full diet. Based on Carey *et al.* (1998; table 1), $n = 100$. The model values were obtained from the resource model (described in § 3) with parameters given in table 2.)

		experiment					model				
age of switch to a full diet, t (days)	cohort	$\overline{X}$	s.d. X	$\overline{F}$	s.d. F	r_{XF}	$\overline{X}$	s.d. X	$\overline{F}$	s.d. F	r_{XF}
—	S	40 ± 2.1[a]	21	24 ± 3.2[a]	32	0.22, $p = 0.03$	40	20	0		0.18
0	P	33 ± 0.9	9	658 ± 45.8	458	0.13, $p = 0.20$	33	18	640	232	0.15
30	P_{30}	30 ± 1.0	10	456 ± 38.9	389	0.49, $p < 0.01$	27	12	385	135	0.54
60	P_{60}	25 ± 1.3	13	160 ± 23.4	2340	0.54, $p < 0.01$	27	10	219	75	0.55
90	P_{90}	26 ± 1.7	17	106 ± 21.2	212	0.48, $p < 0.01$	27	9	101	40	0.54

[a] Mean ± s.e.m.

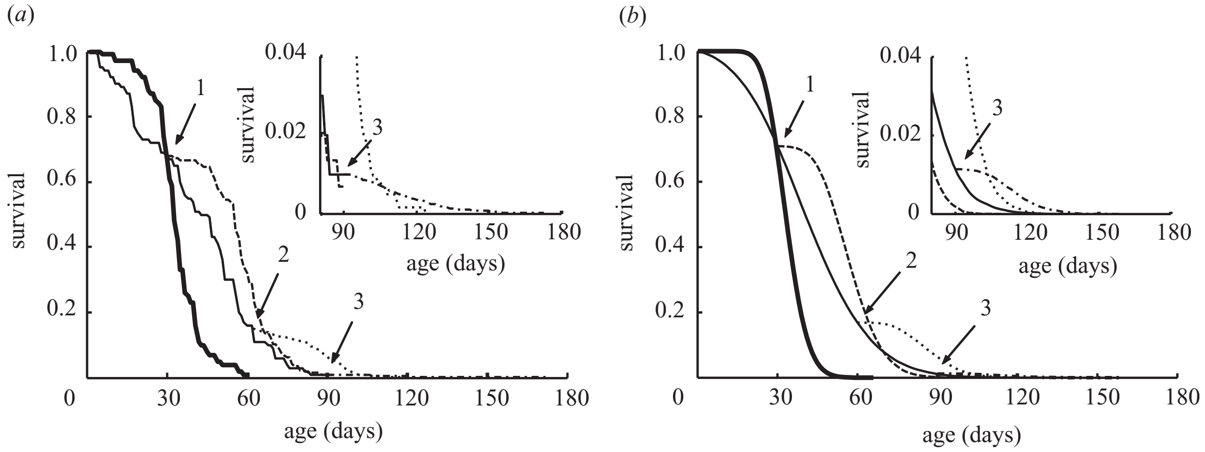

Figure 1. Survival in the (*a*) experimental and (*b*) model cohorts S (thin solid line), P (thick solid line), P_{30} (dashed line), P_{60} (dotted line) and P_{90} (dash-dotted line). The numbers denote ages at dietary change: 1, 30 days; 2, 60 days; 3, 90 days.

(ii) Mediterranean fruitflies that switch from waiting to reproductive mode survive longer than those kept in either mode exclusively.

The data provided in table 1 allow us to examine the relation between the average lifespan, $\overline{F}$, and the average lifetime reproduction, $\overline{X}$, in different cohorts. A larger average lifespan corresponds to a smaller average number of eggs laid (figure 2). This dependence is well fitted by a regression, $0.14\overline{F} + \overline{X} = 123$ (cohort S excluded). Data on cohort S lie aside from the regression line because the lack of necessary nutrition components prevents flies from realizing their reproductive potential. Results of experiments P, P_{30}, P_{60} and P_{90} display a positive correlation between the individual lifespan and lifetime reproduction in cohorts (table 1). But the mean values are negatively correlated between different cohorts (figure 2). To explain this seeming contradiction, we propose a model of resource allocation.

