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Mating opportunity and the evolution of sex-specific mortality rates in a butterfly

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Abstract Life history theory predicts that organisms should only invest resources into intrinsic components of life span to the degree that it pays off in terms of reproductive success. Here, we investigate if the temporal distribution of mating opportunities may have influenced the evolution of intrinsic mortality rates in the butterfly *Pararge aegeria* (Satyrinae). In this species, females mate only once and the frequency of male mating opportunities depends on the temporal emergence pattern of virgin females. As expected, in a population from Madeira where females emerge continuously throughout the year, there was no sex difference in adult life span, while in a Swedish population with synchronised female emergence, males had significantly shorter life spans compared to females. A logistic mortality model provided the best fit to the observed change in age-specific mortality and all categories reached an asymptotic mortality rate of a similar magnitude. However, the Swedish males reached this mortality plateau more rapidly than the other categories. External mortality, due to water and food limitation, affected the pattern of sex-specific mortality but males from Sweden still had higher rates of mortality compared to all other categories. We argue that selection on male longevity is likely to be weaker in Sweden because under synchronised emergence, all females emerge and mate within a short period of time, after which male reproductive value will quickly approach zero. On Madeira, however, male reproductive value decrease more slowly with age since the probability of finding a receptive female is constant over the year.

Key words Life history theory · Longevity · Ageing · Mortality rate · Lepidoptera

Introduction

A major challenge in life history theory is to explain how and why fundamental traits that are closely related to fitness vary among organisms. Explanations are based on the notion that natural selection will maximise individual fitness within the constraints set up by the trade-offs and genetic variation present in each specific case (Roff 1992; Stearns 1992). Therefore, the exact combination of life history traits that satisfies these criteria varies between organisms and environments. Realised adult longevity is a crucial life history trait since it will influence how many times an individual can engage in reproductive activities. As a consequence, evolutionary theories of ageing are largely integrated with the general theories of life history evolution. They suggest that ageing has evolved because external insults to survival and fecundity make the force of natural selection progressively weaker throughout the adult period (Medawar 1952; Williams 1957; Stearns 1992; Charlesworth 1994; McNamara and Houston 1996; Partridge and Barton 1996). Given that ageing does occur, its specific rate in any particular case can be viewed from the perspective of general life history optimisation. Since organisms in the wild are generally killed by external factors such as predation or starvation before they grow old, they should only invest resources into the intrinsic components of life span to the degree that it pays off in terms of reproductive success (Kirkwood 1987; Kirkwood and Rose 1991). From this perspective it seems reasonable to assume that variation between organisms in the intrinsic capacity for longevity may reflect differences in the relative costs or benefits of a long adult life. In this study, we have investigated how the yearly distribution of mating opportunities may influence the relative benefits of a long adult life span. To do this we have compared sex-specific mortality patterns in two populations of the speckled wood butterfly, *Pararge aegeria* (Satyrinae), experiencing different degrees of seasonality.

Temperate insects typically survive the winter in a hormonally controlled diapause, which can only take

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Table 1 Climatic data from the two regions. Statistics from the meteorological stations closest to the location of the sampled populations, obtained from the Swedish Meteorological and Hydrological Institute

Region	Day temperature (°C)	Night temperature (°C)	Precipitation (mm)
Southern Sweden (Malmö)			
January	2	-3	50
April	10	2	35
July	22	13	65
October	12	6	55
Madeira (Funchal)			
January	19	13	65
April	20	14	35
July	24	18	0
October	22	16	90

place in one species-specific life stage (i.e. egg, larva, pupa or adult). As a consequence, the timing of life history events such as growth, development and reproduction is generally well synchronised within a given population. Populations of temperate insects typically have discrete generations of reproductive adults once or a few times during the favourable seasons, depending on the number of generations they have per year. Due to the seasonal synchronisation of adult emergence, most temperate insects are protandrous, which means that males on average enter the reproductive population some time before the females (Wiklund and Fagerström 1977; Fagerström and Wiklund 1982).

