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A multi-environment comparison of senescence between sister species of *Daphnia*

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Abstract Senescence is a general decline of physiological state that accompanies advancing age. It affects nearly all organisms, but patterns of senescence vary markedly, even among closely related taxa. Understanding the evolution of this diversity requires information about environmental effects on the expression of variation among taxa. I examined genetically-based variation of senescence within and between two species complexes of *Daphnia* in four environments. The environments were defined by large differences in food and temperature, two factors known to influence senescence. The species studied were chosen to represent sister species that likely experience divergent (*D. pulex* and *D. pulicaria*) or similar (*D. mendotate* and *D. dentifera*) selection pressures on senescence. Overall, *D. pulex* expressed the greatest demographic senescence, *D. mendotae* and *D. dentifera* were intermediate, and *D. pulicaria* expressed the least. In environments representative of typical natural conditions, *D. pulex* had greater senescence than *D. pulicaria*, regardless of how late-life performance was assessed. This shows that genetic-environment interactions do not confound the interpretation of senescence differences between these species as the result of selective differences between their habitats. Comparison of *D. mendotae* and *D. dentifera* primarily revealed similar life histories, although differences in reproductive declines occurred in some environments. The joint observation of similar mortality patterns but dissimilar fecundity declines suggests that the trade-off between survival and reproduction changes with age. This calls into question the utility of only studying mortality for understanding evolutionary change of senescence in nature.

Keywords Mortality · Fecundity · Phenotypic plasticity · Zooplankton · Aging

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Introduction

One goal of evolutionary ecology is to understand differences among taxa in the way they respond to ecological variation. Such an understanding offers insight into how selection operates in natural systems. Many aspects of life history have been the subject of research in this context, but evolutionary ecologists are only beginning to address senescence. Senescence is a decline of physiological functioning as individuals grow older, resulting in a degraded ability to survive or reproduce. Senescence presents two challenges for evolutionary ecology. First, despite being deleterious, it is present in nearly all organisms. Second, it is both highly variable among taxa and phenotypically plastic. Evolutionary investigations of age-specific fitness components are important for understanding why senescence is a regular component of life histories. To address the variability, such studies must be conducted on multiple taxa in multiple environments.

In recent years, ecologists have capitalized on long-term data to show that senescence can be detected in terms of both survival and reproduction in wild populations, despite the belief that most individuals die due to extrinsic causes. For example, McDonald et al. (1997) found increasing mortality rates with age in Florida scrub jays, even though it was masked by selection and group size effects. Reliance on long-term monitoring generally precludes an evaluation of the role of plasticity in senescence diversity (but see Beverton 1987; Kirk 1997) or examination of differences between taxa. This paper reports an experimental study using short-lived zooplankton to evaluate the role of the environment in amplifying

or muting genetic differences between taxa in their age-specific fitness components.

Senescence evolves as a result of the decreasing force of selection as organisms grow older. Traits appearing early in life have a greater effect on total fitness than those appearing later, causing the later traits to be less exposed to selection than early traits (Medawar 1952; Williams 1957; Rose 1991). Because extrinsic mortality shapes the potential contribution of different ages to fitness, ecological variation among populations can lead to differentiation of investment in longevity and late-life reproduction (Williams 1957; Hamilton 1966; Edney and Gill 1968; Abrams 1993). In this paper, I use the term "senescence" to mean physiological degradation of an individual, and "demographic senescence" to refer to the population-level consequences of senescence that are measurable in terms of age-specific fitness components.

Closely related taxa that experience different mortality risks due to distinct ecologies provide an opportunity to study the evolution of senescence in nature (Austad 1993a; Reznick 1993). Comparing adult performance in a common environment lets one test the hypothesis that different mortality risks lead to genetic differentiation of senescence. Evidence supporting the evolutionary theory of senescence has been found in comparisons of opossums (Austad 1993b), grasshoppers (Tatar et al. 1997), ants (Keller and Genoud 1997) and *Daphnia* (Dudycha and Tessier 1999; Dudycha 2001). Although common-garden experiments reveal genetically based variation, they may be misinterpreted if the chosen environment substantially favors one taxon. In addition, natural habitats are temporally variable and are likely to differ among taxa, making it difficult to determine the best environment in which to compare trait expression. A possible solution is to make comparisons in a variety of environments.

Two ecological variables have been repeatedly shown to influence longevity and senescence of animals: food level and temperature (Finch 1990; Rose 1991). Extended longevity under low food and temperatures are well known in a variety of organisms (reviewed in Comfort 1979; Rose 1991), including *Daphnia* (MacArthur and Baillie 1929; Ingle et al. 1937; Korpelainen 1986). Few studies have examined naturally evolved differences in the influence of the environment on demographic senescence (but see Tatar et al. 1997), addressed fecundity, or considered the range of environments naturally experienced.

In this paper, I report on the environmental responsiveness of late-life performance and age-specific fitness components in the crustacean *Daphnia*. Previous work showed substantial diversity of demographic senescence patterns in the *D. pulex-pulicaria* complex in a single environment (Dudycha and Tessier 1999; Dudycha 2001). My primary goal here is to evaluate the degree to which interspecific comparisons of senescence are influenced by the environment in which traits are measured. To achieve this, I quantified life history in two species complexes of *Daphnia*. In one complex selection pressures on senescence differ greatly, in the other they differ slightly, if at all. I conducted life table experiments in four environments, defined by two temperatures and extremes of food availability. These environmental variables were chosen because their effects on senescence are well-characterized, they vary widely in nature, and I sought to maximize the chance of observing differences in levels of interspecific variation.

