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Review

Senescence in the wild: Insights from a long-term study on Seychelles warblers

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ABSTRACT

Senescence – the progressive age-dependent decline in performance – occurs in most organisms. There is considerable variation in the onset and rate of senescence between and within species. Yet the causes of this variation are still poorly understood, despite being central to understanding the evolution of senescence. Long-term longitudinal studies on wild animals are extremely well-suited to studying the impact of environmental and individual characteristics (and the interaction between the two) on senescence, and can help us to understand the mechanisms that shape the evolution of senescence. In this review, we summarize and discuss the insights gained from our comprehensive long-term individual-based study of the Seychelles warbler (*Acrocephalus sechellensis*). This species provides an excellent model system in which to investigate the evolution of senescence in the wild. We found that Seychelles warblers show senescent declines in survival and reproduction, and discuss how individual characteristics (body condition, body size) and environmental effects (low- versus high-quality environments) may affect the onset and rate of senescence. Further, we highlight the evidence for trade-offs between early-life investment and senescence. We describe how key cellular and physiological processes (oxidative stress and telomere shortening) underpinning senescence are affected by individual and environmental characteristics in the Seychelles warbler (e.g. food availability, reproductive investment, disease) and we discuss how such physiological variation may mediate the relationship between environmental characteristics and senescence. Based on our work using Seychelles warblers as a model system, we show how insights from long-term studies of wild animals may help unravel the causes of the remarkable variation in senescence observed in natural systems, and highlight areas for promising future research.

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1. Introduction

Senescence is generally defined as the progressive decline in performance of organisms with advancing age (Kirkwood and Austad, 2000). Senescent declines in physiological and cellular functions result in age-dependent declines in reproductive output and/or survival – the major determinants of fitness (Stearns, 1992). Senescence occurs in most organisms, but its onset and rate varies considerably within and among species (Nussey et al., 2013), and this striking variation remains poorly understood (Jones et al., 2014). Important outstanding questions are which factors determine: i) how long an individual will live, ii) from which age individuals suffer senescence, and iii) how fast performance declines from the onset of senescence. Other important questions include whether certain lifestyles are associated with accelerated or delayed senescence, and how physiological pathways influence senescence. Identifying the proximate and ultimate factors that cause this variation will help us to understand the evolution of senescence.

Until recently, the majority of studies on senescence have focused on captive model organisms held under controlled laboratory settings, such as mice and fruit flies (e.g. Kirkwood and Rose, 1991; Zwaan et al., 1995; Charlesworth and Hughes, 1996; Sgro and Partridge, 1999; Hughes et al., 2002). These studies have provided fundamental insights into the evolutionary and mechanistic basis of senescence (Guarente and Kenyon, 2000; Kirkwood and Austad, 2000). However, the protected and stable laboratory environments in which these studies are usually conducted are not comparable to the variable abiotic and social environments organisms experience in the wild (Partridge and Gems, 2007). For example, fitness costs of being of poor intrinsic quality are often only expressed under stressful environmental conditions (Cheptou and Donohue, 2011), and therefore may be offset by ad libitum food conditions or benign climates in the laboratory. As such, the selection pressures in natural and laboratory populations may differ to the extent that the balance of the factors governing the onset and rate of senescence is affected. In addition, laboratory studies often use animals that have relatively low levels of genetic and phenotypic variation, that have been selected for high rates of reproduction, and/or that show different longevity compared to wild individuals (Partridge and Gems, 2007). For example, laboratory studies tend to select on a few traits, whereas natural selection acts on multiple traits in concert (Morrissey et al., 2010). A topic that has received less attention is how social conditions and senescence are related (but see Bourke, 2007). As life-histories and fitness are shaped by social interactions between individuals, the social environment may be an important evolutionary force driving variation in the onset and rate of senescence. For example, individuals in highly social species generally have longer lifespans than those in less social species (Keller and Genoud, 1997; Bourke, 2007). However, we still know very little about the exact relationships that exist between social conditions and senescence. Thus, although we now know a lot about senescence in model organisms under controlled circumstances, we still have limited understanding of i) how the onset and rate of senescence relates to individual characteristics (e.g. life history traits, individual "quality", body condition), and ii) how variable social (e.g. interactions with other individuals, cooperative breeding behaviour) and environmental conditions (e.g. adverse weather conditions, food availability) shape senescence in the wild (Partridge and Gems, 2007; Monaghan et al., 2008; Nussey et al., 2013).

Three main non-mutually exclusive hypotheses are often cited to explain the evolution of senescence, all of which are based on the fundamental concept that selection is strongest early in life and decreases with age (Medawar, 1952; Williams, 1957; Hamilton, 1966; Charlesworth, 1994; Kirkwood and Austad, 2000). The mutation accumulation hypothesis proposes that the accumulation of late-acting deleterious mutations over multiple generations causes senescence (Medawar, 1952). The antagonistic pleiotropy hypothesis, meanwhile, assumes that genes with beneficial effects early in life are favoured by selection despite their potential deleterious effects later in life (Williams, 1957). This hypothesis therefore predicts a trade-off between early- and late-life fitness (Williams, 1957; Kirkwood and Rose, 1991; Kirkwood and Austad, 2000). Finally, the disposable soma hypothesis (Kirkwood, 1977; Kirkwood and Holliday, 1979) is similar to antagonistic pleiotropy, but focuses on the trade-offs between the allocation of resources to reproduction versus somatic repair. Specifically, it assumes that early-life investment in repair or maintenance of the soma is costly and traded-off against investments in other costly activities, such as future reproduction and late-life survival (Kirkwood and Rose, 1991; Kirkwood and Austad, 2000). Although laboratory studies generally provide support for evolutionary theories of senescence (Stearns et al., 2000; Chen and Maklakov, 2012), the results from the smaller number of studies of natural populations are mixed (Reznick et al., 2004; Nussey et al., 2013; Hämäläinen et al., 2014). Furthermore, research has tended to focus on distinguishing between the relative importance of these three hypotheses without clear mutually exclusive predictions, perhaps at the cost of leaving important gaps in our understanding of other aspects of the phenomenon of senescence.

Investigating senescence in natural populations is challenging for a number of reasons. First, in many wild populations the majority of

Fig. 1. The Seychelles warbler on Cousin Island. Panel A shows a Seychelles warbler with three colour rings and one metal ring. Panel B shows the intensively monitored Cousin Island with Cousine Island behind. Translocations of Seychelles warblers to nearby islands have led to the successful establishment of Seychelles warblers on four other islands, including Cousine. Photos by M. Hammers.