The two populations originate from southern Sweden and the Atlantic island of Madeira, and because of climatic differences (Table 1), the phenologies of these populations differ. In southern Sweden, butterfly growth and development is restricted to approximately 7 months of the year (April to October) and the winter is survived in diapause (as half-grown larvae or as pupae). This Swedish population of *P. aegeria* has two to three generations each year and reproduction occurs during each flight period lasting between 3 and 4 weeks (C. Wiklund, unpublished data). On Madeira, temperatures allow development and growth during the whole year and the main seasonality feature is the lack of rain during July and August on some parts of the island (Table 1). There is no evidence from the field that the Madeiran butterflies enter diapause and it could not be experimentally induced in the laboratory (Nylin et al. 1995). Further evidence comes from the fact that, on Madeira, all developmental stages of *P. aegeria* can be found simultaneously in the field (Shreeve and Smith 1992; Nylin et al. 1993), and adults fly more or less all year round at lower elevations (Higgins and Hargreaves 1983; Jones and Lacey 1992; Shreeve and Smith 1992; personal observations). Hence, in southern Sweden, generations are discrete and non-overlapping, while the Madeiran population reproduces continuously through the year and well-defined generations do not occur. In line with theory, the Swedish population is protandrous and males have shorter development times than females while there is no protandry or sexual difference in development time in the Madeiran population (Nylin et al. 1993; Gotthard et al. 1994). Thus, there is evidence that sex-specific selection

pressures on development time differ between these populations.

We expected that the population differences in phenology would also result in different, sex-specific, selection pressures on intrinsic mortality rates. Females of *P. aegeria* generally only mate once in their lives while males can mate with several virgin females (Wiklund and Forsberg 1991). In Sweden, where the adult period of the whole population is highly synchronised, the probability that a male will find a non-mated female outside the relatively brief period of female emergence is very low. Therefore, we expected that there would be no strong selection in Swedish males favouring an intrinsic capacity for a long adult life. On Madeira on the other hand, virgin females emerge more or less continuously and the probability of a male finding a receptive female during his lifetime increases monotonously with male age. Reformulated in more theoretical terms, we expected the reproductive value (Fisher 1930) of a Madeiran male to decrease more slowly during his adult life than it does for a male in Sweden. As a consequence, selection for the intrinsic capacity of long adult life should be stronger in the Madeiran males. Predictions for population differences in female intrinsic life span are not as obvious since female reproductive success in both populations should depend not only on the time that is available for egg laying but also on the availability of suitable host plants. In the case of females, therefore, the only prediction was that female intrinsic life span should be longer in both populations than that of Swedish males.

The observed differences between the populations in life span could potentially be altered in the presence of extrinsic sources of mortality. Since the climate on Madeira is very dry and hot during parts of the year, we anticipated that the availability of water and nectar sources may be a relevant environmental dimension to manipulate. Therefore, we investigated adult longevity in a range of water- and food-limited conditions with the expectation that the Madeiran population should be relatively better in surviving these stressful conditions.

Materials and methods

Study organism

The speckled wood butterfly, *P. aegeria*, is widely distributed throughout Europe, Asia and northern Africa. The larvae feed on various grasses from several genera. In Europe, two subspecies are recognised: north of the Alps *P. aegeria tircis* and south of this latitude *P. aegeria aegeria*. The two subspecies hybridise and intermediate forms are found where they meet in the field (Higgins and Hargreaves 1983). In the 1970s, the southern subspecies *P. a. aegeria* colonised the Atlantic island of Madeira from an unknown source (Higgins 1977) and since then has spread all over the island (Jones and Lace 1992; Shreeve and Smith 1992). The mean adult life span expectancy of *P. aegeria* males in the field has been estimated to approximately 6 days both in England and in Sweden, although individual males could survive up to 28 days (Davies 1978; Wickman and Wiklund 1983).

Laboratory stocks

In March 1995, eight mated females of *P. aegeria* were caught in the surroundings of Funchal, Madeira (33°N), and were brought back to the laboratory in Stockholm. Their consecutive offspring are the base for the stock of Madeiran butterflies that was used in experiments performed during the winters of 1995/1996 and 1996/1997. During the breeding of the Madeiran butterflies, we actively tried to avoid selection by collecting eggs in equal amounts from the whole period of female oviposition. For practical reasons, new Swedish butterflies were caught in 1995 and 1996 and, therefore, the stock from southern Sweden differed in the 2 years of experiments. In both years, they originated from approximately ten mated females caught in August. Their offspring were kept in conditions leading to direct development (20 h light:4 h dark, 20°C). All larvae from both populations were reared individually in plastic jars where a tuft of the grass *Dactylis glomerata* was cultured. The sex of individuals was determined at the pupal stage and confirmed in the adults.