Materials and methods

Study system

The species of *Daphnia* chosen for this study have a long history of ecological research in Michigan, USA. *D. pulex* and *D. pulicaria* are sister species in the *Daphnia* subgenus; *D. mendotae* (formerly *D. galeata mendotae*) and *D. dentifera* (formerly *D. rosea*) are sister species in the *Hyalodaphnia* subgenus (Hebert 1995). Each pair of sisters form a complex composed of two parental (nominal) species and naturally occurring hybrid populations (Taylor and Hebert 1992; Hebert 1995; Colbourne and Hebert 1996). Despite low divergence and common hybridization within each complex (Lehman et al. 1995; Crease et al. 1997; Taylor and Hebert 1992; Taylor et al. 1996), each parental species differs in habitat use and seasonal phenology.

Daphnia pulex is found in temporary ponds, while *D. pulicaria* is found in deep lakes (Hebert 1995; Deng 1997). Populations of *D. pulex* recruit from resting eggs in early spring. The length of time ponds are habitable by *D. pulex* varies, but all ponds in this study dry by summer. This constrains maximum lifespan to a few months. In local ponds, water temperature varies from 6° to 28°, with potentially large diel fluctuation, over the period that *D. pulex* populations are active. Food levels for *D. pulex* are typically high, but can reach low levels when the population peaks and resting egg production begins (Tessier and Woodruff 2002a).

In contrast, *D. pulicaria* lives in deep lakes, and populations persist year-round (Geedey et al. 1996; Geedey 1997). Aggregate mortality risk of *D. pulex* in the study populations is much higher than *D. pulicaria* (Dudycha 1999, 2001). During much of the year food availability is low (Tessier and Woodruff 2002b). Lakes are uniformly cold in winter (<4°), but in summer, only the upper waters become warm (20–28°). *D. pulicaria* generally remains in the cool (~10°) bottom waters during summer, but can migrate into the warm surface waters at night (Leibold and Tessier 1991, 1998). *D. pulicaria* thus experiences a colder average temperature than *D. pulex*, whose temperature ranges from the cold of late winter to the warmth of late spring.

D. mendotae and *D. dentifera* are ecologically less distinct than *D. pulex-pulicaria*, because both species inhabit thermally stratified lakes. In southwest Michigan, *D. mendotae* is typically found in warm, pelagic surface waters of large lakes. Its density peaks in summer, but it also persists through the winter (Leibold and Tessier 1991; Taylor and Hebert 1992). *D. dentifera* is found in smaller lakes, mostly in the summer and fall. In these lakes, fish planktivory may be high, and consequently *D. dentifera* typically has strong diel vertical migration (Hall 1964; Dodson 1972; Threlkeld 1979; Leibold and Tessier 1991, 1998). Both species experience wide temperature variation, albeit at different temporal scales, with an average somewhat warmer than either *D. pulex* or *D. pulicaria*. Unlike the *D. pulex-pulicaria* contrast, it is unclear which, if either, species faces greater mortality risks.

Mortality rates of all four species have been measured in the field, and overall, mortality risk is greatest for *D. pulex*, intermediate for *D. mendotae* and *D. dentifera*, and least for *D. pulicaria* (Hall 1964; Threlkeld 1979, 1980; Hu and Tessier 1995; Leibold and Tessier 1998; Dudycha 1999, 2001). Consequently, we expect demographic senescence to be greatest in *D. pulex*, followed by *D. mendotae-dentifera* and least in *D. pulicaria*.

Methods

Life tables

Life table experiments were conducted on three replicate populations each of *D. pulex*, *D. pulicaria*, *D. mendotae* and *D. dentifera*. In addition, life tables on two populations of each naturally occurring hybrid type were conducted to use in comparisons between species complexes. I used populations of *D. pulex* and *D. pulicaria* from the extremes of the habitat permanence gradient. Such habitats are typical for their respective species, but are not a random sample of available *D. pulicaria* populations. For *D. mendotae* and *D. dentifera*, I chose populations where the target species was the dominant member of the species complex present, as determined by the diagnostic AO allozyme locus (Taylor and Hebert 1992). *D. mendotae* and *D. dentifera* do not coexist in the chosen populations, but some coexist with hybrids. I isolated five individuals from each population, in early spring (*D. pulex-pulicaria*) or early summer (*D. mendotae-dentifera*) to maximize the genetic variation sampled (Lynch 1984; Tessier et al. 1992; Geedey et al. 1996). Clonal lineages were established from all individuals and acclimated to the laboratory (20–22°, satiating food) for $\geq$3 generations prior to life tables (Tessier and Consolatti 1991). The purpose of using multiple clones was not to evaluate variation within populations; rather, it permits a more accurate assessment of populations as replicate samples of their taxon.

