Ecology Letters, (2001) **4**: 102–105

LETTER

The senescence of *Daphnia* from risky and safe habitats

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Abstract

Evaluating life history in an ecological context is critical for understanding the diversity of life histories found in nature. Lifespan and senescence differ greatly among taxa, but their ecological context is not well known. Life history theory proposes that senescence is ultimately caused by a reduction of the effectiveness of natural selection as organisms age. A key prediction is that different levels of extrinsic mortality risk lead to the evolution of different senescence patterns. I quantified both mortality risk and investment in late-life fitness of *Daphnia pulex-pulicaria*, a common freshwater zooplankter. I found that *Daphnia* from high-risk pond habitats invest relatively little in late-life fitness, whereas those from low-risk lake habitats invest relatively more in late-life fitness. This suggests that ecological approaches can be useful for understanding senescence variation.

Keywords
Ageing, zooplankton, life history, mortality rate, pond–lake gradient.

Ecology Letters (2001) 4: 102–105

Senescence is the decline of physiological capabilities that accompanies advancing age. The degree to which organisms senesce and their associated lifespans vary widely among taxa (Comfort 1979; Rose 1991; Finch & Tanzi 1997). This is usually attributed to nonecological factors, despite a strong theoretical argument that ecological variation may lead to the evolution of different senescence patterns. Life history theory predicts that genetic variation of senescence will be related to ecological variation of mortality risk (Williams 1957; Rose 1991). The prediction results from the notion that the force of natural selection necessarily declines as age increases, because traits expressed after an individual has begun reproduction can be inherited by the next generation regardless of their deleteriousness. This decline is not uniform in all taxa; it varies with mortality risk (Medawar 1952; Williams 1957; Hamilton 1966). Ecological variation of predation, competition, parasitism and abiotic factors creates mortality risk variation. A greater risk of being killed means that an individual should invest less in late-life fitness because the investment is unlikely to pay-off, leading to the evolution of a specialized life history with rapid senescence. In relatively safe habitats, investment in bodily maintenance may be advantageous by allowing prolonged reproduction, leading to slow senescence (Williams 1957). However, few data address the potential for senescence variation to reflect life history specialization to habitat differences.

A few reports have related variation of senescence or lifespan to supposed differences in mortality risk (Keller & Genoud 1997; Tatar *et al.* 1997; Dudycha & Tessier 1999), but none directly measured risk. I present data comparing quantitative estimates of extrinsic mortality risk to naturally evolved variation of senescence in the common freshwater zooplankter, *Daphnia pulex-pulicaria.*

Daphnia pulex-pulicaria are cyclically parthenogenetic microcrustaceans that are morphologically indistinguishable. Hybridization is frequent (Crease *et al.* 1989, 1990; Hebert *et al.* 1993) and the nominal species are not distinct lineages (Lehman *et al.* 1995; Crease *et al.* 1997; Colbourne *et al.* 1998). However, they typically occupy the extreme ends of the pond–lake waterbody size gradient (Hebert 1995; Deng 1997). *Daphnia pulex* inhabits temporary ponds where ecological conditions change rapidly. *Daphnia pulicaria* generally inhabits deep lakes that provide a permanent, relatively stable environment year-round (Hu & Tessier 1995; Geedey *et al.* 1996). Many ecological differences that influence *Daphnia* mortality risk (e.g. predation, resource availability and abiotic factors) coincide with this habitat difference (Wellborn *et al.* 1996). *Daphnia pulicaria* populations have low death rates even when planktivory is highest (Leibold & Tessier 1998), but death rates for *D. pulex* have not been reported. Dispersal between habitats occurs readily and hybrids inhabit both types of waterbodies. Thus, alleles that promote or retard senescence may be exposed to selection in both habitats, regardless of origin.

Five individuals were isolated from each of 11 populations shortly after sexually produced diapause eggs hatch, i.e. when within-population genetic diversity is expected to be greatest (Lynch 1984; Geedey *et al.* 1996). Stock lineages were established under lab conditions (satiating food, 20°C), acclimating them for $\geqslant 3$ generations before measuring senescence. All populations experience these resource and temperature conditions naturally, but they more closely reflect the average condition in ponds; lakes are cooler with fewer resources on average (Hu & Tessier 1995; Geedey *et al.* 1996; Dudycha, unpublished data). Life history measurements were made on cohorts of 30 female neonates per population (6/lineage). Extrinsic mortality was excluded; thus, the senescence measurements reflect the intrinsic capabilities of individuals. Details on the life tables and comparative ecology of *D. pulex-pulicaria* are elsewhere (Dudycha & Tessier 1999).