Experiment 1

During the winter of 1995/1996 we measured adult life span of butterflies from both populations in standard laboratory conditions. One day after adult emergence from the pupa, all individuals were marked individually and put in flying cages (0.5×1×1 m). To avoid matings, sexes were kept in separate cages. The floor of the cages was covered with paper napkins which were kept moist by watering once a day. Sugar water and grass for oviposition were available all the time (unmated females oviposit). The photoperiod was 8 h light:16 h dark, and each cage was lit with a 400-W, HQIL lamp. Temperature was 25°C when the lights were on, and 20°C at night. The cages were checked each day for dead butterflies. Adults from both populations were tested side by side during the same period.

Experiment 2

This experiment was performed during the winter of 1996/1997 to replicate experiment 1 and to test the combined effect of drought and food limitation on the adult life span of both populations. All individuals in the experiments were marked individually and assigned to either of three treatments. Treatment 1 was standard laboratory conditions: access to sugar water all the time and watering of the cages once a day. Treatment 2 meant access to sugar water and watering of cages every 2nd day, while individuals in treatment 3 were given sugar water and a moist cage every 3rd day. The experiment was done twice on two consecutive generations from both populations. As in the previous experiment, sexes were kept in separate cages using the same experimental protocol as in experiment 1.

Statistical treatment

To investigate differences in mortality patterns between sexes and populations we used survival analysis, which is a suite of statistical techniques that can be used to evaluate data consisting of elapsed time between two events of interest (StatView 5.0 1998). In this particular instance, the time between pupal hatch and death is the quantity of interest. Survival curves for each category and replicate were estimated with the Kaplan-Meier method, which is appropriate for continuously censored event times. Potential differences between categories in survival curves were tested by log-rank tests (StatView 5.0 1998).

There were three replicates in the analysis of mortality in standard laboratory conditions: experiment 1 and the two replicates of treatment 1 in experiment 2. With the data we tested whether mortality differed among sexes within population, and whether mortality differed between populations within sex. Replicate was treated as a stratification variable. The data from experiment 2 were also used to determine whether nectar and water limitation affected potential sex differences in mortality. We investigated the effect of the treatment within each population with log-rank tests stratified by replicate. We then tested whether the sex differences in mortality stayed constant over the food/water gradient, using the same test but stratifying by experimental treatment. We adjusted significance levels of tests with the sequential Bonferroni method (Rice 1989).

To investigate the underlying mechanisms of differences in overall mortality we estimated the parameters of the best-fit mortality model for each category of butterflies. Mortality rate (μ_x) is the continuous-time form of age-specific mortality (q_x) where $\mu_x \approx -\ln(1-q_x)$, and $q_x = d_x/n_x$; d_x is the number of dead in the period x to $x+1$ and n_x is the number of individuals alive at age x (Lee 1992; Carey 1993). A series of parametric mortality models were fitted to the data by maximum likelihood using the software WinModest 1.0 (Pletcher 1999a), and likelihood ratio tests were used to determine which model provided the best fit (Pletcher 1999a, 1999b). Finally, we investigated whether there were differences in the parameter values of the sexes within each population using testing procedures supported by WinModest 1.0 (Pletcher 1999a). For each population we computed the log-likelihood for the maximally constrained model (sexes are constrained to have identical parameter values). We then computed the same statistic for all models where there is a difference between sexes in one parameter (number of possible models=number of parameters in the model). A likelihood ratio test can then determine whether the mortality data are significantly better explained by any of the less constrained models (in this case H_0 =no difference between sexes, H_1 =sexes differ in one parameter) (Pletcher 1999b). If the H_0 could be rejected for any parameter, we proceeded to compare the single case that had the highest log-likelihood with even less constrained models (next step, two parameters differ between sexes: i.e. new H_0 =sexes differ in one parameter, new H_1 =sexes differ in two parameters). This stepwise procedure was continued until a further unconstraining of the model did not produce a significantly better fit to the data.

