

Population Biology of Aging in the Wild

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Abstract

Empirical studies reveal aging occurs in wild populations. Consideration of the ecological and evolutionary consequences of these findings is critical for many areas of research, including life-history evolution, sexual selection, behavior, and applied ecology. Variation in the patterns of age-dependent declines of phenotypic traits has been found both within and among individuals, and this raises future questions aimed at understanding what determines these trajectories across traits and across the tree of life. The presence of older, aging, individuals in populations can have transgenerational effects on offspring and can influence how individuals interact. In some species older individuals in populations can have positive impacts, influencing knowledge and leadership, postreproductive care, and population cycle stabilization. Aging and long life span also need to be recognized in an applied ecology context including management plans, vector-borne disease transmission, and ecotoxicology.

Aging: also senescence; a decline in physiology or morphology that eventually leads to an increased risk of death

Biodemography: the integration of biology and demography

1. INTRODUCTION

Aging does occur in wild populations. A large number of recent empirical studies now demonstrate that individuals, of many species, show a progressive decline in phenotype with advancing age. One of the outcomes of aging is not simply death but rather the creation of a subset of elderly individuals in a population. Ecologists, behaviorists, and evolutionary biologists have generally neglected the importance of older individuals in the social groups and communities of which they are a part. A consideration of the ecological and evolutionary consequences of aging in the wild may potentially set the agenda for future research across diverse areas from life-history evolution to applied ecology.

There are at least four reasons why understanding aging in the wild is important. First, perspectives on the diversity of phenotypic change with age are central to our understanding of life-history evolution and will provide a more complete picture of the diversity of these patterns across the tree of life. Second, emphasis on research on the elderly will encourage biologists to reevaluate the evolutionary theories of aging. Theories may need to be reformulated to account for the wide range of situations in which older individuals continue to reproduce and individuals who are past their prime survive in populations. Third, the concept of the roles of the elderly provides an organizational theme for interdisciplinary aspects of aging. Fourth, a more complete understanding of the life course of individuals is important not only to basic research but also to management decisions of applied ecology. This article is not an exhaustive literature review, but rather it will summarize our current understanding of the patterns of aging and life span extension and then evaluate their ecological and evolutionary impacts. We limit our scope to studies of animals and plants in the wild. Gurven & Kaplan (2007) cover similar topics on the ecology and evolution of the human life course through studies of hunter-gatherer societies.

2. AGING IN THE WILD

2.1. Actuarial Aging

Studies on the biodemography of aging have traditionally quantified aging as an increase with age in age-specific mortality, q_x , a life table parameter defined as the probability of dying in the interval x to $x + 1$. Besides q_x , the conventional life table provides four additional functions that characterize the actuarial properties of a cohort, including survival from birth to age x (l_x), age-specific survival (p_x , i.e., the complement of q_x), deaths in a cohort at age x (d_x), and expectation of life at age x (e_x) (see Carey 2001, his table 1). Although each of these functions can be independently derived from the original cohort data, and all but life expectancy can be used to derive the other functions, age-specific mortality schedule, q_x (or force of mortality), serves as the actuarial foundation for the remaining life table functions as well as for many other cohort actuarial metrics (see the sidebar, Mortality as an Actuarial Foundation).

The basic role of mortality is evident by considering the following. First, death is an event that changes the state of an individual from living to dead. The concept of events (changes of state) is fundamental to the analysis of risk and actuarial analyses (see the sidebar, Mortality as an Actuarial Foundation). Second, an individual can die due to a number of causes, such as an accident, a predator, or a disease. Therefore, mortality rates can be disaggregated by cause of death and thus shed light on the biology, ecology, and epidemiology of deaths, the frequency distribution of causes, and the likelihood of dying of a particular cause by age and sex. Although there are obviously underlying reasons (causes) for why individuals continue to live, an analogous concept to “cause of death” (i.e., conditions responsible for the change of state from live to dead) does not apply to survival. Third, the value of age-specific mortality rate, q_x (and also its complement, p_x), at

MORTALITY AS AN ACTUARIAL FOUNDATION

Although cohort survival to age x (l_x) and age-specific survival (p_x) are the life table parameters most used in ecology and evolutionary literature, age-specific mortality (q_x) represents the most fundamental actuarial concept in the life table (see Carey 2001, his tables 1 and 3) and the statistical foundation for the actuarial sciences—risk (Land et al. 2005). Indeed mortality modeling (e.g., Gompertz model) and the concepts of actuarial aging, relative risk, odds ratio, sex mortality differentials, cause-specific and all-cause mortality, and average lifetime mortality are all based on risk concepts. For example, the ratio of daily survival for two cohorts, one with a value of 99.9% and the other 99.0%, is slightly over 1.0. However, their relative risk of dying [i.e., $(0.01/0.001) = 10$] and their ratio of remaining life expectancies [i.e., $(1.0/0.01) = 100$; $(1.0/0.001) = 1,000$] differ by tenfold. These and many other quantitative relationships between the two hypothetical cohorts are not evident without considering risk. Although the life table continues to be central to demographic analyses in ecology and evolution, bringing mortality concepts to bear on field demographic data not only increases the actuarial depth of the study but also provides a more fundamental understanding of demographic processes that shape populations.

a specified age is independent of demographic events at other ages. In contrast, cohort survival (l_x) to older ages is conditional upon survival to each of the previous ages, life expectancy at age x (e_x) is a summary measure of the consequences of death rates over all ages greater than x , and the deaths (d_x) that occur at young ages determine how many individuals remain to die at older ages. This independence of mortality rate relative to events at other ages is important because age-specific mortality rates can be directly compared among ages or between populations that, in turn, may shed light on differences in relative age-specific frailty or robustness. Fourth, a number of different mathematical models of mortality have been developed (e.g., Gompertz, Weibull, logistic) that provide simple and concise means for expressing the actuarial properties of cohorts with a few parameters. These models provide the analytical foundation for the comparative actuarial analyses of cohorts and populations.