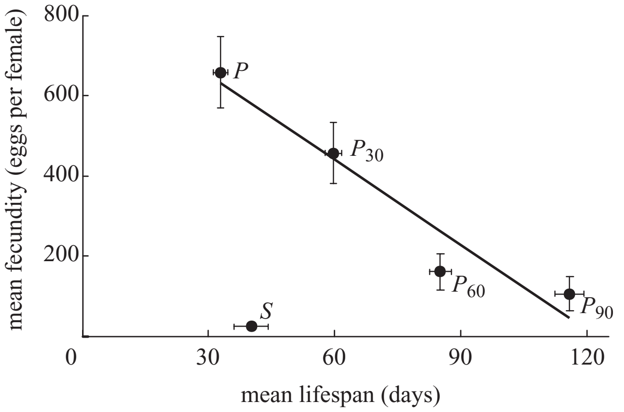

Figure 2. Mean lifespan and mean lifetime reproduction are inversely correlated between different cohorts except S. Diet containing only sugar (diet *s*) blocks egg production; thus the reproduction–lifespan trade-off is not observed in the corresponding cohort S and the resource directed to reproduction is wasted when such an individual dies. Thick solid line denotes regression line (with cohort S excluded from the fit). Crosses denote 95% confidence intervals.

3. THE MODEL

Suppose that the lifespan and fecundity of a female fly are defined by the amount of resources allocated to these functions. At eclosion, a female fly has a non-renewable resource R. It is subdivided into resource R_f allocated to

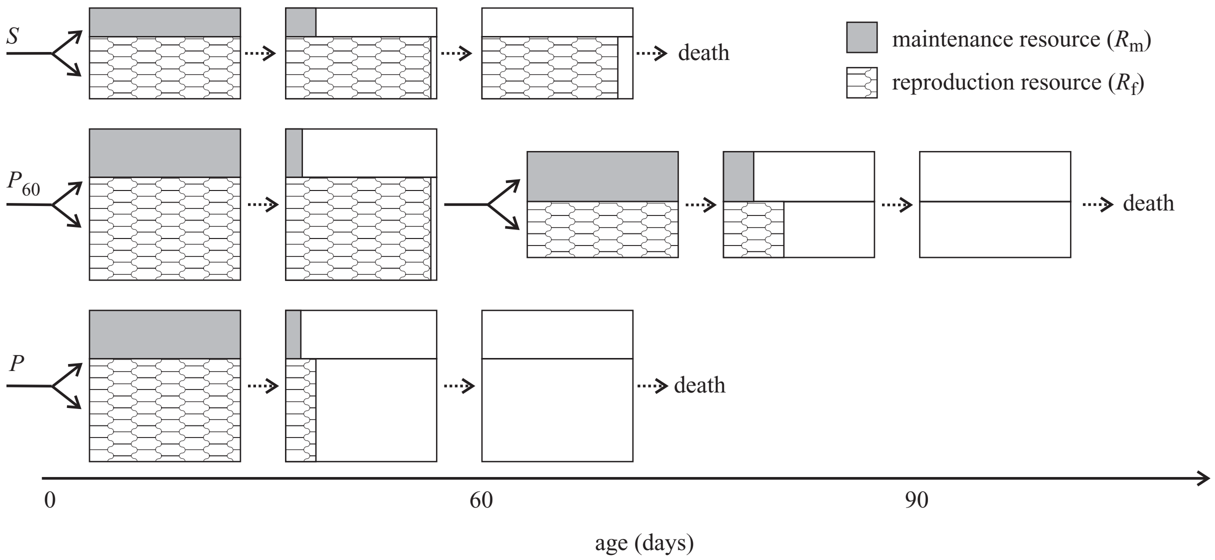

Figure 3. Examples of life histories, described by the resource allocation model for three flies in different experiments. The filled area is proportional to the amount of resources for reproduction or maintenance that a fly has at each specific age. The forked lines denote resource (re) allocations and the dotted lines a change of resource content with time. The maintenance resource of the first fly from cohort S (upper row) was depleted by day 60 and the fly died not having used all of her reproduction resource. The second fly from cohort P_{60} (middle row) nearly depleted her maintenance resource by day 60. However, after a dietary change at day 60, the resources were reallocated, and maintenance resource R_m increased. This gave the fly extra life days and allowed it to make better use of its reproductive potential. The third fly from cohort P (bottom row) depleted both resources before death and used all of its reproductive potential.

reproduction and resource R_m allocated to maintenance. The division is regulated by the individual value of an allocation parameter, c: $R_f = Rc$, $R_m = R(1-c)$. We assume that lifespan X is proportional to the allocated maintenance resource: $X = R_m/\alpha_m$, where α_m is an amount spent daily. Similarly, the number of eggs a fly lays is assumed to be proportional to reproduction resource: $F = R_f/\alpha_f$, where α_f defines the resource cost of one egg. Egg laying is possible and prolific on diet p. Negligibly little resource R_f is spent and zero or negligibly few eggs are laid on diet s.