Results

Adult mortality in standard laboratory conditions

The three replicates consisted in total of 328 individuals with known adult life spans (151 from Sweden and 177 from Madeira). Individual adult life spans ranged from 5 to 47 days in the southern Swedish population and from 3 to 49 days in the Madeiran population. In the Swedish population, males died significantly faster than females (Fig. 1a; log-rank test stratified by replicate: $\chi^2=52.98$, $df=1$, $P<0.0001$). However, in the Madeiran population,

there was no longevity difference between the sexes (Fig. 1b; log-rank test stratified by replicate: $\chi^2=0.05$, $df=1$, $P=0.82$). Furthermore, Madeiran butterflies of both sexes had significantly lower mortality rates although the difference was larger for males (Table 2; log-rank test for differences between populations stratified by replicate: females $\chi^2=8.23$, $df=1$, $P=0.004$; males $\chi^2=78.09$, $df=1$,

$P<0.0001$). Hence, the Swedish males had shorter life spans than any of the other three categories.

Age-specific mortality rates

When investigating the change in mortality rate (μ_x) with age we pooled the three replicates, and determined the most representative mortality models for each sex within populations [four related mortality models were tested: the Gompertz, the Gompertz-Makeham, the logistic and the logistic-Makeham (Pletcher 1999a, 1999b)]. In all four cases, a logistic mortality model fitted the data significantly better than either the Gompertz or the Gompertz-Makeham models (likelihood ratio test for difference between Gompertz and logistic models, $df=1$ in all four cases: Madeiran females $\chi^2=8.54$, $P=0.003$; Madeiran males $\chi^2=6.80$, $P=0.009$; Swedish females $\chi^2=25.76$, $P<0.0001$; Swedish males $\chi^2=38.70$, $P<0.0001$). The logistic-Makeham model fitted the data equally well but included one more parameter which represents extrinsic, age-independent mortality (Pletcher 1999b) and therefore the logistic model was chosen as the most representative (for parameter estimates see Table 3).

The logistic mortality model includes three parameters and can be written:

$$\mu_t = ae^{bt} / [1 + (as/b)(e^{bt} - 1)]$$

where a is the mortality rate at birth and b is the rate of exponential increase in mortality with age early in life while s describes the degree of deceleration in mortality rate at older ages (Vaupel 1990). An s value of zero indicates no deceleration and the mortality model reduces to

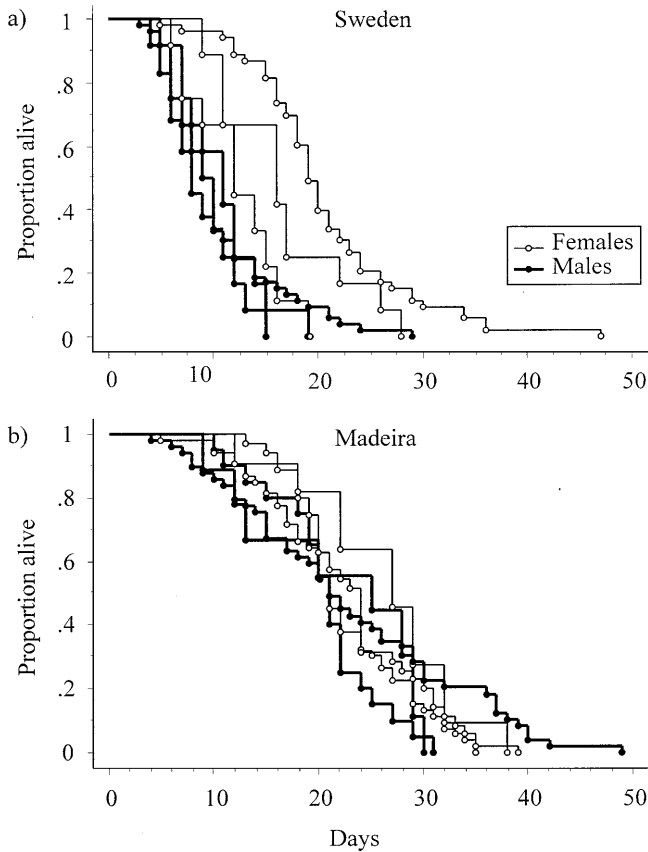


Fig. 1 Proportional adult survival of Swedish (a) and Madeiran (b) butterflies by day in standard laboratory conditions. All three replicates are plotted together with the corresponding Kaplan-Meier survival functions. Females are represented by open symbols and thin lines while males are shown with filled symbols and heavy lines. The number of butterflies in each replicate were: Swedish females 53, 9, 12; Swedish males 53, 12, 12; Madeiran females 56, 11, 35; Madeiran males 49, 9, 20