2.2. Evidence for Aging Across Multiple Traits

An increase in the force of mortality with age is caused by a decline of the phenotype and may be manifest as a decrease in physiological function, reproduction, behavior, morphology and/or an accumulation of damage at the cellular level. Studies of aging in the wild have increasingly quantified not only mortality but also the change in other phenotypic traits with age. These studies have shown that biological age varies not only among individuals within populations, but also within individuals (Bronikowski & Promislow 2005, Nussey et al. 2013). A recent review of the literature (Nussey et al. 2013) demonstrates widespread evidence for aging of birds and mammals in the wild and documents the cumulative increase in the number of studies that have been done on this subject in recent years. The alternative hypothesis would be that most individuals die healthy; that is, there is no decline in phenotype with advancing age. The demonstration that aging occurs in many species in the wild is significant because it was not predicted by the classic theories on the evolution of aging (see the sidebar, Why Did We Think Aging Would Not Occur in the Wild?).

2.2.1. Advances in biodemography. These observations are also significant because such patterns could not have been revealed without recent advances in empirical approaches to the study of biodemography. High rates of ecological mortality, which are characteristic of wild populations, not only led to the predictions that there would be no aging but they also can obscure experimental

WHY DID WE THINK AGING WOULD NOT OCCUR IN THE WILD?

Our expectations about aging in wild populations have been influenced by the classic evolutionary theories of aging and empirical shortcomings. The general hypothesis was that life in the wild is short, and hard, and that genes governing late life processes in the wild do not matter because few survive to old age. Evolutionary theories of aging suggest that aging exists because of the declining force of selection on late age-specific traits (Hamilton 1966, Medawar 1952, Williams 1957). Medawar (1952) suggested that aging could only be demonstrated in “captive,” protected environments, in which animals are protected from natural hazards and can thus survive to ages never seen in the wild. This expectation, that aging cannot be found in the wild, has been quoted for the past 50 years (Kirkwood & Austad 2000), and empirically there were few demographic studies of individuals of known age to contradict this assertion. Recent theoretical work (Baudisch 2005, Williams et al. 2006) challenges some of these classic expectations, and long-term empirical studies of marked individuals demonstrate that the aging phenotype is an important phase of the life history in wild populations.

results because, inevitably, sample size declines with age as individuals die. The common protocol of recent studies is to include large sample sizes and multiple age groups to minimize some of these problems. Most importantly, nearly all the recent demographic studies demonstrating aging have been the result of longitudinal studies of marked individuals of very long duration, including some studies conducted over 40 years on birds (Berman et al. 2009, Bouwhuis et al. 2012, Pardo et al. 2013a) and turtles (Congdon et al. 2013). Longitudinal studies are critical both because aging is a within individual process and because aging can be confounded by selective mortality and changes in the composition of a population (Balbontin et al. 2012, Dugdale et al. 2011, Hayward et al. 2013). Our understanding of the breadth of variation in senescent processes has greatly expanded as the result of these advances.

2.2.2. Fitness and physiological traits. In the Nussey et al. (2013) review, the coverage of species, from the Asian elephant (Robinson et al. 2012) to the white-faced darter dragonfly (Sherratt et al. 2011), and the number of different traits, from survival and reproduction to age-dependent changes in secondary sexual traits (Balbontin et al. 2011), are impressive. There are, however, things to note that suggest directions for future research. First, most studies evaluate a single trait in isolation, and there have been few longitudinal studies that include multiple traits. Integrative studies broaden our knowledge of aging in wild populations not only because they increase our understanding of the number of traits that contribute to declining health and vulnerability but also because the age-dependent declines of different traits may vary. For example, in a study of four traits associated with reproductive senescence in female Soay sheep, Hayward et al. (2013) found declines in annual fecundity, lamb birth rate, and early survival, but not in litter size or twinning rate. This variation was particularly surprising because twinning is a key component of fitness and is under relatively strong selection. Similarly, the two major fitness components, survival and reproduction, can decline at different rates within and among species. In bighorn ewes, declines in age-dependent reproduction begin 6 years after the onset of survival senescence, and three years after the onset of senescence-related loss in body mass (Berube et al. 1999, Jorgenson et al. 1997). If there is a decoupling of patterns of decline, then this suggests that different mechanisms underlie the cause of aging in different traits.

Studies that include both fitness components and physiological traits may help to explain some of the variation in these trajectories, but in the few studies that have been done, the results are mixed. In a wild population of the common lizard, Massot et al. (2011) found contrasting age

MEASURING OXIDATIVE STRESS

A complete understanding of oxidative stress requires measuring all four components, including free radical production, antioxidant defenses, oxidative damage, and repair mechanisms (Monaghan et al. 2009, Selman et al. 2012). The balance between these components determines the consequences of reactive oxygen species for life histories. For example, increased free radical production together with increased antioxidant defenses may reduce oxidative damage to the body but with the added cost of reduced investment in reproduction. The optimal investment in antioxidant defense depends on the fitness consequences and is species and environment dependent.

variation across different fitness components and physiological traits. Similarly, Lecomte et al. (2010) found that age strongly affected reproductive performance and foraging behavior but not baseline physiology in the wandering albatross. One of the key challenges to understand aging in the wild is to understand why trait-specific age trajectories vary among individuals, across sexes (Pardo et al. 2013b, Tafani et al. 2013) and between species (Nussey et al. 2009). Moreover, it is not clear how this variation in rates of decline across fitness traits or physiological systems fits with the expectations of a general decline from the evolutionary theories (Hayward et al. 2013). Given this variability in the trajectories of trait decline, not only is it important to measure multiple traits but it also needs to be recognized that combining fitness measures may impede our understanding of the form of aging particularly as it ignores trade-offs that mediate independent responses between different fitness components (Massot et al. 2011).

2.2.3. Molecular traits. There have been a few studies that integrate fitness declines with the mechanisms underlying the declines, including oxidative stress, telomeres, and metabolic rate, but these results have been mixed. In one of the first studies of oxidative stress with a mammal, Nussey et al. (2009) found high levels of oxidative damage (see the sidebar, Measuring Oxidative Stress) in Soay sheep lambs that were correlated with rates of early growth, but there was no evidence for a change in damage with age. More recently, one of several studies included a longitudinal study on barn swallows and showed that high levels of antioxidant protection positively predicted long-term survival (Saino et al. 2011). There have only been two studies evaluating oxidative stress and whole plant aging in the wild, and these have shown mixed results (Morales et al. 2013, Munne-Bosch & Lalueza 2007).