Suppose that after a switch from diet s to diet p, the remaining resources R_f and R_m are combined and reallocated using a new value of the allocation parameter (figure 3).

We interpret the intercept of the regression line in figure 2 as an average 'metabolic resource' spent by flies during their lives and measured in arbitrary 'metabolic units' (m.u.). Thus, the mean population $R = 123$ m.u. We assume that the metabolic cost of one day of life is the same for all flies and equals to $\alpha_f = 1$ m.u. The regression coefficient is interpreted as a metabolic cost of one egg and is equal to $\alpha_f = 0.14$ m.u. The individual values of allocation parameters c_S, c_P, c_{P30}, c_{P60} and c_{P90} were supposed to be normally distributed between 0 and 1. We modelled them using a 'truncated' normal distribution normalized so that the random values belong to the range [0, 1] with a probability of 1. Individual values of R were modelled by a non-negative truncated normal distribution normalized to 1. The mean of c_P and variances of c_P and R were estimated from the data for group P using the maximum-likelihood method. After that the mean and variance of parameters c_S, c_P, c_{P30}, c_{P60} and c_{P90} were estimated using obtained parameters for R and the maximum-likelihood method from the data for groups S, P_{30}, P_{60} and P_{90} correspondingly. The parameters are given in table 2.

We used these parameter estimations for modelling cohorts P, P_{30}, P_{60}, P_{90} and S. A cohort of 100 000 flies was modelled for each of the five diet patterns. The mean population value of allocation parameter $\bar{c}$ depends on the type of diet: $\bar{c}_P > \bar{c}_S$ (table 2). The results of the modelling are given in figure 1*b*.

4. RESULTS OF THE MODELLING AND DISCUSSION

A comparison of survival in the model population (figure 1*b*) with survival in the experiments (figure 1*a*) shows that the model describes a decrease of mortality after a switch from diet s to diet p and differences between the survival curves in different experiments rather well. The proximity of correlation between individual lifespan and fecundity for the experimental and the modelled data (table 1) shows that the resource allocation model also captures relations between longevity and fecundity that were observed during adaptation to variable environmental conditions.

Our modelling revealed that selection plays an important role in the described experiments. Average initial resource $\bar{R}$ in the group of survivors depends on the length of time that the flies were kept on sugar only (table 3). Flies are selected according to their longevity as age x increases. An average initial amount of metabolic resource R at eclosion for the group of flies that have survived increases because $r_{XR} = r(R(1-c_S)/\alpha_m, R) > 0$. $\bar{R}$ in flies that survived the longest selection (90 days on diet s) is 32% greater than in all cohorts at birth. The mean cohort value of allocation parameter $\bar{c}$ decreases during selection from 0.67 to 0.46. This result demonstrates that only individuals with a higher R and a lower c survive on diet s up to day 90 (table 3, last row). However, this seems to

Table 2. Parameters of the resource allocation model.

notation	value	description
α_f	0.14	metabolic cost of one egg (m.u.)
α_m	1	metabolic cost of 1 day of life (m.u.)
R	123; 40[a]	initial metabolic resource (m.u.)
c_S	0.67; 0.12	allocation parameter for diet *s*
c_P	0.73; 0.12	allocation parameter for diet *p*
c_{P30}	0.67; 0.08	reallocation parameter of transition to diet *p* at day 30
c_{P60}	0.53; 0.08	reallocation parameter of transition to diet *p* at day 60
c_{P90}	0.35; 0.08	reallocation parameter of transition to diet *p* at day 90
μ_R	0.012	spontaneous resource loss rate (day^{-1})

[a] Mean and s.d.

