Roots might be the base of rhizosphere food webs, but Martha Hawes (University of Arizona, Tucson, AZ, USA) reported that the release of microbial substrates from young healthy roots is dominated by 'border' cells that detach from the root cap, rather than by exudation distributed along the entire root. The food web in the rhizosphere of lupines includes root-feeding insects parasitized by nematodes, which use toxin-producing symbiotic bacteria to kill their prey, whilst being preyed on, in turn, by nematode-trapping fungi (Don Strong, University of California, Davis). This system is characterized by periodic die-offs and recoveries of the lupine population.

In spite of the shared enthusiasm for the rhizosphere system, and for increasing crossdisciplinary collaboration, molecular biologists and ecologists still have some bridges to build. Some participants questioned the use of harmless anthropomorphisms, such as 'partner choice' or 'host recognition', to describe the behavior of organisms without nervous systems. Some were unaware of – or reluctant to accept – key ideas from evolutionary biology, such as the severe constraints on the ability of natural selection to ensure the long-term survival of species, let alone ecosystems[8]. Differences among disciplines in the use of seemingly simple words, such as 'why?', are likely to persist. But the challenges and opportunities posed by rhizosphere research, and the eagerness of most of the participants to expand their scientific worldviews, made this an unusually stimulating and enjoyable meeting.

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The biodemography of life span: resources, allocation and metabolism

Lloyd Goldwasser

A workshop on Life Span: Evolutionary, Ecological and Demographic Perspectives was held at the Petros M. Nomikos Conference Centre in Santorini, Greece, from 14 to 18 May 2001.

Evolutionary ecology is more often interdisciplinary in intent than in practice, but, when combined with demography and applied to questions about life span, it can weave together parts of physiology, molecular and cell biology, anthropology and the social sciences. This workshop brought together workers in several of these fields and papers from it will be published in 2002 in a supplement to *Population and Development Review*.

Building on a 1996 workshop on longevity[1], this workshop was designed to focus attention on longevity rather than on mortality, motivated by Sacher's[2] rephrasing of the question, 'Why do we grow old?' to 'Why do we live as long as we do?' Two shifts were evident: (1) away from specific age-related diseases and towards

changes that accompany aging *per se* (Jay Olshansky, University of Chicago, IL, USA); and (2) away from aging as a separate, late-in-life phenomenon and towards processes common to all life stages[3]. Accordingly, much of the work reported focused on the structure and plasticity of life span and its integration with other traits. James Carey (University of California, Davis, CA, USA) emphasized the role of natural selection in shaping life span; Ken Wachter (University of California, Berkeley, CA, USA) pointed out that events after reaching reproductive maturity are no less a part of individual development than are those before; and Ronald Lee (University of California, Berkeley) and Joshua Goldstein (Princeton University, NJ, USA) suggested that human life stages might be stretched, shrunk, or even iterated by their interplay with social and economic forces.

One of the simple successes of this workshop was a group of definitions that removes the inconsistencies that have surrounded the use of life span and related terms (Box 1; John Wilmouth, University of California, Berkeley). Useful distinctions were also drawn between aging (which reflects chronological time) and senescence (which reflects loss of function). Recent interest in health span in addition to life span makes this distinction relevant, but also highlights the difficulty of quantifying senescence or the related concept of frailty. Advances in physiological tools that might make such quantification possible were of particular interest.

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Patterns of mortality and life span

During human adulthood, per capita mortality rates double with about every eight years of age, and such exponentially increasing rates, first described in 1825 by Benjamin Gompertz, are the standard of comparison for patterns of mortality. After ~80 years of age, the rate of increase of mortality declines and mortality rates may even plateau. Beyond ~105 years, mortality rates may decline, but small sample sizes make these estimates uncertain. However, a clear exponential increase followed by a leveling off and then a decline in mortality rates have been found consistently in species as diverse as *Drosophila melanogaster*, medflies *Ceratitis capitata* and three *Anastrepha* spp., a parasitoid wasp *Diachasmimorpha longiacaudtis*, the nematode *Caenorhabditis elegans* and yeast *Saccharomyces cerevisiae* (Carey; James Vaupel, Max Planck Institute for Demographic Studies, Rostock, Germany). The explanation that heterogeneity among individuals causes the decline in mortality rates (those with weaker constitutions die out earlier, leaving those with stronger constitutions) is reasonable but incomplete: the observed declines would require an unrealistically high level of heterogeneity[4], and they occur even in genetically uniform strains of *Drosophila* and yeast. The ubiquity of these patterns suggests that the determinants of life span, however subtle, are closely tied to fundamental life processes.

Intriguing ideas about patterns of life span are now being refined and tested with new data[5] and comparative approaches, as focus shifts from life-history invariants towards different types of variation and their maintenance (Shripad Tuljapurkar, Mountain View Research, CA, USA). Robert Ricklefs (University of Missouri, St Louis, USA) showed that avian life span correlates with mass, genome size, incubation period and growth rate, and that these correlations occur at differing taxonomic levels. Correlations for other groups include the timing of peak mortality, the length of the tail of the survival curve, age-related changes in mortality rates, litter size and social behavior (Vaupel; Shiro Horiuchi, Rockefeller University, New York, NY, USA; Carey; Debra Judge, University of California, Davis). Distinctions between different sources of mortality, especially as they change with age, seem crucial (Jean-Marie Robine, INSERM Démographie et Santé, Montpellier, France). However, even the 'simple' distinction between intrinsic and extrinsic sources of mortality proved difficult, because of interactions among physiological condition, behavior and ecological relations.