Table 2 Sex-specific life spans of the two populations in standard laboratory conditions (mean \pm 1 SE in days). The statistics were obtained by pooling the three replicates

Madeira		Sweden	
Females	Males	Females	Males
22.8 \pm 0.7	22.1 \pm 1.1	19.0 \pm 0.9	10.1 \pm 0.6
$n=102$	$n=78$	$n=74$	$n=77$

Table 3 Parameter estimates and their confidence intervals (in parentheses) for the logistic model describing the change in mortality rate with age. Estimates are obtained by maximum likelihood. The corresponding fitted means for each model are also given

Parameter	a	b	s	Predicted mean longevity (days)
Madeiran females	5.3×10^{-4} (7.0×10^{-5} – 3.9×10^{-3})	0.29 (0.18–0.47)	1.42 (0.53–3.8)	22.8
Madeiran males	3.8×10^{-3} (1.1×10^{-3} – 1.3×10^{-2})	0.19 (0.10–0.34)	1.22 (0.39–3.8)	22.0
Swedish females	1.3×10^{-3} (2.8×10^{-4} – 5.9×10^{-3})	0.32 (0.21–0.49)	1.87 (0.93–3.7)	19.0
Swedish males	4.1×10^{-5} (2.0×10^{-7} – 8.9×10^{-3})	1.7 (0.84–3.6)	9.4 (4.0–21.7)	10.1

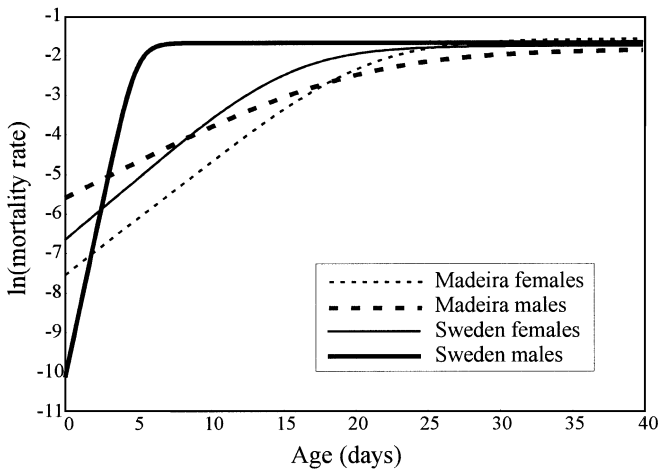


Fig. 2 Estimated mortality functions describing the change in $\ln(\text{mortality rate})$ with age in all four categories of butterfly. See Table 3 for parameter estimates

the Gompertz ($\mu_t = ae^{bt}$). In all four categories of butterfly there was a significant deceleration in mortality rate at advanced ages (Fig. 2). Moreover, there was a very good correspondence between the actual and the model-predicted mean longevity (compare Tables 2, 3).

We could not detect any significant differences in parameter values between the sexes in the Madeiran population (likelihood ratio test comparing a model with no sex differences in parameter values with models where sexes are allowed to differ in one parameter in turn, $df=1$ in all cases; difference in a : $\chi^2=1.32$, $P=0.25$; difference in b : $\chi^2=0.16$, $P=0.69$; difference in s : $\chi^2=2.74$, $P=0.10$). In the Swedish population, the first step in the testing procedure suggested that a model with sex-specific values of b had a significantly higher log-likelihood than the fully constrained model (likelihood ratio test with $df=1$, $\chi^2=63.24$, $P<0.0001$). In the next step we compared this new model with models where the other two parameters were allowed to vary in turn. This showed that allowing each sex to have unique values of b and s gave a significantly better fit (likelihood ratio test with $df=1$, $\chi^2=9.46$, $P=0.002$). A further step allowing all three parameters to take sex-specific values did not produce a significantly higher log-likelihood value (likelihood ratio test with $df=1$, $\chi^2=2.32$, $P=0.13$). Hence, there was no significant difference in a , which can most likely be attributed to the wide confidence intervals attached to the estimates of this parameter (Table 3). In conclusion, this procedure detected significant sex-differences in the Swedish population with respect to the rate of increase in mortality early in life (b) and the degree of deceleration later in life (s) but not in the mortality rate at birth (a).