Mothers of experimental animals were raised concurrently from birth for several weeks at low density (1/50 ml) to reduce variation due to maternal effects. Life tables were initiated with neonates ~12 h old. Three cohorts composed of two neonates from each of the five clones were made for each population. Occasionally, mothers failed to produce an adequate number of female neonates when a life table began. Other neonates derived from the same population were used as substitutes when this happened. Animals were kept in incubators on a 16:8 L:D cycle. Every 2 days, animals were moved to fresh, filtered (1 μm) lake water. As animals grew and died, water volume was adjusted so cohorts could not filter >50% of the water between feedings (Knoechel and Holtby 1986). A small amount of cetyl alcohol was floated on the water to prevent surface film entrapment (Desmarais 1997). Mortality was recorded daily and fecundity (number of neonates) every 2 days until all animals died.

Life history variation was assayed under four environmental conditions: 20° or 26° at high or low food (20,000 or 3,000 cells/ml *Ankistrodesmus falcatus* fed daily), abbreviated 26°H, 26°L, 20°H and 20°L below. All species studied experience a range of variation that includes these temperatures and food levels in the wild, despite differences in their mean environment (J.L. Dudycha and A.J. Tessier, unpublished data). At 26°L, one population of *D. pulicaria* failed to mature and was removed from all analyses. Similarly, at 20°L, a population of *D. pulex* produced only one clutch of offspring, and was removed from analyses that included fecundity.

Logistic limitations prevented life tables on all populations in all environments from being conducted concurrently. However, because the focus of this study is on interspecific comparisons and whether those comparisons are generally influenced by the environment, all eight populations of a particular complex were always run together in each environment. Thus, comparisons between sister species within an environment are not temporally confounded. Attributing differences between environments directly to food or temperature can only be done with caution. For example, in *D. pulex-pulicaria*, life tables at 20°H, 26°H and 26°L broadly overlapped in time, but the 20°L life table was initiated 6 weeks after the 20°H experiment ended. Within *D. mendotae-dentifera*, the 20°L and 26°L were run concurrently, but the high food life tables had been completed while the *D. pulex-pulicaria* life tables were running. Thus differences among the environments may include variation due to unknown laboratory artifacts. However, there are four reasons to believe that any artifactual effects are minor. First, over the entire project there were no apparent changes in food or water quality, the most likely source of artifacts, as evidenced by consistent performance of algal cultures and stock *Daphnia* cultures. Second, phenotypic differences apparently associated with temperature and food level were substantial and consistent with known effects of food and temperature. Third, the effects of food and temperature were consistent between the two species complexes, despite different temporal arrangements of their life tables. Finally, as part of another experiment, two separate life tables were conducted at 20°H on *D. pulex-pulicaria* >8 months apart and their results were indistinguishable (Dudycha 1999, 2001).

Estimation of demographic traits

Senescence is fundamentally a broad trait of individuals, not populations, so no one demographic measure can fully characterize senescence. Nonetheless, it can be instructive to encapsulate senescence in an index reflecting the potential demographic consequences of senescence. Many authors focus exclusively on mortality rates, but interpreting mortality parameters as senescence is complicated by tradeoffs with fecundity. A senescing individual may alter the relative investment in survival versus fecundity, exacerbating the decline of one fitness component, while limiting degradation of the other. To gain insight into the net fitness effects of senescence, I combined investment in late-life survival and fecundity into a single index of late-life performance. First, I estimated age-specific performance as the expected remaining contribution of each age class to R_0, the expected lifetime reproduction. Elsewhere, this measure was called intrinsic value, because it is independent of r and is thus unaffected by clock-time, an extrinsic factor that obscures the use of reproductive value as a measure of senescence (Dudycha and Tessier 1999). Intrinsic value includes current performance and future potential, in terms of both survival and fecundity, and allows comparison among groups that differ in baseline survival and reproductive abilities (Dudycha and Tessier 1999).

The age when intrinsic value declines to 25% of its initial state is a useful index of late-life performance (denoted i_x25). By definition, intrinsic value equals one from birth to maturity and equals zero after reproductive cessation, and consequently other measures would be needed if those time periods were of interest. In *Daphnia*, it declines roughly linearly with age thereafter until it reaches ~0.15–0.20 (Dudycha and Tessier 1999; Dudycha 2001). Thereafter, marked decelerations may occur, probably due to lengthening of the inter-clutch interval. Setting the performance index at 25% avoids the deceleration while still reflecting late life. This index is analogous to lifespan, in that it represents a point in time that is partly dependent on factors other than senescence, but reflects the net phenotype of late-life performance on which selection could act. Unlike lifespan, however, the index is unlikely to be distorted by extreme values.

In addition to exploring an aggregate index of late-life performance, it is helpful to examine its component traits to better understand how late-life performance is organized. Therefore, I present the complete trajectories of age-specific mortality and fecundity for each of the parental species. These trajectories are averages of the traits estimated in the three replicate populations of each species. Actual mortality rates are presented to show the trait as it is expressed and subject to selection. Daily fecundity estimates are averages over all individuals in a cohort, over a 6-day sliding window, and finally across replicate populations.

Statistical analyses

Explicit comparisons of life history plasticity within- and between-species complexes were performed on population growth rate (r), and the index of late-life performance (i_x25). Response of r and i_x25 were tested in an ANOVA model that treated food, temperature and species complex as fixed effects, and taxon nested within species complex as a random effect with GLM in SAS v. 6.09. The test of an effect of taxon nested within complex was done with the Sheffé model, rather than the SAS model, because it tests for genetic

variance due to different taxonomic levels (Fry 1992). When significant genetic variation was indicated, the proportion of variation due to genetic differences within- versus between-species complexes was estimated via maximum likelihood (SAS v. 6.09, proc VARCOMP).

