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Sci. Aging Knowl. Environ., Vol. 2004, Issue 14, pp. pe14, 7 April 2004
[DOI: 10.1126/sageke.2004.14.pe14]

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Document URL: <http://sageke.sciencemag.org/cgi/content/full/2004/14/pe14>

Key words: evolution • mathematical modeling • senescence • population dynamics • mating systems • life history

Introduction

Traditional theories of aging focus on the way in which genetic changes that affect age-specific survival and reproduction evolve against the backdrop of species-specific life histories (1, 2). Although this approach has typically overlooked ecological and social components, there has been a recent increase in interest in understanding how diverse components of an organism's ecology influence the genetic evolution of aging-related characters. These components of an organism's ecology have included interactions between sources of mortality (3) and between males and females (4-6). Such studies show that the aging phenomenon should depend on the features of individuals, such as gender, physiological conditions, and susceptibility to disease. These results highlight the importance of understanding the social and ecological context in which all evolution takes place. In this Perspective, I discuss the results of a recent study by Berec and Boukal (7), which shows that the dynamics of mating and divorce in a population can affect life spans through their effect on population dynamics.

Mating and Aging

The evolution of age-specific mortality rates has traditionally been understood as the resolution of a conflict of interest between increasing current reproductive output and survival (1, 2, 8) (see [Zwaan Perspective](#)). Whenever natural selection alters the amount of time, energy, or risk that is invested in current reproductive efforts, there will be a concomitant change in age-specific mortality and longevity. The nature of this conflict differs between the sexes because of differences in the opportunities for reproduction. In the simplest case, females choose only how much to invest in raising their current offspring, balancing an increase in mortality with an increase in reproductive output. However, social interactions can make the decision more complicated, because the decisions of conspecifics--participating individuals of the same species--change the costs and benefits of making reproductive decisions.

Reproduction for males depends on acquiring a mate, which always involves some sort of social interaction. On the one hand, competition between males for access to females creates age-specific costs of engaging in sexual behavior; for example, younger males may face greater risks when engaging in combat with older males. This can select for delayed maturity and increase selection on survivorship before breeding begins. On the other hand, female preferences can create age-specific benefits whenever their preferences favor males in a particular age class. For example, if females prefer features that are lost as males age, then males will experience more success by attempting to mate when young, even if aging is

accelerated. Extreme variation in sex-specific maturity is thought to evolve in response to intrasexual competition; for example, male northern elephant seals (*Mirounga angustirostris*) typically are more than 6 years of age before their first breeding attempt and only breed for a few years, whereas females begin breeding at ages ranging from 2 to 6 years and can continue breeding up to age 14 (9, 10). In these seals, males compete with each other to monopolize access to females, which creates a steep increase in mating success with male size. This in turn selects for a later age of maturity in males.

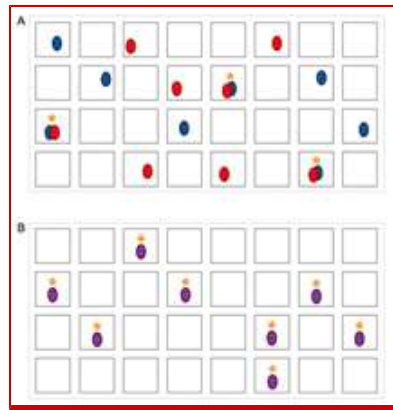
Male reproductive effort and senescence

Regardless of their cause, female preferences can alter the evolution of age-specific mating effort by making particular male age classes more likely to contribute to male reproduction. If females prefer younger males, then a premium is placed on youthful reproduction, and senescence in males will be accelerated. In contrast, if females prefer older males, then senescence in males will be retarded. The prediction that females will express age-specific preferences is based on several ideas. One possibility is that males with higher overall quality have a longer life span. This means that age itself is a window into the genetic quality of an individual, and a female who mates with an older male can ensure that her offspring, both male and female, have high genetic quality and long productive lives (11-13). The opposite position has also been argued: that deviations from the evolved optimal aging schedule create differences in the genetic quality of males as a function of age, so that the oldest males have low genetic quality (14, 15). This position argues that males who do not attempt to reproduce when they are young will live to older ages simply because they avoid reproduction-related mortality. Although this may seem like a reasonable option, these long-lived virginal males actually have lower total lifetime reproductive output, and a female who mates with them will also have offspring with low fitness. Male age could also have a direct negative effect on sperm quality because of mutations that have accumulated in the germ line (16, 17) (see [Walter Perspective](#) and ["Riddled With Errors"](#)). A final possibility is that the "honesty" of males changes with age (4, 6). In many species, females choose mates based on observations over a short period of time and have no future contact with their mate. In this situation, a female must infer the quality of offspring that each male is capable of producing based solely on his appearance and behavior. The handicap theory of signaling predicts that males will signal in an honest way so long as the proportion of future reproduction that a male gives up by signaling is higher for low-quality males (18). When male signals are honest, females are expected to use them in mating decisions. This process causes males with low expected life spans to risk more on current reproduction than high-quality males, and so can result in differences in the rate of aging between males of different quality. This last possibility suggests that a relation between the mating system and aging will exist, at least in males.