Adult mortality in water- and food-limited conditions

The total number of butterflies in the two replicates of experiment 2 was 299 (137 Swedish and 162 Madeiran

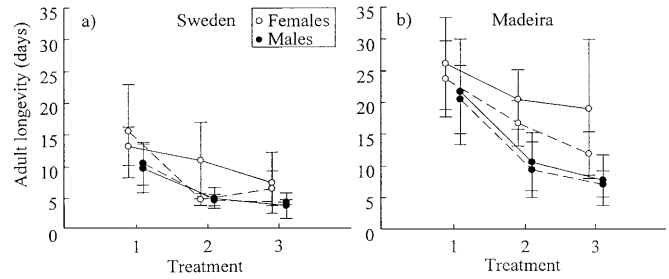


Fig. 3 Results from experiment 2 showing the mean longevity (± 1 SE) of Swedish (a) and Madeiran (b) butterflies, experiencing an increasing level of drought and food shortage from treatment 1 to treatment 3. Sexes are shown with different symbols. The dotted and solid lines connect the two replicates. The sample sizes for each mean of experiment 2 were between 7 and 16 individuals, except in treatment 1 in one of the replicates of Madeiran butterflies (dotted line), where the sample sizes were 35 for the females and 20 for the males

individuals). As expected, the food and water limitation in experiment 2 had a severe impact on the adult life spans of both populations (Fig. 3; log-rank test for differences between treatments stratified by replicate: Sweden $\chi^2=51.26$, $df=1$, $P<0.0001$; Madeira $\chi^2=62.76$, $df=1$, $P<0.0001$). In addition, the patterns of sex differences in mortality were altered by the drought and food limitation (Fig. 3). In these water- and food-limited conditions there were sex mortality differences in both populations (log-rank test for difference between sexes stratified by treatment: Sweden $\chi^2=30.00$, $df=1$, $P<0.0001$; Madeira $\chi^2=39.51$, $df=1$, $P<0.0001$). It seems as if the Madeiran males suffered proportionally more from these limited conditions compared to the other categories. Nevertheless, the Madeiran butterflies of both sexes still had significantly lower mortality rates than their Swedish counterparts (log-rank test for differences between populations stratified by treatment: females $\chi^2=80.52$, $df=1$, $P<0.0001$; males $\chi^2=92.55$, $df=1$, $P<0.0001$).

Discussion

The results suggest that sex-specific selection pressures on age-specific mortality are different in these two populations of *P. aegeria*. Males from southern Sweden stand out as having a different mortality pattern and considerably shorter life spans than the other three categories when water and food is not limited (Figs. 1, 2, Table 2). As predicted, sexual differences in mortality rate and average life span were present in the Swedish but not in the Madeiran population. In general, the butterflies from Madeira had longer adult life spans than their Swedish counterparts, but this difference was considerably larger for the males than for the females (Table 2). The analysis of mortality rates indicated that all categories reach a mortality plateau at approximately the same level but that the Swedish males reach it faster than the other butterflies (Fig. 2).

A similar population difference in sex mortality differentials was also documented in a previous study of these populations (Gotthard et al. 1994). That earlier study was performed on a different stock of butterflies held in the same standard laboratory conditions. The fact that the result is repeatable suggests that the size of field samples or genetic processes in the laboratory populations (genetic drift, inbreeding, selection) are unlikely to have biased the present results.

With additional levels of externally driven mortality (drought and starvation), females were longer lived in both populations (Fig. 3). It appears that the Madeiran males were relatively more sensitive to starvation and drought than their female counterparts. Hence, the expectation that the Madeiran population should be better adapted to water-limited conditions was not supported. Nevertheless, the Swedish males died faster than any other category throughout all treatments of experiment 2. The life spans of the Swedish males were so short in the water- and food-limited conditions that they approached the minimum value (1 day), which might explain the relatively smaller effect of the treatment (Fig. 3).