To facilitate comparison with other studies, I sought to apply a common mortality model to the data. A number of models are available, but these data are inadequate for reliably distinguishing among them. I chose to assume one of the simplest models, since the detailed form of mortality is not of interest in this study. The Gompertz model is a common exponential model that defines the age-specific mortality rate, $\mu_x = ae^{bx}$, in terms of the initial mortality rate (a) and an age-dependent mortality rate (b). If $b > 0$, mortality rate increases with age; this is often interpreted as senescence (e.g., Promislow 1991; Ricklefs 1998; Shaw et al. 1999). Alternate mortality models yielded similar results. Because the breadth of the project and inclusion of fecundity estimates necessitated using relatively small cohorts at the population level, I estimated b for each species by pooling data within species (for a total of ~90 individuals per species) and analyzing mortality at 3-day intervals. Estimates of b and their 95% confidence intervals were obtained via maximum likelihood, using WinModest v. 1.0.2 (Pletcher 1999a, 1999b; Promislow et al. 1999). Sensitivity analyses verified that the estimates were at global likelihood maxima, and that confidence intervals were stable. Within each environment, I tested whether sister species' parameters differed with a likelihood ratio test.

Results

Overall, the data showed that interspecific differences of late-life performance were greater at 20° than at 26°. Food level had little impact on the index of late-life performance (i_x25), but strongly influenced r in all species; temperature had the reverse effects (Fig. 1). These patterns were strikingly similar in both species complexes, so they were analyzed jointly, pooling the effects of environment across complex.

Late-life performance (i_x25), in contrast to r, was primarily influenced by temperature rather than food level, although food effects were significant (Fig. 1, Table 1). Variation was not apparent between the species complexes but was strong among taxa within complexes (Table 1). A significant interaction between taxon within complex and temperature resulted in much more of the variation in late-life performance being due to genetic differentiation within complexes at 20° (54.4% of total variation) than under thermal stress (29.1%).

Food level was the only factor that had a substantial and significant effect on r ($P<0.0001$, $F=249.2$, $df=1, 4.29$; Fig. 1). Temperature had a slight effect ($P=0.018$, $F=13.7$, $df=1, 4.36$), but neither complex ($P=0.21$, $F=2.19$, $df=1, 4.16$) nor taxon nested within complex ($P=0.42$, $F=1.79$, $df=4, 1.68$) had an effect. There were no significant interactions. Driven by food, the model explained >80% of the variation in r. The lack of any taxonomic role in explaining r variation indicates that comparisons of taxa in other aspects of life history are not confounded by differences in fitness with respect to the broad set of environments chosen.

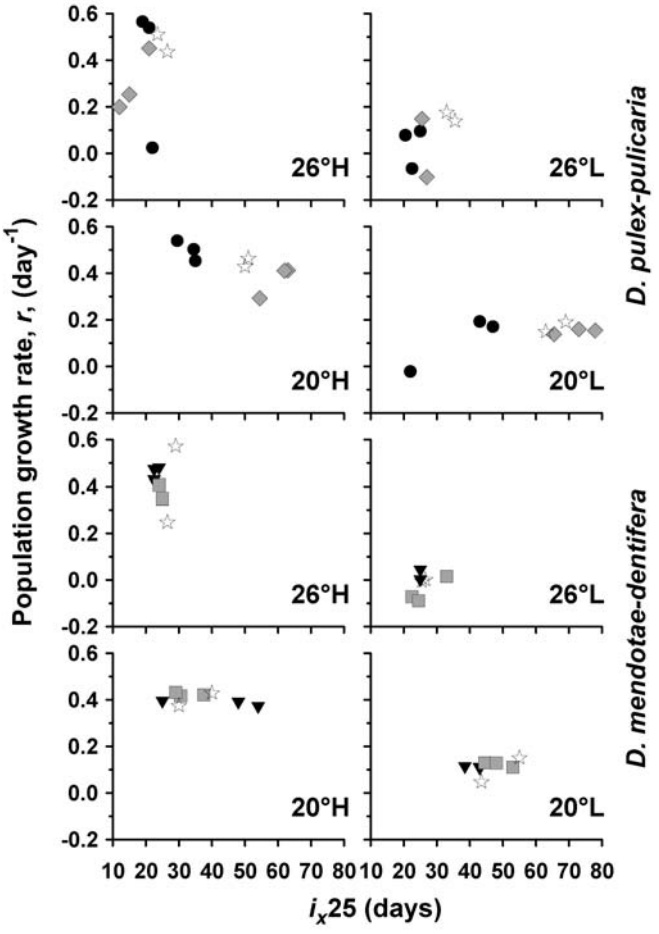

Fig. 1 Estimated late-life performance and population growth rate of *Daphnia* in four laboratory environments. *Black symbols* represent populations of *D. pulex* (*upper quartet*) or *D. mendotae* (*lower quartet*); *grey symbols* are *D. pulicaria* or *D. dentifera*; *white symbols* are hybrids. Environments are identified in the lower right corner of each panel (*Temperature* and *H*= high food, *L*= low food)

Mortality

In all cases, age-specific mortality increased at later ages, but the degree to which it increased and the ages at which it was substantially elevated varied among species and environments (Figs. 2, 3). At 26°, a relatively stressful temperature, the variation between species was much less than that observed at 20°. In addition, at 26° there was little obvious effect of food level on mortality patterns, but at 20° the low food level extended longevity.

