COMMENTARY

Uncovering variation in the patterns of aging

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Do all species experience the declines of old age? No. Do we currently have theories that accurately predict which species escape these declines? In PNAS, Warner et al. (1) demonstrate that the answer to this question is also "no." Understanding the breadth and diversity of the patterns of aging across the tree of life is central to life history evolution, and recent studies demonstrate that there is considerable variation in the age trajectories of traits across species (2–4). In general, the decline in function and increase in mortality that is associated with increasing age is expected, according to classic evolutionary theories, because of the decline in the strength of selection with age (5–7). In other words, the alleles that predispose us to heart disease or dementia have effects primarily at late ages, after we have reproduced, thus their impact on Darwinian fitness is minimal and these deleterious traits—and many others like them—persist. In natural populations, as we look across species, a central premise of the evolutionary theories of aging is that the rate of aging in different species will depend on levels of environmentally imposed mortality (7). All living organisms are subject to a constant risk of mortality posed by accidents, predation, and disease. This environmental, or extrinsic, mortality will influence the probability that individuals will survive to a given age. The hypothesis is that species with the highest levels of environmental mortality should evolve high levels of early reproduction and rapid aging. Conversely, slower rates of aging are expected in populations or species with low environmental mortality, for example in species such as turtles, which have protective shells that reduce predation. In this case natural selection will act to eliminate late-acting deleterious alleles because those individuals who can live longer will have higher lifetime reproductive success. Additionally, turtles increase their size with increasing age, and larger-sized individuals have higher fecundity that may help to maintain a high level of selection on late-age traits.

Fig. 1. A study with the painted turtle (*Chrysemys picta*) shows age-related declines in a reptile with a long lifespan. Image courtesy of Clare Isabel Ming-ch'eng Adams (Iowa State University, Ames, IA).

Warner et al. (1) show that the story about aging in turtles is not this simple. In their study with the painted turtle (*Chrysemys picta*) (Fig. 1), the authors marked more than 1,000 individual turtles living in the backwaters of the Mississippi River, and these individuals were followed for 24 y. Over this long time period, patterns of reproduction and mortality were tracked to determine how the trajectories of these traits changed with advancing age of the individual turtles. Based on evolutionary theories, Warner et al.'s expectation had been that reproduction would increase with age as the turtles grew larger, and that there would be no age-dependent increase in mortality. However, what they found was that reproduction declined and mortality increased as the turtles aged. The oldest females produced eggs with reduced hatchling success. Warner et al.'s analysis also shows acceleration in the probability of mortality across the entire lifespan. Specifically, the mortality rate for the turtles doubled every 13.8 y. Human populations have an approximate mortality rate doubling time of 7.2 y (8), which means that after age 30, our chances of dying double approximately every 7.2 y. The painted turtles are thus aging slower than humans, but these

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results show that the probability of mortality for these turtles is accelerating over their entire lifespan. In the context of the predictions based on theory, the painted turtles' increase in age-dependent mortality and decrease in reproduction was surprising.

There are two aspects of turtle biology that led us to predict that this species should be able to escape aging. First, because of their protective shell, turtles have low rates of predation; however, other sources of environmental mortality, particularly human impacts, may have influenced the patterns of aging found in this study. Warner et al.'s (1) site is used as a recreational area, where boating activity and nearby roads have increased the mortality of the turtles. Importantly, this additional mortality primarily impacts nesting females and older adults in the water column; in other words, the environmental mortality caused by this human activity is age-dependent (9). Fortuitously, the impact of these anthropogenic effects could be evaluated by comparing results from another study of painted turtles. In southeastern Michigan, in a population that is located in a fenced area with limited human access, data were collected for more than 3,000 marked individuals for 38 y (10). Relative to the Michigan population, Warner et al.'s population showed younger and smaller age at maturity, faster growth, and lower annual adult survival (11). Additionally, in the Michigan population there was no evidence for reproductive aging and the survivorship of the oldest and younger females was the same (10). These differences in the life history schedules and patterns of aging across these two populations of painted turtle are consistent with the theoretical expectation that populations with higher rates of adult, environmentally mediated, mortality will show more rapid aging (7, 9). This comparative analysis of populations has provided us with a unique opportunity to understand the variability in the patterns of aging within this species. In a broader sense, and from a more conservation-related perspective, this comparative analysis is an excellent demonstration that long-lived organisms can adjust their life history in response to human activities via plasticity and contemporary evolution (11).

The second aspect of turtle biology that made us predict that there should be no aging was the fact that turtles get larger as they get older, and larger individuals have higher fecundity. These increases in size and reproduction may counterbalance the weakening selection pressures on late ages and lead to negligible or even negative aging, compared with species with determinate growth (12). There is very little longitudinal growth data for species with relatively long lifespans, but in another study of several turtle species, including the painted turtle, it was found that older turtles had a higher chance of having periods of no growth and their growth rates were often lower than younger individuals (13). The Warner et al. (1) study also shows some suggestive data that growth rates decline with age. It is not clear how much these slower growth rates may influence late-age reproduction. Given that, in any environment, there is constant age-independent environmental mortality that is reducing survival, there will always be fewer individuals in the oldest age classes. Therefore, to keep selection pressure on late-age traits high, reproduction needs to continue to increase with age (14). Unfortunately, we do not have empirical data from other indeterminate-growing species to know how selection pressures change over the life cycle.

The Warner et al. (1) paper contributes to a growing number of long-term studies that have followed large numbers of marked individuals of known ages in wild populations. These studies have shown that the patterns of aging in animals and plants are more diverse than we ever predicted from our theories (2–4). One of the strengths of the Warner et al. study (1) is that they confirmed age-related declines with two traits: survival and reproduction. The diversity of aging that is now being uncovered is not only between species, or within species in two different environments, but also among traits within an individual (15–17). Aging is a complex phenotype and our current theories are not adequate to predict all of the diversity that the empirical studies are uncovering.

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