The results from experiment 2 indicate that a sex difference in intrinsic mortality may also be present in the Madeiran population when food and water are in short supply. Therefore, it is of interest to relate the treatment conditions to the natural situation of these butterflies. With the present experimental setup, the flying cages dry up in 24 h, and therefore the butterflies in treatments 2 and 3 were totally deprived of water for 24 and 48 h, respectively. In Sweden where the natural situation of the population is well documented, the adult butterflies will practically never experience these degrees of drought. The exact situation for the Madeiran population is not as well known to us, but it seems possible that the butterflies may occasionally be totally deprived of water for up to 1 day during the dry season (Table 1; this was the rationale for our expectation). However, the dry season only makes up a minor part of the year and during the rest of the year water limitation seems highly unlikely. The degrees of water limitation applied in treatments 2 and 3 were designed to be rather extreme, and most likely mimic events rare even for the Madeiran population. Although there is some uncertainty about the situation on Madeira during the dry season, it is reasonable to assume that treatment 1 (standard laboratory conditions) reflect the most commonly occurring field situation in both populations better than either treatment 2 or 3. Consequently, the difference between populations in sex mortality differentials is likely to be present in the natural situation as well.

With the exception of the drought/low food treatments, life span was measured in conditions where extrinsic sources of mortality were minimised. It is, therefore, reasonable to assume that the variation in longevity and in age-specific mortality between populations and sexes reflects variation in rates of ageing during the adult period. We suggest that the population difference in longevity and mortality rates between males is, at least part-

ly, a result of different selection pressures acting directly on the intrinsic mortality rates. Theoretical and empirical work on the evolution of ageing and longevity have mainly focused on how the magnitude of extrinsic sources of mortality may influence selection pressures on the intrinsic components of mortality (e.g. Williams 1957; Austad and Fischer 1991; Rose 1991; Stearns 1992; Abrams 1993; Partridge and Barton 1996; Keller and Genoud 1997). It is typically expected that when death rates due to predation, starvation or other extrinsic factors are high, there will be no strong selection to lower the rates of ageing. The generality of this prediction has, however, been questioned (Abrams 1993; Partridge and Barton 1996).

There is no information concerning the level of adult mortality due to external factors in the two populations of *P. aegeria* investigated here. There is a possibility that externally imposed mortality rates differ among the populations, but at present there are no a priori reasons to expect it. In any case, a difference in the level of extrinsic mortality rate could not explain the main result of this study, i.e. a population difference in sex mortality differentials. This finding is, however, consistent with the difference in selective regimes predicted by the mating opportunity hypothesis. In Sweden, seasonally synchronised adult emergence in combination with the monandrous habit of *P. aegeria* females is expected to cause a rapid decline in male reproductive value with increasing age. Since discrete adult generations are not present on Madeira, the probability that a male will find a non-mated female is more or less constant over time, and male reproductive value is predicted to decline more slowly with age. Therefore, selection for a slow rate of ageing is expected to be stronger for Madeiran than for Swedish males.

The results also indicate a population difference in the intrinsic mortality of females. This may be related to variation in extrinsic mortality rates, but there are other possible explanations. The reproductive success of a female will depend on the number of eggs she has managed to distribute on suitable host plants at the time of her death. This will in turn be a function of the realised length of her life and the frequency with which she has encountered acceptable oviposition sites. In Sweden suitable grasses are abundant throughout the period when *P. aegeria* is active, whereas the situation on Madeira suggests that during parts of the year, host plant availability is lower and more unpredictable. Hence, to encounter the same total number of suitable host plants, the average female on Madeira must have a longer adult life span compared to the average female in Sweden. Given that the reproductive output per female is similar in the two populations, this difference in abundance and predictability of host plants may influence the strength of selection pressures on female life span. This explanation is, in fact, similar to our argument concerning male life span, in that both sexes are sampling resources that have different spatial and temporal distributions in Sweden and Madeira.