Box 1. Definition of life span and related concepts

Life span, a property of the individual, is the duration of its life, typically from birth to death. Applying this term to a population or species requires a modifier to avoid ambiguity, and the following distinctions are proposed.

- Maximum observed life span is the highest verified age at death, possibly limited to a particular population or time period. The overall highest verified age for a species is also called its world record life span.
- Maximum potential life span is the theoretical highest attainable age. It is also known as the maximum theoretical life span or the species-specific life span. Many experts question whether such an attribute even exists for most species, although, in traditional usage, the unmodified term life span has often been used for this particular concept. Depending on context, maximum life span can refer to either the observed or the potential maximum.
- Mean life span is the average age at death, and is also known as average life span or life expectancy. It can apply to either a real cohort of individuals or a hypothetical cohort derived from a life table. Median life span and modal life span are alternative measures of typical life span.
- The effects of early mortality can be excluded by using just the adult portion of the life span, giving mean adult life span, median adult life span and modal adult life span.

Environmental variability and sociality: models with reinforcement

Several participants showed that environmental variability favors increases in life span through its effects on either the average population growth rate or the probability of extinction (Steven Orzack, Fresh Pond Research Institute, Cambridge, MA, USA; Marc Mangel, University of California, Santa Cruz, CA, USA). By contrast, the effect of variability on reproductive span depends on the type of temporal correlations that are involved (Orzack). Environmental conditions can also affect the degree of heterogeneity among individuals: for example, differences in ungulate vital rates, which follow family lines, manifest themselves only in poor years (Jean-Michel Gaillard, Université Claude Bernard, Lyon, France).

Models of human evolution suggested that both resource scarcity and uncertainty can favor the extension of life span (Carey and Judge; Hillard Kaplan, University of New Mexico, Albuquerque, NM, USA). These extensions can then be self-reinforcing, with positive feedback looping through parental investment, learned skills and intergenerational transfers. Physical structure as well as learning can be treated as a capital investment; the former may decline with age, whereas the latter increases indefinitely, but the payoffs for both increase with life span (Kaplan). This interplay between life span and social changes may apply to social insects as well as to humans[6].

Human historical trends show the potency of technological changes alone: the maximum observed human life span has increased steadily during the past 140 years, with the increase in survival between ages 80 and 100 being especially important (Robine; Wilmoth). The worldwide trend has paralleled the within-country trends[7], which reflects both the sampling issues for maximum observed life spans and the ubiquity of the increase.

Underlying mechanisms: models with tradeoffs

Explicit models of tradeoffs between allocation for survival and for reproduction are the starting points for new and significant investigations of possible mechanisms. Mangel's elegant study of rockfish (*Sebastes* spp.) growth, metabolism, oxidative damage and repair, and population dynamics demonstrated both the importance of these tradeoffs and the relevance of behaviors that mitigate their effects. Tradeoffs are identified, although links among life-history traits are still complex (Tuljapurkar): for instance, selection for increased life span in *Drosophila* also increases stress resistance by increasing expression of the free-radical-destroying enzyme superoxide dismutase, whilst reducing reproduction at lower ages (Larry Harshman, University of Nebraska,

Lincoln, NE, USA). The importance of minimizing metabolically produced oxidative damage is also suggested by the relatively large amounts of antioxidants that some birds put into their eggs. Severe restriction in caloric intake prolongs life in many species by slowing metabolism, and preventing reproduction in medflies by restricting protein has a similar effect. However, recent genetic work has also shown that neither reproduction nor metabolic rate *per se* tells the whole story about the determinants of life span[8,9]; quantifying costs involved in the tradeoffs appears to be crucial. New molecular developments are rapidly improving our understanding and, potentially, our ability to measure and manipulate key molecular entities.

Prospects for humans and for science

The trend of increasing human life span is almost certain to continue (Robine and Wilmoth)[10]. Discussions about the nature, extent and ramifications of future changes are, however, more speculative than scientific. Without joining, say, the hawkers of miracle substances, scientists might contribute their ideas about possible scenarios – but it was argued that even such contributions would be misleading at best (Olshansky). Clearly labeling such discussions as speculative seems necessary, but there was no consensus about whether doing so is sufficient.

Many levels of biology are making major contributions to demographic studies of life span. In the constructive spirit of this workshop, some participants wondered about contributions in the other direction, and were reminded that demographic techniques have long constituted some of the fundamental tools of population biology (Wachter). Additionally, human data have detail and scope that ecologists can barely dream of, and seeing such data used to address fundamental questions in the common ground of biology and demography can help population biologists sharpen their own ideas, methods of data collection, and analyses.

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