Longevity and Population Dynamics

Most thinking about the evolution of aging focuses on genetics and excludes ecological and population-dynamic effects--factors that affect the variability of populations over time and space. The recent study by Berc and Boukal (7) has examined the way in which mating decisions restrict aging-related phenomena through their effect on population dynamics. Their approach was to design models of population growth that take into account the way individuals compete for geographically local resources, mate acquisition, and the breakdown of pair bonds (termed divorce). In doing so, they showed that some populations will become extinct, even when females are capable of producing enough offspring to replace themselves. An important question that they ask is: "How do longevity and mating decisions interact to determine population persistence?" Although they do not model the evolution of mate choice or aging-related genes directly, they determine sets of conditions that are not allowed in nature and thus cannot represent end points of evolution.

Berc and Boukal show that sexual reproduction between two separate sexes can create an Allee effect; that is, a decline in birth rate at low population densities (for example, because of the increased difficulty of finding a mate) (Fig. 1) (7, 19, 20). The Allee effect occurs when small populations become extinct under environmental conditions that allow larger populations to thrive. This effect is caused by sexual reproduction, because unmated individuals may not find an acceptable mate quickly enough to achieve their full reproductive potential (that is, they don't reproduce as often as they are able). Berc and Boukal also include the possibility of divorce, where mating partnerships break up, which again reduces the amount of actual time that females spend breeding. In order for populations to avoid the Allee effect and become established, the initial population has to be large enough, individuals must live long enough, mating pairs must form readily enough, and divorce must be rare enough. This means that each of these features interacts to determine the minimum longevity that allows a population to persist. Even if evolutionary dynamics force the population to enter the parameter ranges that cause extinction (through evolutionary suicide) (21-24), these parameter values will not be observed in nature, because the population goes extinct: If a species evolves its way into extinction, we can know this to be the case only through the fossil record or by noting that extant species never have the properties that would make them prone to evolutionary extinction. The overall pattern predicted by this theory is that neither high divorce rates nor low mate acceptance rates can be associated with short life spans.



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Fig. 1. The Allee effect. Red ovals, female; blue ovals, male; purple ovals, hermaphrodite; stars indicate reproduction. In (A), only mated pairs can reproduce. Each square represents a spatial location, and a mated pair must occupy the same spot in order to reproduce. When females spend time unmated, either because of divorce or because they cannot find acceptable mates, they cannot reproduce. The spatial clumping of mated pairs can also have a negative effect on population growth if offspring compete for sites. The hermaphroditic species, shown in (B), does not need to search for mates. This means that there is no Allee effect, and the population will generally grow faster than will populations of species with separate sexes.

The Allee effect is often associated with social behavior, and Berc and Boukal find support for this idea in their study. The type of mate search strategy that individuals use has an effect on both the likelihood of pair formation and the degree to which offspring are clumped. They compare passive search models (in which individuals wander until they find a mate) with active search models (in which individuals move directly toward potential mates) and find that passive search tends to decrease the likelihood of population persistence. This happens in their model because clumping causes local competition between offspring for sites, for instance, because only a limited number of nest sites are available. Berc and Boukal suggest that colonial species can persist with higher divorce rates because new mates are easy to find. However, to understand how these effects play out in nature, we need a better understanding of the relation between local competition for resources and the ability to find mates. These results suggest that species with very short life spans must have either active mate search or mating aggregations.

Berc and Boukal's study assumes complete monogamy, and this makes the population dynamics depend symmetrically on the number of males and females. It is likely, however, that females play a larger role than males in defining population growth rates, because even socially monogamous species often show some degree of promiscuity (25). This suggests that population-dynamic forces place a larger emphasis on female longevity.

Population Dynamics, Evolution, and Aging

The work by Berc and Boukal explores the population-dynamic consequences of mating decisions and shows that these consequences depend on birth rates and longevity. But how do we expect mating decisions and senescence to coevolve? In other words, even though there is a minimum bound on longevity as a function of pair formation, will evolution move populations far away from this bound, or will they be on the edge of evolutionary suicide? In order to answer this question, we need to have models that include spatial population dynamics--those that occur in a defined region or space--as well as evolutionary changes that result from genetic mutations. It is becoming more and more apparent that ecological forces play a large role in shaping what have traditionally been thought of as purely genetic problems; these new results remind us that the evolution of aging is no exception.

April 7, 2004

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Citation: S. R. Proulx, Does Sex Age You? *Sci. Aging Knowl. Environ.* **2004** (14), pe14 (2004).

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