Table 4 Life history data on the two populations of *Pararge aegeria*, in photoperiods inducing direct development at 17°C. Result (means \pm 1 SE) are from two previous studies (*N* Nylin et al. 1993; *G* Gotthard et al. 1994). Significance levels refer to ANOVAs testing for differences between sexes

Population	Sex	<i>n</i>	Larval time (days)	Pupal weight (mg)	Growth rate (%/day)
S. Sweden (N)	Males	24	32.8 \pm 0.7	137.9 \pm 3.2	20.2 \pm 0.5
	Females	30	35.7 \pm 0.5**	165.7 \pm 3.2**	18.9 \pm 0.3*
Madeira (N)	Males	24	34.9 \pm 0.3	132.7 \pm 2.0	19.6 \pm 1.0
	Females	20	35.1 \pm 0.4 n.s.	153.1 \pm 2.1**	20.0 \pm 0.3 n.s.
S. Sweden (G)	Males	80	27.4 \pm 0.2	143.1 \pm 1.3	24.8 \pm 0.2
	Females	83	30.7 \pm 0.2***	162.6 \pm 1.4***	22.4 \pm 0.2***
Madeira (G)	Males	65	33.0 \pm 0.3	125.0 \pm 1.2	20.2 \pm 0.2
	Females	59	32.0 \pm 0.3*	150.6 \pm 1.5***	21.6 \pm 0.2***

n.s. $P>0.05$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$

The frequency of breeding opportunities has been suggested to explain variation in life span among several species of tropical fruitflies (Sevenster and VanAlphen 1993), and a comparative study of flesh flies showed that non-diapausing species with a desynchronised phenology had longer adult life spans compared to diapausing species with synchronised development (Denlinger et al. 1988). Moreover, Tatar et al. (1997) suggested that high-elevation populations in a sibling species complex of *Melanoplus* grasshoppers had evolved accelerated rates of ageing due to selection on reproductive schedules, which are truncated by the early onset of winter at high altitudes. Our results fit well into the experimental program suggested by Tatar et al. (1997): i.e. to derive testable predictions about population differences in the rate of ageing from known differences in the biology of these populations.

Another recurrent issue in evolutionary studies of ageing is to identify the trade-offs linked to longevity and intrinsic mortality rates (e.g. Rose 1984, 1991; Hillesheim and Stearns 1992; Stearns 1992; Promislow 1993; Sevenster and VanAlphen 1993; Chippindale et al. 1994, 1997; Zwaan et al. 1995a, 1995b). Age at reproduction and body size are traits that have been proposed to be positively correlated with longevity, based on the idea that a prolonged period of growth would result in a larger and higher-quality soma. However, results from the best studied species, *Drosophila melanogaster*, are not conclusive on this issue (Rose 1984; Hillesheim and Stearns 1992; Partridge and Fowler 1992; Chippindale et al. 1994, 1997; Partridge et al. 1995; Zwaan et al. 1995a, 1995b). In the case of *P. aegeria*, variation in body size between populations is clearly not positively associated with longevity in the laboratory, since the longer-lived Madeiran butterflies are significantly smaller than their Swedish conspecifics (Table 4; Nylin et al. 1993, 1995; Gotthard et al. 1994). However, the Madeiran butterflies typically have lower larval growth rates compared to the Swedish butterflies. A likely explanation is that in a continuously reproducing population, the yearly timing of life history events is less important, and when there is nothing to "be in time for" it may be better to avoid possible costs of fast development (Gotthard et al. 1994). Typically, the Swedish males have higher larval growth rates than the other categories (Table 4), and therefore

we have suggested that there may be a trade-off between larval growth rate and somatic quality of adults, which in turn could be reflected by survival rates in the laboratory (Gotthard et al. 1994). If so, the population differences in sex-specific mortality rates could also have evolved as an indirect effect of different selection pressures on larval growth rate.

The present investigation of sex-specific mortality in these populations is more rigorous than our earlier study (Gotthard et al. 1994). Moreover, the direct selection on life span proposed here may be a more plausible explanation for the population difference in sex mortality differentials, compared to the possibility of an indirect effect of selection on larval growth rates. However, direct selection on life span and the possibility of indirect effects of selection on growth rate are not mutually exclusive alternatives (Tatar et al. 1997). The present study supports the hypothesis that the seasonality in Sweden creates a selective regime that favours individuals able to emerge as adults when the probability of finding mates is high. This seasonality hypothesis is also supported by the results for the Madeiran population: i.e. in the absence of strong seasonality, selection is predicted to favour traits that allow adults to sample a relatively longer period of the year. Due to the different reproductive schedules of males and females, however, these population differences in selective regimes should have sex-specific consequences. If the evolutionary scenario envisioned here is correct, both direct and indirect selection pressures may explain the variation in longevity seen in these populations of *P. aegeria*.

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