The difference between mortality patterns of *D. pulex* and *D. pulicaria* changed across environments (Fig. 2). At 26°H, these taxa were quite similar. At 26°L, substantially elevated mortality occurred in *D. pulex* about 10 days earlier than in *D. pulicaria*. This gap expanded to ~40 days at 20°H and was >60 days at 20°L (Fig. 2). Changes in the mortality gap between *D. pulex* and *D. pulicaria* occurred largely because the mortality pattern of *D. pulicaria* was notably more plastic than that of *D. pulex*. In most

Table 1 Sources of variation of an index of late-life performance (i_x25) described in the text; for the full model r^2=0.91

Source	*df*	MSE	*F*	*P*
Species complex	1, 4.0	437.92	1.03	0.37
Temperature	1, 4.0	7826.01	22.32	**0.0091**
Food level	1, 4.1	719.35	10.00	**0.0332**
Taxon (complex)	4, 39	434.09	12.29	**<0.0001**
Complex × temperature	1, 4.0	597.38	1.70	0.27
Complex × food level	1, 4.1	64.05	0.89	0.40
Complex × food × temperature	1, 4.2	40.03	1.43	0.29
Temperature × food level	1, 4.2	175.51	6.28	0.0634
Taxon (complex) × temperature	4, 4	356.56	12.8	**0.0149**
Taxon (complex) × food level	4, 4	72.59	2.61	0.19
Taxon (complex) × food × temperature	4, 39	27.78	0.79	0.54

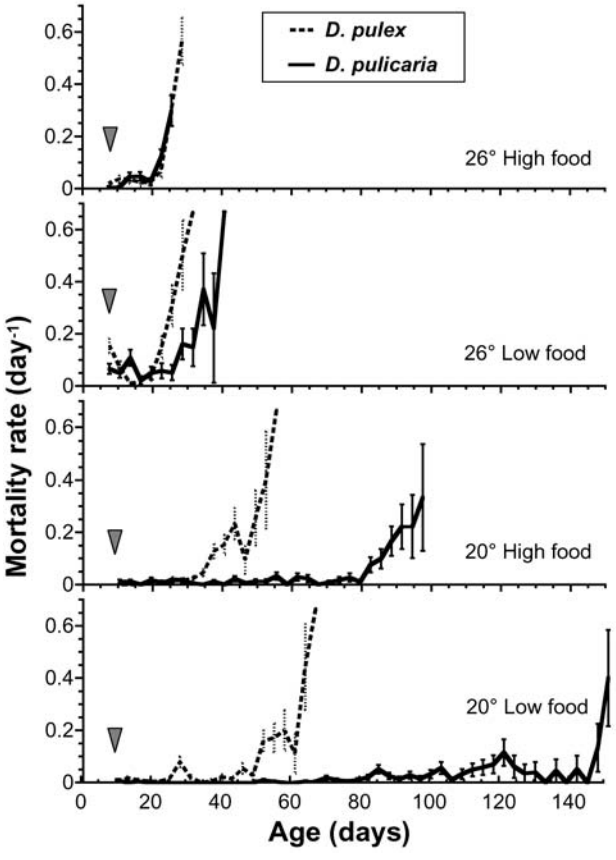

Fig. 2 Mortality rates of *Daphnia pulex-pulicaria* in four environments. Mean±1 SE of three replicate populations per species. *Triangles* point down to the age at maturation

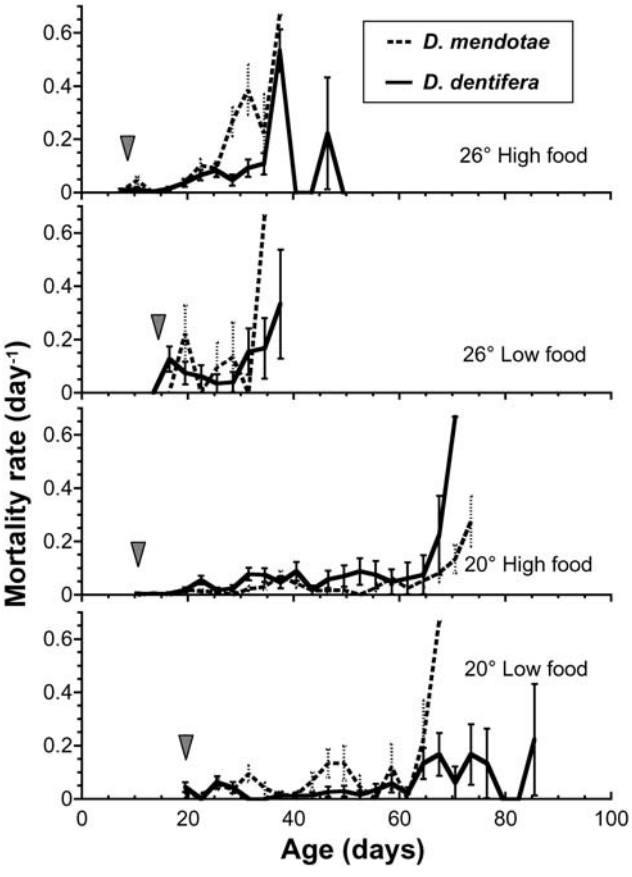

Fig. 3 Mortality rates of *Daphnia mendotae-dentifera* in four environments. Mean±1 SE of three replicate populations per species. *Triangles* point down to the age at maturation. Note that the Age scale differs from that of Fig. 2

environments, the estimated Gompertz *b* of *D. pulex* was significantly greater than in *D. pulicaria* (Fig. 4). The estimates of *b* for *D. pulex* were strikingly different across environments (particularly with respect to food), whereas those of *D. pulicaria* were indistinguishable among three environments.