Telomere dynamics predict life expectancy in the wild in some species (Bize et al. 2009, Cohen & McGraw 2009, Salomons et al. 2009). In a 17-year study with Seychelles warblers, for example, shorter telomeres and faster shortening of the telomeres predicted future mortality (Barrett et al. 2013). The causal connection between telomere dynamics and life span is not clear, and it may be that telomere shortening is an indicator of stress, for example, due to parasites (Barrett et al. 2013) or organismal condition (Monaghan 2010). Clearly, our current understanding of the underlying molecular mechanisms of aging in the wild is limited.

2.2.4. Model organisms in the wild. Laboratory studies provide a more complete understanding of the molecular mechanisms of aging in many model organisms, but research has only just begun on the population biology of aging in the wild for these species. The model organisms used for most aging research are the same as those used in basic biomedical research, including brewer's yeast (*Saccharomyces cerevisiae*), round worms (*Caenorhabditis elegans*), fruit flies (*Drosophila melanogaster*), zebrafish (*Danio rerio*), laboratory mice (*Mus musculus*), and the rhesus macaque (*Macaca mulatta*). An online search for papers published in 2013 on the biology of *M. musculus*, *D. melanogaster*, and

C. elegans yielded over a quarter of a million results. In sharp contrast, a similar search on three species that are closely related to each of these yielded less than 2,000 publications. On the basis of differences in available literature, the potential for laboratory-field complementarity differs by more than two orders of magnitude between model and many nonmodel species. Although the basic natural history is known for many of these species, virtually nothing is known about aging, survival, and life span in the wild for any of them.

Information on aging in the wild does exist for *D. melanogaster*, but even here a critical mass of information requires including information derived from field studies on three other *Drosophila* species. Izquierdo (1991) demonstrated that overwintering of *D. melanogaster* in temperate regions of Europe (northern Spain) was possible only in young mated females that survived through the cooler periods for up to 6 months. Thus the older, overwintering females were responsible for regenerating populations in the spring. Begon (1976) used temporal variation in the reproductive condition of *D. obscura* and *D. subobscura* to estimate changes in reproductive age structure for both species. He reported continuous population aging as surviving, nonreproducing adults passed the winter followed by four to five generations with no clear patterns of aging owing either to generation overlap or because the monthly analysis hid age-structure cycles of short periodicity. Relatively long life spans of 40 days for *D. serrata* (Robson et al. 2006) and greater than two months for *D. melanogaster* (E. Behrman, S. Watson, K. O'Brien, M.S. Heschel, and P. Schmidt, submitted manuscript) have been reported from wild population studies.

2.3. Patterns of Aging

The patterns of aging may be defined in a number of different ways. Here we discuss age-dependent versus -independent declines, condition-dependent aging, and the possibility of escaping aging.

2.3.1. Age-dependent or age-independent declines? Ecology and selective pressures across life stages can influence the patterns of aging declines. Gradual decline is predicted by the evolutionary theories and is expected to begin at the age of reproductive maturity. For some species there may be an initial increase and then a gradual age-dependent decline at later stages (Jones et al. 2008). These postmaturity increases may occur for several reasons, including continued increases in size (Sparkman et al. 2007) or due to increased parental experience (Balbontin et al. 2007). An alternative, age-independent pattern may be observed such that the age of onset and rate of decline can be indexed to the time interval before death (age at death minus age) for each individual (Martin & Festa-Bianchet 2011, McNamara et al. 2009). Several studies have shown that age-dependent and -independent aging can co-occur. In a study with a short-lived perennial herb, *Plantago lanceolata*, reverse age analysis showed that size decreased (individuals shrank), and reproductive output declined in the three years before death regardless of overall age, suggesting physiological deterioration (Shefferson et al. 2013). The progressive nature of these declines over several years suggests that this was not due to a terminal illness. Age-dependent declines were then manifesting as steeper declines for the oldest individuals (Shefferson et al. 2013). Similar patterns of both age-dependent and -independent declines have been found for reproduction in Seychelles warblers (Hammers et al. 2012) and bighorn ewes (Martin & Festa-Bianchet 2011). Even with the limited number of studies to date, there is considerable variation in the type of pattern found, including among sexes (Tafari et al. 2013), among reproductive traits within a species (Martin & Festa-Bianchet 2011), and among closely related species (Nussey et al. 2011). Doing analysis of both chronological and reverse-age approaches to study aging in the wild requires detailed monitoring of individuals, but it will offer important new insights on health of wild plants and animals in relation to age at death.

2.3.2. Age-by-environment interaction. The patterns of aging can also depend on the condition of the individual, that is, the senescent state can interact with a mortality factor to increase the risk of mortality. This is likely to occur in wild populations in which differential mortality is determined by abiotic conditions and/or biotic pressures of predation, disease, and competition (Abrams 1993, Williams & Day 2003, Williams et al. 2006). Condition-dependent aging has been found in the black-brown albatross (Pardo et al. 2013a), snail kites (Reichert et al. 2010), the common gull (Brommer et al. 2010), and a plant species *Plantago lanceolata* (Roach 2012, Roach et al. 2009), and at high densities for Soay sheep (Coulson et al. 2001). This increased susceptibility of older individuals can change how selection acts on traits, and life span might evolve to be longer under some conditions (Abrams 1993, Descamps et al. 2008, Williams & Day 2003). For example, in a comparative study of populations in which bears showed differential predation of older senescent salmon, the salmon in streams with higher predation showed lower rates of senescence (Carlson et al. 2007). In other words, higher levels of condition-dependent mortality increased the strength of selection against aging deterioration and slowed the rate of aging. A more complete understanding of how physiological state interacts with variable levels of ecological mortality is needed to broaden our understanding of how selection has acted to shape the evolution of aging.