Table 3. Cohort survival (l_x), life expectancy, e_0 (days) and average initial resource, $\overline{R}$ (m.u.) for flies of cohort S that survived to age x (days).

	experiment		model		
x	l_x	$e_0\vert_{X\geqslant x}$	l_x	$e_0\vert_{X\geqslant x}$	$\overline{R}\vert_{X\geqslant x}$
0	1.00	40	1.00	40	123
30	0.68	52	0.66	51	111
60	0.16	71	0.16	74	147
90	0.01	92	0.02	102	162

contradict figure 2 where experimental data demonstrate that the mean initial amount of resources in cohorts P, P_{30}, P_{60} and P_{90} is 123 m.u.

This discrepancy may be explained if we revise the indirect assumption that the cost of one day alive is constant and similar for all females. One strong factor of heterogeneity is the body mass, m, and the base metabolic rate (maintenance energy expenditures) is expected to scale as $m^{0.75}$ (Gillooly *et al.* 2001). Still the body mass was not measured in experiments, and there are no data on the relationship of R_f and R_m with m. That is why for the first approximation we assumed that not only R_m but also R_f decreases with time on diet *s*: $R_f(t) = \exp(-\mu_R R_t)R_f(0)$. Such addition to the model allows us to reproduce a relationship similar to that shown in figure 2.

These results reveal that population heterogeneity plays an important role in lifespan increase after switching from diet *s* to diet *p*. A challenging question arose: does reallocation depend on the resource at the moment of dietary change? To answer this question, each cohort was divided into three groups: 25 flies with the lowest, 50 flies with an intermediate and 25 flies with a maximum lifespan. Figure 4 shows that the trade-off between the mean lifespan and the mean number of eggs laid took place at any level of resource. In the group of the lowest lifespan, resource reallocation led to zero fecundity in experiments P_{60} and P_{90}.

Regression lines shown in figure 4*a* are defined by equations $0.16\overline{F} + \overline{X} = 85$ (groups with the shortest lifespan), $0.12\overline{F} + \overline{X} = 115$ (middle lifespan groups), and $0.2\overline{F} + \overline{X} = 188$ (longest lifespan groups). As one can see, the mean amount of resources (defined previously as the intercept in the regression equation) in the longest lifespan groups is 2.2 times that of the shortest lifespan groups. The relative cost of laid eggs and life maintenance also shows significant differences between the selected groups. The flies of the intermediate lifespan groups are most effective in reproduction, for those in the extreme (lowest and highest) lifespan groups reproduction is less effective. We may therefore suppose that flies in the extreme groups are fitter for survival and reproduction in extreme conditions and that flies in the intermediate groups have a higher reproduction in standard conditions.

Figure 4*b* demonstrates the dependence between lifespan after a diet change and the number of egg-laying days. In the groups of low and medium lifespan, the number of reproduction days is proportional to the length of the reproduction period. Keeping in mind the data from figure 4*a*, we make the supposition that the mean daily reproduction of flies does not change significantly between the groups and the value of the allocation parameter is constant.

The group of flies with the longest lifespan shows a weak dependence between the number of egg-laying days and the lifespan between the cohorts. For example, cohort P_{90} is characterized by a minimal number of egg-laying days, but the longest lifespan. One may assume that one of the life-history features of flies in this group is the maximization of resources allocated to maintenance. The proportion of egg-laying days in this group is smaller but the number of eggs laid in each egg-laying day remains fairly constant.

Flies that survived until day 90 on sugar are very much selected according to lifespan (1% of newborns). As a trade-off they are characterized by very low fecundity (Carey *et al.* 1992).

The analysis of the experimental data described above shows that the lifespan of female Mediterranean fruitflies and the number of eggs laid depend on at least two