D. mendotae and *D. dentifera* had similar mortality patterns (Fig. 3). The data suggest that *D. mendotae* may have a higher mortality rate than *D. dentifera* under some conditions (e.g., older than 25 days at 26°H). However, these apparent differences may be exaggerated due to distinctly non-monotonic changes of mortality in these species (Fig. 3). There is some evidence of a greater response to temperature in *D. mendotae* at high food than in *D. dentifera*. Mortality patterns of these two species differ across environments more than those of *D. pulex*, but less than *D. pulicaria*. Estimates of Gompertz *b* are fairly stable across environments, with some evidence for elevation at the higher temperature (Fig. 4). The only difference between the species occurred at 26°H, with a higher *b* for *D. mendotae*.

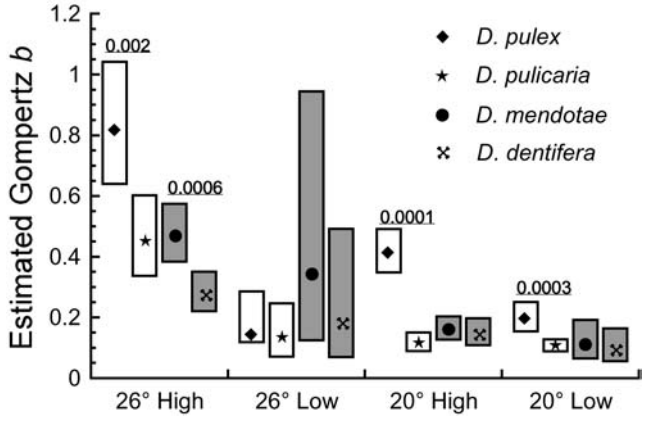

Fig. 4 Estimated Gompertz senescence parameters of *Daphnia* in four environments (defined by temperature and High or Low food). Symbols indicate global maximum likelihood estimates, bars show 95% CI. Data are pooled within species. *White bars* show *D. pulex-pulicaria*, *grey bars* show *D. mendotae-dentifera*. *P*-values from a likelihood-ratio test appear over sister species in environments where the two species' *b* was significantly different

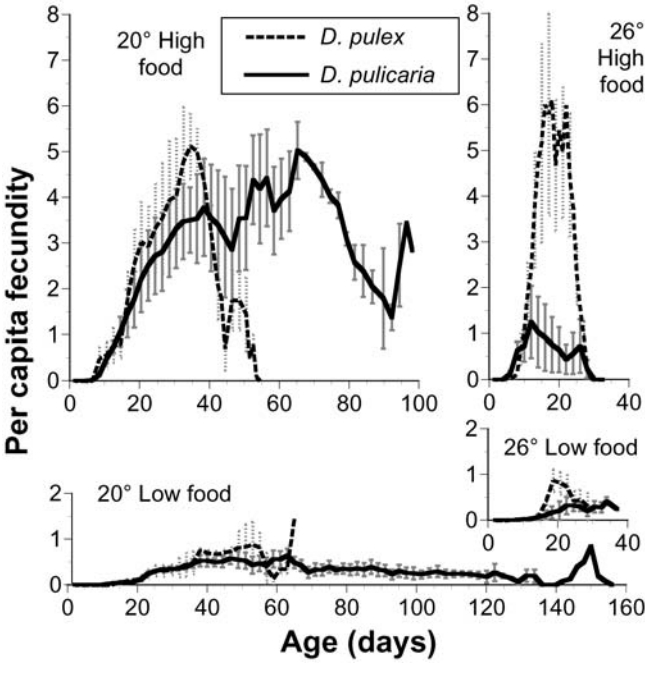

Fig. 5 Fecundity of *Daphnia pulex-pulicaria* in four environments defined by temperature and food level. Curves indicate mean fecundity (offspring per female per day, in a 6-day moving window) of three replicate populations per species. *Error bars* are 1 SE. Scales for all environments are identical, but note that the horizontal axes of the two low food environments are offset

Fecundity

In most species in most environments fecundity clearly declined following a peak (Figs. 5, 6). Steepness (i.e., rate) of fecundity decline, and the effect of environment on the steepness, varied among species. Declines were typically steeper at high food than low food, probably due