2.3.3. Escaping aging? Do all organisms age? No, but for extremely long-lived species we will rarely, if ever, have the opportunity to longitudinally monitor large numbers of individuals through to the latest stages of their life. Hamilton's (1966) classic theory suggested that senescence tends to creep in, because of the decline in the strength of selection with age, and thus should be found in all species. Recent reexamination of the assumptions of these theories (Baudisch 2005, Vaupel et al. 2004) suggests that senescence is not inevitable, particularly for species that can continue to increase in size and hence reproduce with increasing size and age. A number of species have been identified as having negligible senescence (Finch 2009). Species with extreme life spans, such as the naked mole rat (Perez et al. 2009) and ocean quahog (Ungvari et al. 2011), show reduced oxidative stress. Most information that we do have about species with negligible senescence is from cross-sectional studies in which traits are compared across individuals of different ages. For example, in a study of the very long-lived plant species *Borderea pyrenaica*, which has life spans of up to 300 years, age determination was based on shoot scars, and five years of demographic data were used to construct an age-size-structured population projection model (Garcia et al. 2011). Results showed that mortality stayed constant, or possibly even decreased, with age for old plants. Recent physiological studies with this species have also not identified any deterioration of plant function with age (Morales et al. 2013). Longitudinal studies would be impossible for these species, but unfortunately long-term variation in selective mortality and early-life environmental conditions may mask the true aging patterns.

A rare exception is a study of 9 turtle species in which marked individuals were followed for more than 40 years (Congdon et al. 2013). This study showed that older individuals not only laid more eggs but also more consistently reproduced than younger individuals. In contrast to expectations, this study also demonstrated that growth in a species with negligible senescence is not strictly indeterminate as many individuals stopped growing, some for a decade or more, before recommencing.

3. LIFE SPAN AND AGING

3.1. Definitions

There is now good evidence that the rates of decline in traits that contribute to the aging phenotype vary within individuals for different traits and across individuals within and among populations. It

Negligible senescence:

refers to a species with neither apparent functional declines nor increases in mortality with age

LIFE SPAN CONCEPTS

Life span, a property of individuals, is the duration of 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: (a) Maximum observed life span is the highest verified age at death, possibly limited to a particular population or time period. (b) Maximum potential life span (MPLS) is the theoretically highest attainable age 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. (c) 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. And (d) 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 (Goldwasser 2004).

is interesting to ask what broader patterns in the rate of aging may exist across all species (Jones et al. 2014). Life span (see the sidebar, Life Span Concepts) is integral to this because aging in the wild cannot be understood without a basic understanding of an individual's life course and a species life history, the boundaries of each of which are set by life span. Sacher (1978) made a sharp distinction between the approaches needed to study aging versus life span when he noted that even though important parallels exist in how rats and humans senesce, because both are mammals, an understanding of the differences in their aging rates sheds little light on an understanding of their evolved differences in life spans. Thus aging is deprived of important meaning without being considered in the complementary domain of life span, which is an evolved trait and a life-history metric.

3.2. Phylogenetic Context

A species' life span must be considered in the context of its phylogeny and thus its bauplan (see the sidebar, What Is a Bauplan?). Design concepts, for example, differ between lepidopterans (butterflies, moths) and coleopterans (beetles), between nematodes and gastropods, and between birds and mammals. To ignore differences in the types and levels of mortality risk across these groups would be to disregard differences in mortality risk and life spans resulting from their respective phylogenetic legacies. For example, by virtue of their design, nearly all adult butterflies are subject to fundamentally different risks and have shorter life spans than most adult beetles.

3.2.1. Bauplan. The bauplan frames not only developmental processes but also life histories and life span potential. For example, many species within the Radiata are sessile because their radially

WHAT IS A BAUPLAN?

Bauplan refers to the common new and original (homologous) properties of the members of a systematic group (taxon) (Purves et al. 2004). The best-known example is the evolution of the vertebrate bauplan—the laying down of the gut, the formation of the neural tube, the notochord, and the muscle somites. These are features of all vertebrates. As this clade evolved from fish to amphibians to reptiles, the bauplan and developmental sequence from one group were used as the foundation for the next.

symmetric bauplan makes it difficult to evolve traits for rapid movement. Therefore, many species evolved defense mechanisms, such as poisons or spines, to increase their survival rates and enable them to reproduce over long periods.

Another example is the hexapod (insect) bauplan. The insect clade is thought to have originated in the Devonian (410 Mya), a period of near-drought conditions worldwide (Grimaldi & Engel 2005). The life spans were shaped by the bauplans of each of the four holometabolous groups of insects (i.e., lepidopterans, coleopterans, dipterans, and hymenopterans). For these groups there are clear morphological, and thus ecological, separations of preadult and adult stages that enabled them to exploit different niches. The preadult stages are mainly for acquiring food for growth, whereas the adult stage is for mating, food foraging, and resource storing for offspring. For example, the bauplan for lepidopterans consists of herbivorous preadults that are able to quickly exploit resource-rich habitats. This group evolved dispersive adults not burdened with highly protective armor. Protection is through camouflage and flight, and most lepidopterans are short-lived. In contrast, the bauplan for coleopterans is that of preadults investing much of their resources into growth and adult cuticle for protection. Investment in thick cuticle requires that adults forage for proteinaceous food for egg production using their chewing mouthparts. Thus many coleopterans are long-lived.

3.2.2. Comparative studies. This phylogenetic approach to understanding life span then raises questions about whether variation in the life history and bauplan of different species influences the relationship between life span and aging. Jones et al. (2008) evaluated the patterns of aging across 19 species of different-sized birds and mammals and showed that aging patterns were often found for survival across different sizes, but reproductive aging was more often found in large, longer-lived, mammals than small mammals. Their analysis also showed that birds generally have a lower senescence rate than mammals because birds have a longer generation time, hence slower life history, than mammals for a given body size. In other words, senescence is determined by the speed of the life history (Jones et al. 2008, Ricklefs 2010). Interestingly, in angiosperms, a comparison of age trajectories of 290 species also showed that long-lived plants show stronger senescence and that there is a phylogenetic component to this variation (Baudisch et al. 2013). A broader study of 46 diverse species, from Japanese women to desert tortoise, that used smoothed trajectories of fertility and mortality showed no correlation between the degree of senescence and the length of life. However, some clustering of taxonomic groups was found, suggesting that traits related to the bauplan may be important determinants of aging (Jones et al. 2014).