Measures of senescence that combine survival and fecundity eliminate the possibility that tradeoffs between survival and fecundity will obscure comparisons of senescence (Partridge & Barton 1993, 1996; Dudycha & Tessier 1999). To describe senescence, I combined daily survival and fecundity data into a single measurement, defined as the contribution to expected lifetime fecundity remaining at a specific age. This measure of age-specific fitness, called intrinsic value, represents the physiological state of an average individual using a currency that is directly related to evolutionary fitness (Dudycha & Tessier 1999). I summarized senescence as the index i_x25, the age when the remaining contribution to lifetime fecundity has declined to 25% of its initial value (Dudycha & Tessier 1999). Younger values of i_x25 indicate more rapid senescence. The index is directly analogous to lifespan, but more completely represents physiological state and the persistence of fitness into late life because it incorporates fecundity. Therefore, it allows comparison of relative investment in late-life performance. As with the use of lifespan as an indicator of senescence, nonsenescent mortality (i.e. age-independent) is assumed to be constant across populations. This assumption is reasonable for laboratory cohorts raised under identical conditions.

Field mortality risk was quantified as death rate (d), the difference between population growth (r = log change in population density) and birth (b) rates. *Daphnia* carry their eggs, allowing accurate estimates of b based on temperature and the egg stage distribution (Threlkeld 1979). Population density, temperature and egg stage distribution were estimated at time intervals approximating the egg development time. Ecological influences on population dynamics vary seasonally, so I estimated $d \geqslant 5$ times during the year in each population, covering all phases of natural population dynamics. The average daily mortality risk individuals experienced in each population was the average of the d estimates, weighted by population density, over one year.

Age-specific contribution to lifetime fitness declines much more rapidly in populations from ponds than in those from lakes (Fig. 1), confirming an earlier report on a subset of these populations (Dudycha & Tessier 1999). There are striking differences between the habitat types' riskiness (Fig. 2), with rapid senescence of populations from risky habitats, and slow senescence of populations from safe habitats. This assumes that risk differences are consistent across years, which is likely between habitat types, but not necessarily within habitat types. Because estimates of field mortality risk were weighted by population density, the comparison reflects the average daily mortality risk, rather than extreme mortality risks that may occur periodically. Senescence itself is not an important direct factor for field mortality: field life expectancy was 4–10 days, but median laboratory lifespans

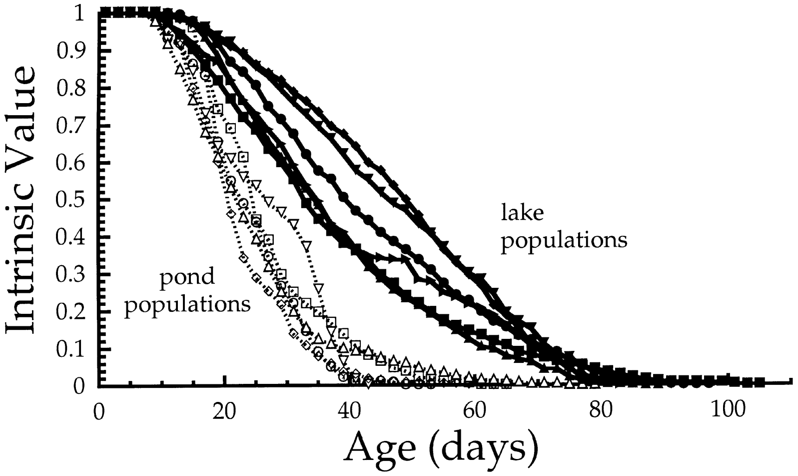

Figure 1 Age-specific fitness (intrinsic value) in populations of *Daphnia pulex-pulicaria*, estimated as the proportion of expected lifetime fecundity remaining. Dashed lines and open symbols represent temporary pond populations (*D. pulex*); solid lines and closed symbols represent perennial lake populations (*D. pulicaria.*).