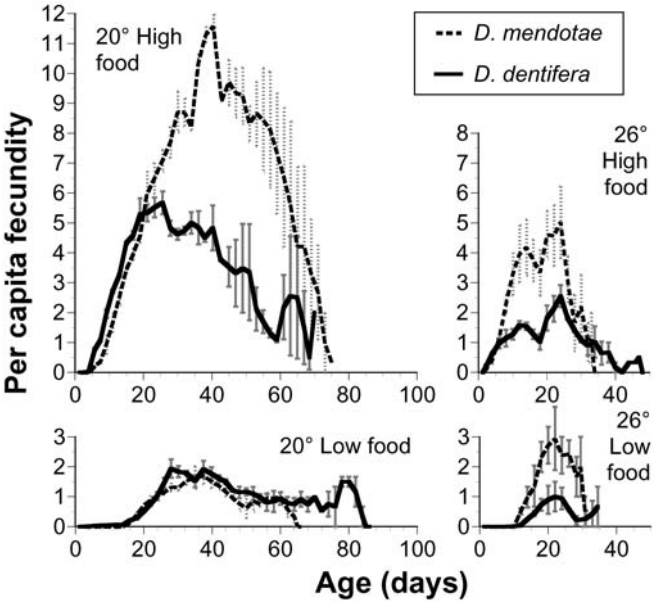

Fig. 6 Fecundity of *Daphnia mendotae-dentifera* in four environments defined by temperature and food level. Curves indicate mean fecundity (offspring per female per day, in a 6-day moving window) of three replicate populations per species. *Error bars* are 1 SE

to a strong effect of food on maximum fecundity. Fecundity usually declined to zero, but not always (e.g., *D. pulicaria* at 20°H).

Although the route differs among environments, reproductive decline in *D. pulex* appeared more rapid than in *D. pulicaria* (Fig. 5). For example, both species reached a similar maximum fecundity at 20°H, but *D. pulex* reached that level ~30 days earlier, then dropped rapidly to zero. Fecundity of *D. pulicaria* declined over a longer period, and to roughly 30% of the maximum rather than zero. In contrast, the steeper decline of *D. pulex* at 26°H occurred because *D. pulex* reached a higher fecundity than *D. pulicaria*. Fecundity differences between these species were less pronounced under low food, although *D. pulicaria's* fecundity tapered off slowly (20°L) or not at all (26°L). Fecundity patterns of *D. pulex* were largely unaffected by temperature, but temperature affected fecundity of *D. pulicaria* dramatically when food was high (Fig. 5). In addition, the steepness of fecundity decline in *D. pulicaria* was clearly much shallower under low food than high, but a difference was not apparent for *D. pulex*.

Fecundity differed strongly between *D. mendotae* and *D. dentifera* in three environments (not 20°L), in contrast to their similar mortality patterns (Fig. 6). At 26°H, 26°L and 20°H, *D. mendotae* reached a substantially higher fecundity level than *D. dentifera*, resulting in steeper fecundity declines. At high food, both species' fecundity was roughly halved in magnitude from 20° to 26°, but a similar change did not occur at low food. Thus there is no strong evidence that reproductive decline responds to

environment differently in *D. mendotae* versus *D. dentifera*.

Discussion

The expected pattern of increased demographic senescence under higher temperature and food level was evident in all four species of *Daphnia*. This is consistent with prior studies of these factors on *Daphnia* longevity (MacArthur and Baillie 1929; Ingle 1933; Ingle et al. 1937; Korpelainen 1986). By studying temperature and food level jointly, we see that the response of demographic senescence to food was curtailed under thermal stress. Even though there were broad similarities, clear differences between species emerged. Across environments, the general ranking of least demographic senescence in *D. pulicaria*, moderate in *D. mendotae-dentifera* and greatest in *D. pulex* shows a lack of correspondence to taxonomy at the species level despite >150 millions of years divergence between the complexes (Colbourne and Hebert 1996). Instead, this ranking roughly matches the known ecological variation in the aggregate extrinsic mortality risk these species face, with *D. pulicaria* inhabiting a stable, low-risk environment, *D. mendotae-dentifera* facing moderate risks, and *D. pulex* facing much higher risks.

Genetic differentiation of phenotypic plasticity was evident among taxa within complexes, but no obvious difference between complexes was observed. Specifically, the effect of temperature on late-life performance was strong in both complexes while the effect of food was modest. Temperature also affected the magnitude of expressed genetic differentiation within species complexes, which accounts for more than half of the phenotypic variation at 20°, but less than a third at 26°. This means that the phenotypic variation on which selection could act is greater at the benign temperature. Conversely, it shows that differences in late-life performance are limited under stressful conditions. Though the pattern occurred in all species, the temperature response was most pronounced in *D. pulex-pulicaria*. Two general conclusions can be drawn: First, differentiation of both late-life performance and its plasticity is pronounced at the taxon-within-complex level, but not between complexes. Second, the differentiation is greater within *D. pulex-pulicaria* than within *D. mendotae-dentifera*.

The life tables in this experiment used replicate populations to compare species, and consequently relied on genetically heterogeneous cohorts. This obscures the age-specific life history traits of individual genotypes, and thus we do not know the basis of variation within populations. At one extreme, all genotypes in the population may exhibit similar life histories, as might be expected in populations subject to strong stabilizing selection on life history. Populations may instead be a composite of distinctly different life histories, such as short-lived highly fecund genotypes cohabiting with long-lived low-fecundity genotypes. This scenario may be expected where distinct life histories have complementary advantages, for example if there is habitat heterogeneity available to a population. Further work at the within-population level will be needed to elucidate the manifestation of senescence for particular genotypes, and whether the among-genotype variation differs between species.