To address the same question in a different way, Turbill & Ruf (2010) compared the mean and maximum life spans of different species. Their premise was that species that have relatively similar mean and maximum life spans are more likely to experience aging than species in which the mean occurs at a much younger age. A comparison of 125 mammal species showed that long-lived mammals have relatively similar mean and maximum life spans and are thus more likely to experience aging than short-lived mammal species. These results are consistent with the finding that large, longer-lived, mammals are more likely to show reproductive senescence (Jones et al. 2008) and that aging patterns vary with life span, and there is more decoupling of declines of different traits in longer-lived species (Bouwhuis et al. 2012).

3.3. Sociality

Living as a breeding pair or living in a large social group creates conditions for increasing life span because of reduced mortality from predation, resource shortages, and other stochastic sources. For

example, helpers can allow a population to increase rapidly during favorable years while buffering the population from rapid decline during periods of harshness (Rowley 1976). Group living can enhance predator avoidance through different mechanisms, including possible early detection, safety in numbers, or confusion effects (Jullien & Clobert 2000). Group living can also create infrastructural and/or behavioral assets that enhance survival in offspring or relatives in the form of ecological inheritance, including the bequeathing of mounts, nests, dens, territory, and/or rank (Odling-Smee et al. 2003). Constraints imposed by ecological stochasticity (e.g., rainfall) may cause resources to be widely distributed. Living in large social groups may allow better exploitation of these ecological niches through cooperation and reproductive suppression (Brockmann 1997). The evolution of extended longevity in African mole rats, for example, is considered first a response to environment that is then augmented by its sociality (Faulkes 1998). These and other arguments form the basis for theories for the evolution of eusociality in insects in which comparative studies across species show that queen life spans are long, inversely correlated with queen number, and are directly correlated with mode of colony founding (Keller & Genoud 1997). Improved environmental conditions, due to nesting behavior and sociality, and increased longevity are evolutionarily self-reinforcing (Carey & Judge 2001). This positive feedback relationship is based on the demographic concept that increased survival from birth to sexual maturity reduces the number of replacement-level offspring needed to be produced by females, *ceteris paribus*.

In social wasps, the situation may be reversed such that social behavior may be an outcome of extended longevity (Carey 2001). An adult female wasp must live long enough to still be present when her offspring emerge as adults; generation overlap is thus a prerequisite for the evolution of incipient sociality (Evans 1958). Progressive (as needed) provisioning evolved after the evolution of extended longevity because here the mothers provide food directly to their offspring larvae. Among sphecid wasps, progressively provisioning *Bembix* live two to four times as long as the mass provisioning *Gorytes* (i.e., mass provisioning wasps stockpile hosts in their nest and then lay their eggs). Field et al. (2000) found that helpers in a tropical hover wasp (*Liostenogaster flavolineata*) have an insurance-based advantage over lone foundresses because after a helper dies, most of the brood that she has partly reared will be brought to maturity by surviving nest-mates.

4. ECOLOGICAL AND EVOLUTIONARY IMPACT OF AGING

Aging in the wild can influence how natural selection acts on traits in populations as well as how organisms interact. As noted earlier, age-by-environment interactions result when older individuals are more vulnerable to environmental conditions, and selection may act on traits to decrease this vulnerability. In addition, declining reproductive quality with age influences the evolution of traits. We also discuss the impact of aging on sexual selection and behavior.

4.1. Reproductive Aging and Transgenerational Effects

Age may have transgenerational effects on offspring phenotype. Several species show parental age effects on offspring, including a decrease in offspring survival in meerkats (Sharp & Clutton-Brock 2010), red squirrel (Descamps et al. 2008), and free-ranging moose (Ericsson & Wallin 2001), and a decrease in the probability of recruitment in the offspring of older parents of blue-footed booby (Ericsson & Wallin 2001). In great tit birds, offspring hatched from older mothers perform better early in life but suffer from an earlier onset and faster rate of reproductive senescence later in life (Bouwhuis et al. 2010). A decline in quality of the germ line, either from the maternal (Bouwhuis et al. 2010) or the paternal side (Pizzari et al. 2008, White et al. 2008), may cause these declines

in fitness of the offspring. In the blue-footed booby, for example, oxidative damage to DNA of sperm increases with age (Velando et al. 2011); as a consequence, progeny of senescent males are at high risk of genetic disorders.

In addition to declines in quality of the germ line, transgenerational age effects may be caused by parental care behavior or resource investment in early-life reproduction. In species as diverse as moose (Ericsson & Wallin 2001) and blue-footed booby (Beamonte-Barrientos et al. 2010), there is a correlation between a decrease in parental care with maternal age and an increase in offspring mortality. In addition, early-life reproductive effort can increase somatic deterioration and reduce parental performance of older parents, for either mothers and/or fathers (Torres et al. 2011). Not all studies have found declines in fitness with parental age (Low et al. 2007), and some studies have shown increased offspring survival with maternal age, for example, in Weddell seals (Hadley et al. 2007). In some of these cases, however, population averages are reported instead of variation in the quality of offspring for individuals as they age; thus these results may not reflect true age effects at the level of the individual (Reid et al. 2010).

At the population level, breeding by senescent parents may increase the population mutational load and cause a reduction in mean fitness. Kim et al. (2011) found a genotype-by-paternal age interaction such that there was more genetic variation in progeny of younger fathers of the blue-footed booby. This decrease in genetic variance with father's age was possibly due to age-related changes in germ line mutations and a general reduction in gene expression. Parental age-specific environmental effects, for example, the stressful conditions created by reduced care by senescent parents during early development of offspring, may also reduce the genetic variance of offspring traits (Kim et al. 2011). These results suggest that the strength of selection for evolutionary change is influenced not only by age-dependent variation in survival and fecundity but also by parental age-dependent heritable variance. Predicting the genetic response of a population to selection becomes more complex if the genetic variation among individuals within a population varies with the age of their parents; this response then depends on the age structure of the population.

