IN FOCUS

Senescence in nature: New insights from a long-term seabird study

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Christophe Barbraud, Centre d'Etudes Biologiques de Chizé, UMR7372 - CNRS & Université La Rochelle, 79360 Villiers en Bois, France.
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Abstract

In Focus: Tompkins, E. M., & Anderson, D. J. (2019). Sex-specific patterns of senescencein Nazca boobies linked to mating system. *Journal of Animal Ecology, 88*, 986-1000. https://doi.org/10.1111/1365-2656.12944. Sex-specific differences in senescence and environmental impacts on senescence in both sexes remain poorly understood. Tompkins and Anderson (2019) studied senescence in survival (hereafter called actuarial senescence) and in reproduction (hereafter called reproductive senescence) in Nazca boobies using 33 years of individual-based capture–recapture data. Senescence patterns (life-history traits, ages at onset, senescence rates) differed between sexes and were affected by environmental conditions (food availability) faced by individuals during their younger ages. Patterns of sex differences in senescence may result from the mating dynamics due to the population's male-biased sex ratio.

KEYWORDS
early-life diet, mate dynamics, Nazca booby, senescence, sex

Understanding the eco-evolution of senescence–the decrease in whole-organism performance with age–remains a major puzzle in evolutionary ecology. Although the theoretical foundations of the evolution of senescence were established during the first half of the 20th century (Fisher, 1930; Haldane, 1941; Medawar, 1952; Williams, 1957), the first mathematically explicit versions of the theory of senescence started more recently (Charlesworth, 1980; Hamilton, 1966). Therefore, empirical tests of the theoretical ideas of senescence have a relatively short history. This is particularly true for the study of senescence in wild animals, which necessitates large sample sizes and long-term individual-based studies. However, there was acceleration in the study of senescence in the wild since the beginning of the 21st century partly due to the increasing number of long-term studies of wild populations (Nussey, Froy, Lemaitre, Gaillard, & Austad, 2013). Some of these empirical findings, together with recent theoretical studies, appear to contradict major predictions of the senescence theories, pointing to the need for a broader and more integrative theory of senescence (Cohen, 2017; Jones et al., 2014). Therefore, the study of senescence in the wild is a growing field of research and, despite the fact that actuarial and reproductive senescence are now recognized in many vertebrate species, many

unresolved questions remain (Bouwhuis & Vedder, 2017; Lemaître & Gaillard, 2017). For example, whether environmental variations have sex-specific effects on actuarial and reproductive senescence remains an open question. Tompkins and Anderson (2019) explore these issues and others, using a long-term study of a long-lived seabird species.

Nazca boobies (*Sula granti*) have been studied on Española Island in the Galápagos archipelago since 1984. During most breeding seasons until 2017, fledglings were banded and annual band resight surveys provided individual capture histories of known-age birds as well as information on their breeding performances. Tompkins and Anderson (2019) used 1,564 individual capture histories to estimate sex-and age-specific survival and between 1,781 and 2,057 individual capture histories to estimate sex-and age-specific reproductive parameters including annual breeding success, breeding probability and fledging success. Using state-of-the-art analytical approaches, Tompkins and Anderson (2019) first tested for different sex-specific rates and ages at onset of senescence. They detected actuarial and reproductive senescence in both sexes, but with clear sex differences. The increase in mortality rates in males, which are 16% lighter than in females, started later in life than in females and was
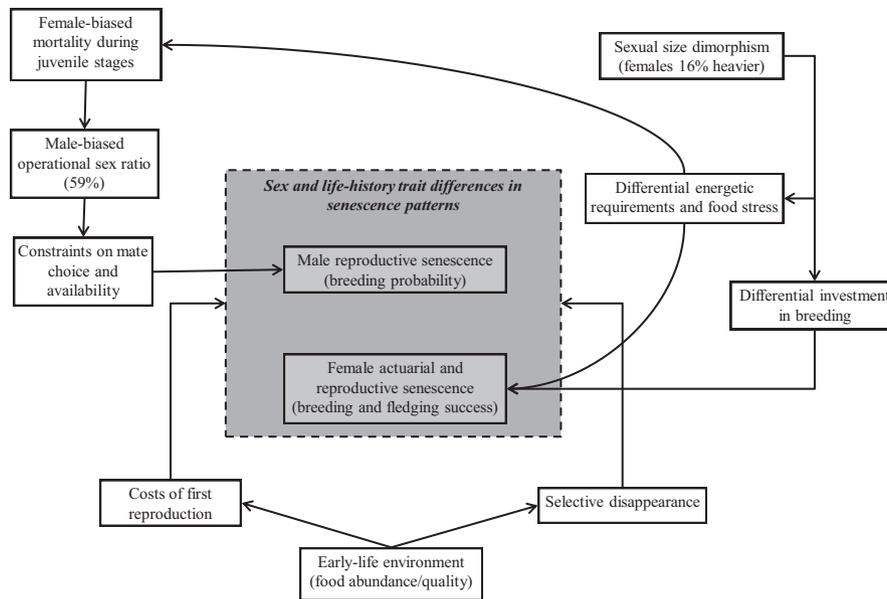
FIGURE 1 A schematic overview illustrating how mating dynamics may generate senescence differences between sexes and life-history traits at the population level in monogamous species in populations with biased sex ratios, as proposed by Tompkins and Anderson (2019). During the juvenile stage, female Nazca booby breeding Española Island in the Galápagos archipelago experience higher mortality than males (Maness, Westbrock, & Anderson, 2007). A direct consequence is a male-biased operational sex ratio with 59% males (Maness & Anderson, 2007). This results in an excess of unmated males trying to breed each year. Since females control pair formation and maintenance (Maness & Anderson, 2008) and may prefer younger and pre-senescent males, as in the closely related blue-footed booby (Ramos, Garnier, Gonzalez-Solis, & Boulinier, 2014; Torres & Velando, 2007), older males may be less likely to breed, generating senescence at the population level. Females being 16% heavier than males have higher energy requirements and may experience food stress at fledging, which may explain their lower survival during the juvenile stage, as well as actuarial and reproductive senescence. Early-life environmental conditions also affect sex-specific senescence patterns through different pathways. Enhanced costs of first reproduction during early life may negatively impact mortality risks and reproductive investment later in life. Alternatively, but not exclusively, differential mortality of poor-quality (frail) individuals during early life (selective disappearance) may affect senescence patterns found at the population level