Demographic senescence in *D. pulex-pulicaria*

The comparisons of life history between *D. pulex* and *D. pulicaria* suggest that in their natural habitats, *D. pulicaria* can extend longevity and reproduction longer than *D. pulex*. At the benign temperature (20°) fitness declined more substantially against age in *D. pulex* than in *D. pulicaria*, regardless of which fitness component is examined. This is true at resource levels that are satiating or near starvation. At the stressful temperature (26°), interspecific differences were evident only at high food levels. *Daphnia* experience a lower average temperature in the field than those studied here, but it is unlikely that the observed rankings switch at lower temperatures. Similarly, although *D. pulex* inhabits a boom-bust community, it is possible that at food levels intermediate to those used here *D. pulex* may extend longevity (as in *Drosophila*; Chapman and Partridge 1996). Nonetheless, it seems improbable that *D. pulex* would live longer than *D. pulicaria*, since that would require living longer than the ponds' hydroperiod. Despite substantial genetic-environment interactions, the species facing higher extrinsic mortality risks (Dudycha 2001) has greater senescence, as generally predicted by the evolutionary theory of senescence. However, theory indicates that the relationship between selection and senescence is more complicated that the coarse pattern described here (Abrams 1993). These results suggest that it will be fruitful to further investigate how selection is shaping senescence in the wild, incorporating seasonal environmental change of risks, and the age-structure of mortality risk and of density-dependent effects on fecundity and mortality.

The goal of this project was to explore the effects of environment on comparisons between species, not to test hypotheses of adaptive plasticity. However, noting that plasticity differs between *D. pulex* and *D. pulicaria* we can speculate as to why. Consider that an individual seeking to maintain a stable demographic phenotype across a wide range of environments must be able to adjust the underlying physiology that determines its life history. By varying physiological investment in maintenance with respect to temperature and resources, *D. pulex* may more fully exploit the environmentally limited time it has available. Conversely, an adjustable life history may result from a stable physiology whose life history consequences are environment-dependent. In the habitats of *D. pulicaria*, the advantages of longer life are more pronounced under ecological conditions that are associated with greater longevity. Habitat quality varies seasonally in the lakes *D. pulicaria* inhabits, with periods

of very poor quality in the summer (due to low resources) and winter (due to cold). A physiology that permits extended reproductive longevity when the environment is poor, but does not apparently require increasing investment in maintenance, may be advantageous.

Demographic senescence in *D. mendotae-dentifera*

The life histories of *D. mendotae* and *D. dentifera* are much more similar to each other than those of *D. pulex* and *D. pulicaria*, despite a longer time for evolutionary divergence (3.5 million years versus 500,000 years; Colbourne and Hebert 1996). This is expected if selection is more important for senescence than neutral processes, because the habitat differences between *D. mendotae* and *D. dentifera* are not as large. Although the species did not express appreciably different plasticities, the *D. mendotae-dentifera* complex as a whole fits the pattern of a fairly stable physiology producing a flexible life history. Mortality patterns and Gompertz *b* were similar between the species, but suggested modestly greater demographic senescence in *D. mendotae*. By contrast, fecundity differences were sharp, with higher levels that declined faster in *D. mendotae* than *D. dentifera* in three environments. Therefore, overall performance typically declined faster in *D. mendotae* than *D. dentifera*, but the difference was less than between *D. pulex* and *D. pulicaria*.

These results suggest that the relative investment in fecundity and survival can change with age. For example, at 20°H there is no difference between *D. mendotae* and *D. dentifera* in either mortality pattern or Gompertz *b*, indicating a similar age-specific investment in survival. From age 25–70 days, fecundity of *D. dentifera* declines more or less linearly from 5 to 1 offspring per female per day. Fecundity of *D. mendotae* declines from 11 to 1 over ages 40–75 days. Therefore, age-specific changes in reproduction differ strongly between species, and consequently, in at least one species the ratio of investment in survival to reproduction changes with age. Evolutionary studies of senescence that examine only mortality necessarily assume that this ratio is invariant across ages. In the case of *D. mendotae-dentifera*, this would be misleading. Many studies of senescence are specifically interested in the detailed form of mortality patterns, and necessarily require large cohorts where measuring fecundity is impractical. However, if age-specific tradeoffs are typical of life histories, difficulties arise in interpreting mortality-only studies in terms of evolution by natural selection, and thus in linking them to the natural diversity of life histories. Research on beetles (Tatar and Carey 1995) has also shown age-dependence in the tradeoff between survival and fecundity. The importance of this phenomenon to interpreting senescence warrants research aimed directly at determining the age-structure of survival versus fecundity allocation in a number of species.

Consequences of phenotypic plasticity for selection

Both *r* and late-life performance (i_x25) were strongly influenced by environment. Food level had a strong positive effect on *r* through its effect on fecundity, but its effect on late-life performance was much smaller. The reverse was true of temperature. Benign temperature led to improved late-life performance relative to stressful temperature, but it had only a minor effect on *r*. These differences suggest that the opportunity for evolution by natural selection differs among environments. Temperature notably influenced the degree to which genetic differentiation in late-life performance was expressed. At the stressful temperature, variation of late-life performance among taxa was lower than at the benign temperature (Fig. 1), suggesting that the impact selection could have is reduced under temperature stress. Furthermore, high food level elevated population growth rate, so the consequences of even small trait differences would be rapidly manifest under conditions where population size is limited. Thus selection should be most efficient in the most benign environment (20°H), and the late-life traits of *Daphnia* relatively optimized for such an environment.

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