4.2. Sexual Selection

Aging and life span can influence the magnitude and direction of sexual selection. On the one hand, long life span is an indication of high genetic quality, but as the reproductive system ages, the increased probability of reduced fertility or offspring viability should favor female discrimination (Pizzari et al. 2008). In the blue-footed booby, germ line damage in males is correlated with a decline in sexual attractiveness (Torres & Velando 2007, Velando et al. 2011), but our understanding of the role of mate choice in selecting against older animals with germ line damage is limited (Velando et al. 2011). Females may benefit from polyandry if sperm competition reduces risk of fertilization from lower-quality old males (Gasparini et al. 2010, Radwan 2003). The intensity of sexual conflict can also be modulated by an interaction between male age, male status, and the social environment. In a seminatural population of domestic fowl, reproductive senescence influenced intrasexual competition, which then influenced sexual conflict over mating (Dean et al. 2010). Old males were less likely to dominate male-biased groups, but in female-biased groups in which competition was less intense, old males had an equal probability of being dominant. Moreover, when they were dominant, old males fertilized more eggs, which resulted in reduced fertility for females. There are still many open questions about how much of the variation among populations in sexual selection is due to environmental effects on aging or life span and, conversely, how much variation among populations in aging and life span is due to variation in sexual selection or sexually antagonistic coevolution (Bonduriansky et al. 2008).

4.3. Behavior

Two examples of age effects on behavior in the wild are predation and foraging. It is well known that aging impairs athletic performance in animals, such as horses (Mota et al. 2005), shrews (Punzo & Chavez 2003), birds (Cosantini et al. 2008), fish (Reznick et al. 2004), and insects (Schumacher et al. 1997), and that athletic senescence predisposes older animals to predation (Fuller & Keith 1980, Slobodkin 1968). MacNulty et al. (2009) showed that individual predatory performance in wolves initially improved to a peak but then declined with age. They found that adult wolves were maximally proficient predators for only around one quarter of their lives, and therefore declining adult performance reduced the quantity of prey killed by wolves as the ratio of senescent hunters increased in the pack.

In a long-term study of the grey-headed albatross, Catry et al. (2006) demonstrated that long-lived birds display a senescence-related decline in both reproductive function and foraging performance years before their death. Studies on another albatross species, the wandering albatross, reported similar patterns of aging, and observations on sex-specific foraging efficiency—that is, the ability of individuals to extract energy from their environment—suggest that foraging might play a central role in shaping aging patterns in natural conditions (Lecomte et al. 2010).

5. ROLES OF LONG-LIVED INDIVIDUALS

Although older individuals often constitute a small proportion of the population of which they are a part, in many species the longest-lived individuals play extremely important roles in group dynamics and welfare or in population renewal and stabilization. In this section we discuss these roles in several different contexts and for a number of different species or species groups (see also Carey & Gruenfelder 1997).

5.1. Knowledge and Leadership

Experience and wisdom are two of the defining traits for the elderly in species that are both highly intelligent and social. Here we describe the roles of older individuals with these traits in two such groups—elephants and primates.

5.1.1. Elephants. Despite disease and deterioration, aging females have an important role in elephant society (Freeman 1980). Elephant age, size, and dominance are all positively correlated, and because elephants' social organization is matriarchal, the oldest females are usually the leaders and the largest in the herd (DiSilvestro 1991). As old subherd leaders they have more experience and unique knowledge, such as the location of scarce resources during dearth periods, the intensity of predation threats, or safe migration routes (King 2010). The female leader also provides fitness benefits to the group from an improvement in ecological knowledge that accompanies aging (McComb et al. 2001). The possession of enhanced discriminatory abilities by the oldest female can influence social knowledge of the group as a whole and influence reproductive success because resources for defensive behavior are more efficiently allocated to appropriate situations.

5.1.2. Primates. Little attention has been given to old animals in the vast literature on primate behavior because it has long been thought that very few primates in natural habitats could evade predators and disease long enough to grow old (Hrdy 1981). There is, however, evidence across many primate species that long-lived aging individuals occupy high rank and are critical for leadership and defense. The social rank of macaque females increases with age when a daughter of a high-ranked female can adopt a home range overlapping her mother's range. When the mother

dies, the young female gains access to resources from which she would otherwise be excluded (Clutton-Brock 1991). Hrdy (1981) suggested that in Japanese macaques the rank of the older females has a potential effect on her genetic contribution to subsequent generations because her daughters inherit her rank. Leadership is a primary role of many older individuals in primate groups. Old silverback gorillas make troop decisions, including when and where to forage, rest, and sleep, and arbitrate disputes within their harems (Harcourt & Stewart 2007). Hrdy (1981) showed that older, postreproductive langurs are low ranking but participate vigorously in defending the troop, advancing troop interests, and protecting and caring for infants and juveniles of close relatives.

5.2. Postreproduction

Females in many nonhuman species, ranging from round worms and fruit flies to primates and cetaceans, experience a postreproductive period before death. Although this nonfertile period for most species is likely a residual, nonadaptive, terminal segment of their life course, for several species or species groups that we discuss below this postreproductive period appears to be adaptive.

5.2.1. Tooth cetaceans. There are several roles that elderly odontocetes perform in their societies, including guardian, aunt, and nurse. For example, in old bottle-nosed dolphins (Wells 1991) and very old Hawaiian spinner dolphins (Johnson & Norris 1994), males watch over the juveniles while the rest of the group forages. By exercising these parent-like duties, the older males are allowing the younger parents to forage, an activity that the old male may not be able to do as efficiently. There is reciprocity in work allocation that requires the active involvement of all age classes (Tyack 1986).