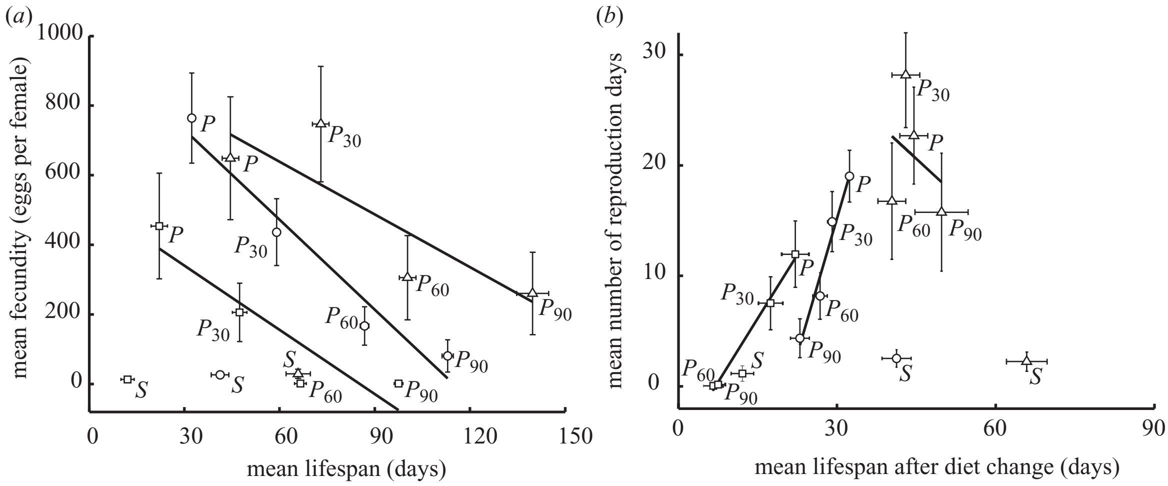

Figure 4. Influence of cohort heterogeneity on the relation between lifespan and fertility. Flies of each cohort are analysed in three groups: 25 flies with shortest lifespan (squares), 50 flies with medium lifespan (circles) and 25 flies with longest lifespan (triangles). (*a*) Trade-off between mean lifespans and mean number of eggs in groups of flies selected by lifespan; (*b*) correlation between mean lifespan after a change in diet and mean number of egg-laying days. The linear regression is shown in thick lines. Crosses denote a 95% confidence interval for estimations of means.

factors. The first is the presence of yeast hydrolysate in the diet. This component increases egg production 27 times in comparison with a sugar-only diet on average. Carey *et al.* (2002) and O'Brien *et al.* (2002) propose that uptake of amino acids increases egg production. We propose that other critical components of yeast hydrolysate are sterols. Insects do not synthesize these substances but obtain them from the environment (Highnam & Hill 1977). These substances are necessary because steroid hormones, which play the principal role in ontogenesis, are synthesized from them (Thummel 1996; Gilbert *et al.* 2002).

The second factor is the ability to maintain the metabolism and support energy transformations necessary for maintenance and egg production. From our data analysis it is evident (see figure 2) that some resource exists that may be used either for individual maintenance or for reproduction. We propose that mitochondria, or more precisely their ability to transform energy, may play the role of such a resource. The function of mitochondria is to provide energy for the synthesis processes. It is known that mitochondria are localized near cell structures demanding energy. One such structure is the endoplasmic reticulum—a place where proteins vital for maintenance and the regeneration of body cells and egg production are synthesized. The types and amounts of synthesized proteins are defined by the mRNA currently synthesized in the nucleus. During ATP production, mitochondria are damaged by oxidative radicals that lead to a gradual decrease of their function, ageing and death (Vain & Webster 1977; Miguel & Fleming 1986; Kalous & Drahota 1996). It follows that the allocation of resources of this type takes place naturally according to a genetic programme. One of our motives to develop this model of resource reallocation was the intention to explain the correlation between the number of produced eggs and lifespan that is positive for cohorts P, P_{30}, P_{60} and P_{90} but negative between the cohort means (figure 2). Hence, we supposed that the diet change is a signal for realization of a physiological trade-off between longevity and fertility. This individual trade-off may be masked by the population heterogeneity of the total amount of resource (Van Noordwijk & de Jong 1986). The proposed computer model allowed us to check this hypothesis and provided good quantitative coincidence with the data (see figure 1*b*). Numerical experiments demonstrated the key role of the population heterogeneity in realization of this trade-off (see parameter R in table 3). One of the probable explanations of the revealed dynamics of the reallocation parameter is that the reallocation is a result of competition of the cell metabolic systems for ATP after activation of the reproductive metabolic mode.

Finally, note that adaptation ability through resource reallocation is obviously limited as it is observed only in individuals with a high initial resource level and for small changes in environmental conditions.

5. CONCLUSIONS

Resource allocation is a probable mechanism explaining an increase of lifespan of *C. capitata* females when they are switched from a sugar-only to a protein-containing diet.

The heterogeneity of the initial female cohort in terms of the total amount of resources and its allocation to the processes of maintenance and reproduction plays a significant role in the discovered resource allocation.

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