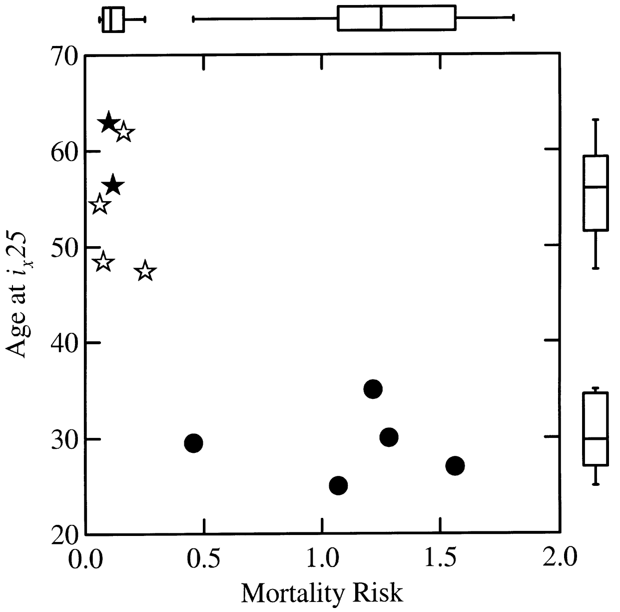

Figure 2 Senescence and mortality risk in 11 populations of *Daphnia pulex-pulicaria.* Stars indicate populations from permanent lakes, circles represent temporary ponds. Solid symbols are populations that comprise one phylogenetic mtDNA clade; open symbols comprise a distinct clade. Senescence is indexed as i_x25, the age (in days) when only 25% of expected lifetime fitness remained in a laboratory life table experiment. Average mortality risk is the per-capita death rate (per day) that occurs in the field, estimated from multiple measurements over one year that were then averaged, weighted by population density. Boxplots show the univariate distributions of variables for each habitat.

were 20–90 days. Nonetheless, susceptibility to extrinsic mortality risks (e.g. predators) may increase with age in the field. It is unlikely that the association between senescence and risk is driven by senescence itself. If it were, the relationship would not be expected to map onto habitat type, because dispersal between habitat types would tend to erode systematic differences between them. It is also unlikely that genotype–environment interaction drives the association. The lab environment was closer to that of ponds, but those were the populations with poor late-life performance. In addition, life tables run at other environmental conditions never showed superior late-life performance of pond populations (Dudycha 1999).

The data presented here show a pattern dominated by differences between the two habitats, which are confounded with taxonomic nominal status. However, the current view is that *D. pulex* and *D. pulicaria* are an interbreeding species complex (Lehman *et al.* 1995; Crease *et al.* 1997; Colbourne *et al.* 1998). Furthermore, an mtDNA phylogeny of these same populations (Dudycha 1999) is inconsistent with the hypothesis that senescence differences were congruent with population relatedness. The tree comprised two sharply distinct clades, but one clade included both habitats (identified in Fig. 2). This is evidence that genes have successfully crossed the habitat boundary, but genes governing senescence did not accompany them. This suggests that selection is an important factor in the evolutionary divergence of senescence. Such a conclusion needs confirmation by examining additional pairs of *Daphnia* taxa whose members occupy different habitats along the pond–lake gradient. Further work should also determine how variable riskiness is among years, include habitats with intermediate riskiness, and be scaled to detect the smaller life history differences expected within habitat types. Selection experiments, such as manipulating habitat riskiness in mesocosms and measuring senescence changes after many generations, would also be illuminating.

Considering the incomplete divergence among these populations, the potential for migration among habitats and the large magnitude of senescence differences, the data suggest that selection is an important force contributing to senescence differences between *D. pulex* and *D. pulicaria.* This indicates that an understanding of ecological interactions and their effects on mortality risk can contribute to our comprehension of senescence variation. Because senescence is less closely tied to fitness than early life-history traits, uncovering differentiation of senescence shows that ecological studies are a strong approach to understanding the evolutionary origin of trait diversity. The data presented here aggregate all field mortality into a single estimate of risk, and all life history information into a single index. Both are considerable simplifications of complex phenomena. Elaborations on the life history theory have shown that the age-structure of risk should also influence senescence evolution (Abrams 1993). By incorporating age-structure and environmental correlates of risk, ecologists may contribute to explaining the diversity of senescence at multiple biological scales and reveal an evolutionary basis for environmental modulation of senescence.

ACKNOWLEDGEMENTS

The author thanks Alan Tessier for comments and discussion of this work and Pam Woodruff for technical assistance. Three anonymous reviewers provided constructive criticism of an earlier version of this paper. The research was supported by the U.S. National Science Foundation through grants DEB-9421539 (to A.J. Tessier), DEB-9701209 (to AJT and JLD), and research training grants (DIR-9113598 and DBI-9602252) to the Kellogg Biological Station. This is KBS contribution # 944.

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BIOSKETCH

Jeff Dudycha is interested in the evolutionary ecology of life history. He is working towards understanding trait evolution across multiple levels of biological organization, from genes to communities. His research has focused on the ecological context in which senescence evolves, and the ecological consequences of senescence in natural populations.

Editor, M.M. Lambrechts
Manuscript received 13 October 2000
First decision made 8 November 2000
Manuscript accepted 9 January 2001