Old female dolphins and killer whales assist younger females during birth and early infant care (Johnson & Norris 1986). Postreproductive females not only help watch, defend, and teach the younger animals but they also nourish the young. Postreproductive female Hawaiian spinner dolphins can produce milk, enabling them to help the younger mothers feed their calves. In pilot whales, females have an exceptionally long postreproductive period, ceasing ovulation at about 40 years, although they often live until age 63 (Foote 2008). In Japanese fisheries, 25% of female pilot whales captured are postreproductive and 25% of the postreproductive females are lactating. This information implies that females have switched their energies from bearing offspring to nurturing the ones already born, although whether these cetaceans suckle only their own offspring is unclear (Tyack 1986).

Killer whales have the longest postreproductive life span of all nonhuman animals; females stop reproducing in their 30s and 40s but can survive into their 90s (Olesiuk et al. 1990). Male killer whales, however, continue reproducing into older ages. Foster et al. (2012) reported that for offspring over 30 years old, the death of a postreproductive mother increased mortality risk 13.9 fold in sons and 5.4 fold in daughters in the year after their mother's death. Given the continued reproduction of older males, old mothers maximize their inclusive fitness benefits by directing care toward sons.

5.2.2. Saturnid moths. Blest (1963) divided New World Saturnid moths into two groups: (a) cryptic, which rely on camouflage to escape the detection of predators but are tasty, and (b) aposematic, which rely on their terrible taste to discourage predators from ever eating a member of that species a second time. Postreproductive survival of the tasty moths is detrimental to conspecifics because a predator's discovery of any member of a cryptic species would establish a search image in the mind of the predator. By contrast, a predator's unpleasant experience with a long-lived aposematic individual would benefit its kin and other conspecifics.

5.3. Population Cycle Stabilization

Older individuals in many species stabilize populations in a variety of ways, for example, by surviving through dearth periods, by serving as main sources of recruitment, or by buffering against predation. Here we describe two examples, one for fish and the other in a predator-prey system.

5.3.1. Old fish. “Storage effects” refer to a suite of demographic conditions, for example, long pupation in insects or seed banks in plants, in which populations can store the gains in good years to help them survive population losses in bad years (Warner & Chesson 1985). Excluding longevity, storage in reproductive potential is figurative, and long-lived individuals are present when conditions are favorable for reproductive and larval survival. One of the best examples of this storage effect is in large, old fish. Big, old, fat, fecund female fish (BOFFFFs) are essential for the successful maintenance of a number of fish species that exhibit long life spans (Field et al. 2008 and references therein). The basic argument is that fish longevity has evolved to deal with the variability in recruitment of young fish into populations whose young stages need to survive variable mid-latitude pelagic environments (Longhurst 2002). Excluding their reproductive contribution, BOFFFFs (*a*) lay exponentially more eggs, thus increasing the chances of replacement; (*b*) produce larger eggs with more fat reserves, resulting in improved chances of larval survival; (*c*) lay their eggs in locations that are more favorable for survival owing to the ability of the mother to dominate the best locations for food and protection; and (*d*) experience earlier and longer spawning periods (Hixon et al. 2013). The species for which BOFFFFs are best demonstrated are long-lived and live in temperate waters, such as Atlantic cod, which can live over 20 years, and Pacific rockfishes, which can exceed 200 years in age.

5.3.2. Predator-prey cycle. Stability within the wolf-moose predator-prey cycle depends on the age of senescence of the moose (Hastings 1984). Under certain assumptions, small numbers of long-lived prey will reduce the predator population, and large numbers of ungulate juvenile prey will allow predators to increase. The age of senescence can have an important stabilizing influence if the large numbers of ungulate prey senesce before producing another large age class on which the predators can feed. However, if the age of senescence is old enough then the age class of the predators slowly decreases, allowing another sizeable prey age class to appear, the result of which is stability in the predator-prey cycle.

6. APPLIED ECOLOGY OF AGING IN THE WILD

Studies on the population biology of aging are relevant to virtually all areas of applied ecology, including studies concerned with conservation and the vulnerability of populations and population and pest management. In this section we focus on selected examples that either historically or more recently contain a critical mass of published papers.

6.1. Population Projection Models

The recognition that aging occurs in the wild is critical to predicting the risk of extinction of vulnerable populations. Structured population models are an essential tool for conservation applications (Finkelstein et al. 2010), and one of the questions to ask is, Does age matter to these population models? A recent analysis (Chu & Adler 2014) showed that integral projection models

of 19 populations of perennial grasses had a higher proportion of vital rate variance explained when age was included. Moreover, populations with a strong Type III survival curve were most sensitive to the inclusion of age because as the cohort ages the surviving individuals are of higher quality, and as the composition of the population increasingly includes only high quality individuals, the population growth rate increases (Kendall et al. 2011). Thus, models that ignore individual heterogeneity may underestimate population growth and abundance for some species and lead to overly pessimistic estimates of extinction risk (Chu & Adler 2014). Conversely, if a population contains a large number of older individuals that are producing low quality offspring, then population risk may be underestimated (Reid et al. 2010).

6.2. Social Structure

The extraordinarily strong fidelity of many social mammalian species (e.g., killer whales, elephants) to their natal units suggests an important and potentially variable contribution of different individuals to their social network (Williams & Lusseau 2006). Social structure of populations cannot be disregarded from management plans that promote the recovery of endangered species. In elephant populations, for example, in which groups rely on older members for their store of social knowledge, whole populations may be affected by the removal of a few key individuals (McComb et al. 2001). The loss of old females disrupts social relationships and has consequences for population health, and the loss of older, reproductive, males can result in the loss of genetic diversity (Archie & Chiyo 2012). Older male elephants tend to be physically larger and possess larger, heavier tusks (J.H. Poole 1994, T.B. Poole 1987), and when these reproductively active old bull elephants are harvested for the ivory trade, their loss can have a critical impact on the population (DiSilvestro 1991).

Trophy hunting may also impact social structure of a population. A concept that has received much attention recently in trophy hunting is the specification of male age minima for killing, which is based on harvesting trophy males just past their prime. For example, simulation studies (Packer et al. 2009, 2011) suggest that a safe minimum age for killing lions and leopards in Tanzania may be 6 and 7 years, respectively. A problem with implementing this hunting policy is that no method exists for reliably aging leopards, although there is a reliable age index for lions (Whitman et al. 2004). A trade-off with harvesting older male lions is that, because males provide extensive paternal care, their removal can harm the population as a whole. Excessive trophy hunting of old males could cause male replacement and associated infanticide to an extent that would prevent cubs from reaching adulthood.