slightly lower. Since female Nazca boobies breed more frequently than males and experience a more wear and tear strategy, these results nicely fit with the predictions from the theoretical framework of senescence (Hamilton, 1966). Regarding reproductive senescence, females had an earlier onset and steeper late-life decline in reproductive performance than males for annual breeding success and fledging success. Again, these results are coherent with the predictions from the theory, although clear predictions about reproductive senescence are lacking and reproductive senescence is usually grounded in the same theoretical framework used to explain actuarial senescence (Lemaître et al., 2015).

A puzzling result found by Tompkins and Anderson (2019) was that, contrary to theoretical predictions (Cody, 1966; Kirkwood, 1977; Williams, 1957), early-adult reproductive effort did not reveal long-term survival and reproductive costs. Tompkins and Anderson (2019) used the number of clutches as a proxy for early-adult reproductive effort, and more traits may be needed to test this hypothesis due to the sequential nature of reproductive senescence in males (pre-and post-copulatory traits, ejaculate quality and quantity, paternal care) and females (quantity and quality of oocytes, maternal care) in free-ranging populations (Lemaître & Gaillard, 2017).

More puzzling is the earlier onset and steeper rate of senescence in males for breeding probability. Males had a lower breeding probability than females for all age classes, and their breeding probability started to decrease two years earlier than females. Although this could be a consequence of senescence in pre-or post-copulatory sexual traits, as observed in a closely related species (Torres & Velando, 2007; Velando, Noguera, Drummond, & Torres, 2011), Tompkins and Anderson (2019) suggest three non-mutually exclusive hypotheses to explain the sex differences in senescence observed at the population level. Two of these explanations (long-term differences in the nestling experience due to sexual size dimorphism and differential reproductive investment by males and females) are hypotheses commonly formulated by the evolutionary theory of senescence, but the third one presents some novelty linked to the mating dynamics of Nazca boobies (Figure 1). It is well known that among-individual heterogeneity in life span may mask, or falsely suggest, senescence patterns at the population level (Vaupel & Yashin, 1985). For example, due to phenotypic heterogeneity, frail individuals are more likely to die young and the proportion of high-survival individuals increases with age. Consequently, the age-specific mortality estimated at the cohort or population level could plateau or even decrease with age as low-frailty individuals compose a larger and larger proportion of the survivors. Tompkins and Anderson (2019) propose a new mechanism (mating choice and mate availability) that may contribute to observed population-level patterns and sex differences of actuarial and reproductive

senescence even in the absence of underlying sex differences in somatic degeneration with age. In essence, female-biased mortality in early life can lead to sex ratio biases in reproduction, with potential consequences for how and when senescence occurs. This mechanism may operate in other monogamous species showing similar mating dynamics and for which sex ratios are unbalanced.

Another important advance in the understanding of senescence in wild populations made by Tompkins and Anderson (2019) is their investigation of the impact of early environmental conditions on both actuarial and reproductive senescence in males and females, a poorly documented aspect in wild populations (Balbontín & Møller, 2015; Cartwright, Nicoll, Jones, Tatayah, & Norris, 2014). Interestingly, actuarial senescence started later and was slower in females experiencing a food-stressed environment during early adulthood than in females experiencing a food-rich environment. Environmental conditions also influenced reproductive senescence in males: males had a steeper decline of fledging success with age when faced with food-rich conditions during early adulthood.

Interestingly, the recent discovery that early and adult social environments modulate actuarial senescence patterns differently between sexes and life stages in cooperative breeding species (Berger, Lemaître, Allainé, Gaillard, & Cohas, 2018) also demonstrates that the proximate determinants of senescence are more complex than previously thought. These observations stress that our understanding of the eco-evolution of senescence in wild populations is still limited when it comes to sex differences and effects of environmental conditions experienced by individuals during their lifetime.

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