6.3. Fisheries Management

There are a number of negative consequences of harvesting the oldest, most fecund, fish (i.e., BOFFFFs), including shortening and changing the timing of the spawning season, decreasing the production of eggs and larvae, reducing the probability that favorable conditions will be encountered by at least some larvae, decreasing the average survival potential of larvae, and reducing genetic heterogeneity (Field et al. 2008). The effects of sustained heavy exploitation may not be reversible. In light of the importance of BOFFFFs in fish populations, Hixon et al. (2013) offered three options for managing fish spawning, including (a) reducing the rate of exploitation significantly, an option they admit may be economically infeasible; (b) instituting slot size limits (maximums and minimums)—an option only available to species that can readily be released unharmed after capture; and (c) designating marine reserves that set aside areas in which fishing is prohibited and older fish can survive and spawn.

6.4. Vector-Borne Disease Transmission

Daily mortality is the most important determinant of an arthropod vector's (e.g., mosquitoes) ability to transmit pathogens, such as those causing malaria, dengue fever, lymphatic filariasis, and viral encephalidites. The longer a vector lives, the more likely it is to encounter an infectious host, survive the incubation period, and transmit an infectious agent during subsequent feeding attempts (Novoseltsev et al. 2012, Styer et al. 2007). Because of the important effect of mortality at several stages in the pathogen transmission cycle, small changes in longevity can result in relatively large changes in arthropod vector-borne pathogen transmission. All other factors being equal, transmission rates are highest if mortality rates decrease with vector age because the vector population will be composed of mostly older vectors that have lived long enough to become infectious. In contrast, when vectors senesce, transmission is expected to decrease because the population age distribution shifts to younger vectors, most of whom will not live long enough to become infectious.

6.5. Ecotoxicology of Long-Lived Vertebrates

One of the consequences of life in the wild for long-lived species is the risk of reduced fitness owing to the long-term accumulation of persistent environmental contaminants (Stark & Banks 2003). As Rowe (2008) noted, species with life-history traits, such as delayed maturation and iteroparity, confer the potential risks from cumulative effects expressed before reproduction, and large parental investments in yolk and milk may threaten offspring. Thus the suite of traits that optimized reproductive fitness in long-lived species while they were evolving may ultimately put species in peril in the modern world of chemical contaminants. For example, Aguilar & Borrell (1994) reported that in fin whales the long period of accumulation of contaminants by females before maturity resulted in very high concentrations in their offspring during the first few breeding seasons. This accumulation caused fetus malformations and mortality, low weight of neonates, various pathological and behavioral alterations, immune incompetence, and decreased or failed reproductive performance of the descendants.

Chronic contaminant exposure in long-lived animals has potential effects on reproductive fitness though a number of pathways (Rowe 2008). For example, in species with large per capita investments in offspring, there is a risk of maternal transfer of high concentrations to the offspring. In species with delayed reproduction, the chronic accumulation of contaminants can be transferred to offspring upon maturation. Additionally, species with long embryonic, preparturition, or preweaning periods risk chronic exposure of offspring to female-derived contaminants (yolk, placenta, milk). These pathways for contaminant transfer can affect fitness, population growth rates, and recovery times.

SUMMARY POINTS

Ecology influences the evolution of aging, and aging influences ecology and evolution. Despite the hundreds of studies done on aging in the wild, we feel that the field is only at the beginning of establishing multidisciplinary approaches.

1. Individuals in the wild do not all die healthy. There are multiple traits that contribute to the aging phenotype, and evidence suggests that not all traits decline at the same time or rate. A better understanding of declines in physiological and molecular traits will help us

to quantify the health of individuals and give us more metrics to investigate species with no apparent aging. Quantifying health will help us to better understand the interaction between health and environment in determining variation in mortality. Indeed, understanding health span of individuals in the wild is a virtually untapped area of research with much to be learned from the human demography literature on this topic conceptually, analytically, and empirically (Siegel 2012).

2. Older individuals can have negative effects on populations, for example, if the quality of their offspring is low, but older individuals can also have stabilizing effects on populations through leadership and intergenerational transfers (Lee 2003). The age-dependent nature of trait variation and its influence on fitness within and between generations is only beginning to be understood, and both individual and population fitness concepts need to consider the roles of some of the longest-lived individuals in populations. Moreover, these findings also suggest that the use of Lotka's intrinsic rate of increase (little r) to characterize fitness is, for many species, inappropriate. Seminal papers on life-history theory (e.g., Lewontin 1965), suggesting that change in the timing of first reproduction has the greatest impact on fitness, are consistent with observations in many fast-growing species, but it is less useful as a fitness measure for species in which the older individuals play an important role in ecology and reproduction.
3. As we consider the state of our knowledge of the patterns of aging across the tree of life, there are several very tractable groups of organisms about which we know very little. Plants, for example, have a diversity of life spans and potentially a diversity of patterns of aging. Insects are the most numerous and diverse group of organisms on the planet, and studies on this group, as well as other invertebrate taxa, that are concerned with the adaptive role of life span as it coevolved with other life-history traits have the potential to open up entirely new avenues of research on the evolutionary biology of aging and life span.
4. Although age is central to virtually all population studies, precise knowledge in field studies of either individual age or population age structure is the exception rather than the rule. Although data sets based on detailed demographic data gathered on individually marked animals will remain the gold standard in population biology research, new concepts are emerging for studying age-related population processes and traits when individual age is unknown. One such method involves monitoring death rates in marked individuals of unknown age to estimate rates of aging (Zajitschek et al. 2009). A related concept involves using the death distribution in the laboratory of wild-captured insects to estimate the age structure of the population from which they were sampled (Behrman et al. 2014, Carey et al. 2012). Although both approaches involve certain restrictive assumptions, we believe they hold great promise for studies on populations in which the age of individuals is not known and particularly for studies in which age marking and recapturing are notoriously difficult.

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