other fitness traits in the field. Genetics *166*, 693–706.
12. Koch, M., Vorwerk, S., Masur, C., Sharifi-Sirchi, G., Olivieri, N., and Schlaich, N.L. (2006). A role for a flavin-containing mono-oxygenase in resistance against microbial pathogens in *Arabidopsis*. Plant J. *47*, 629–639.

13. Zhao, Y., Christensen, S.K., Fankhauser, C., Cashman, J.R., Cohen, J.D., Weigel, D., and Chory, J. (2001). A role for flavin monooxygenase-like enzymes in auxin biosynthesis. Science *291*, 306–309.
14. Kamoun, S. (2007). Groovy times: filamentous pathogen effectors revealed. Curr. Opin. Plant Biol. *10*, 358–365.

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Vertebrate Ageing: An Evolutionary Process with a Genetic Basis?

Theories that explain the persistence of ageing in the face of natural selection implicitly assume that there is a genetic basis for ageing. This has now for the first time been shown to be the case in two free-living populations of mammals.

Jean-Michel Gaillard and Christophe Bonenfant

Senescence (or ageing) is a biological process occurring after the period of development of an organism and involves several mechanisms of deterioration. At first sight, senescence could simply be due to wear reflecting a physiological deterioration of cells with increasing age. This interpretation would explain why senescence occurs in free-ranging populations despite the apparent negative effects of decreasing individual performance with age. However, in our current evolutionary theory senescence is viewed as a life-history process that is moulded by natural selection. This poses the question of why senescence occurs even though it should be selected against. Two main, non-mutually exclusive hypotheses have been proposed to explain this apparent paradox: the mutation-accumulation hypothesis [1] suggests that the strength of selection decreases with age, such that more deteriorating mutations would accumulate; the antagonistic-pleiotropy hypothesis [2] involves positive selection for genes that confer short-term fitness benefits early in life, but at the same time cause fitness reduction in later ages.

In both of these models, senescence has a genetic basis. However, evidence for a genetic basis of variation of senescence had not yet been provided for free-ranging vertebrate populations. In a recent issue of *Current Biology*, Wilson *et al.* [3] fill this gap and report that genetic differences among individuals account for variation in their senescence rates. This offers the first firm empirical support for the current evolutionary theory of senescence in vertebrates — either mutation accumulation or antagonistic pleiotropy, as these hypotheses are not easy to disentangle in practice [3]. This finding is a major contribution to our understanding of senescence in vertebrates. The results of Wilson *et al.* [3] are based on two key components that should shape future empirical studies on senescence in free-ranging populations: the availability of detailed long-term (>30 years) data collected at the individual level and the use of an appropriate metric for measuring senescence. Using exceptionally detailed, long-term monitoring of Red deer and Soay sheep populations living on Scottish Islands, Wilson *et al.* [3] were able to estimate accurately the age-specific variation in both reproductive success and survival for large numbers of individuals. This provided a direct measure of senescence in annual fitness. Moreover, the knowledge of pedigree structures in those populations allowed the authors to apply quantitative genetic models in order to assess whether variation in ageing rates in annual fitness in sheep and deer females had an additive genetic basis.

Detecting Senescence in Free-Ranging Populations of Vertebrates: Is Ageing Universal?
Senescence has always intrigued people, but research on ageing has traditionally focused on humans, laboratory invertebrates or captive vertebrates [4–6]. Whether findings obtained on these models will apply to free-ranging populations is, however, questionable. Unlike experimental animals, free-ranging animals face a large amount of environmental fluctuation and are typically subject to much higher mortality during the first stages of the life-cycle, which indicates that natural selection will operate mainly at early stages of life. As illustrated by Wilson *et al.* [3], the availability of long-term data on an individual level is required to analyse the senescence reliably in the wild. Consequently, empirical evidence of senescence in free-ranging populations of vertebrates has so far almost entirely focused on a few particular groups, such as seabirds and passerines [7] or large herbivore mammals [8]. By contrast, other species, such as fishes or tortoises, were reported not to age in the wild [9], although these conclusions were based on limited sample sizes.

Whether senescence is a universal process cannot be answered without long-term, individual-based data and in particular the duration of a study constitutes a key component for our ability to detect senescence in free-ranging populations. Of course, the required study length will depend on the focal species. Ideally, a study should include several cohorts monitored until extinction. Nowadays, the paucity of data in terms of taxonomic range, sample size and duration prevent a reliable answer to the question of how universal senescence is in the wild. Of course, this also hampers our understanding of the mechanism involved in shaping age-specific changes in life-history traits. Long-term studies involving the monitoring of individual performance from birth to death, such as those reported by Wilson *et al.* [3] for red deer and Soay sheep are badly needed.

Assessing Senescence from an Evolutionary Perspective
From an evolutionary perspective, the effects of senescence should be measured with respect to the fitness of individuals rather than to specific life

history traits [10]. In vertebrates, individual fitness is often measured as an absolute value, such as the lifetime reproductive success [11]. Lifetime reproductive success, however, is not an age-specific measure and thus not suitable for analysing senescence. In most studies performed so far, age-specific survival has been used as a proxy for annual individual fitness to analyse actuarial senescence. However, a possible trade-off between survival and reproduction may confound the interpretation of actuarial senescence in terms of fitness. Decreased survival with age could indeed correspond to an absence of senescence if the reproductive output increases with age at the same time, as expected under the evolutionary hypothesis of 'terminal investment' [12]. This hypothesis states that the reproductive effort of females should increase in populations in which the expected number of offspring a female produces until its death decreases with the female's age. In their analysis, Wilson et al. [3] used a measure of annual fitness that combines survival and reproduction [13] thus accounting for possible trade-offs. This measure is based on the relative contribution of a given individual to the population growth in a given year. By accounting for environmental variations, these individual contributions to the population growth offer a promising metric for studying senescence in free-ranging populations.

Senescence as a Life-History Process
Hamilton [14] showed that senescence should occur as an inevitable consequence of repeated reproductive events that through age-specific mutations should lead to reduced fitness with age in any age-structured population. Both simulations of life-history tactics [15] and empirical studies on fishes [16], birds [7], and large mammalian herbivores [8] supported the contention of a pervasive occurrence of senescence in vertebrates. Kirkwood and Holliday [17] provided a life-history context for the evolution of senescence, the disposable soma theory, that is basically grounded in the energy allocation principle and involves a trade-off between longevity and reproduction. Despite such a strong theoretical context, and some case studies that have provided empirical support of this theory [18], the genetic basis required for such an evolutionary process remains undiscovered. By showing that additive genetic variance in annual relative contributions of individuals to population growth was highest in the oldest age classes of both red deer and Soay sheep living in free-ranging conditions, Wilson et al. [3] established a strong link between observations and theory. Whether a genetic basis generally underlies senescence in annual fitness among vertebrates, providing thereby a direct support for evolutionary theories of aging, deserves clearly further investigation.

References
1. Medawar, P.B. (1952). An Unsolved Problem of Biology (London: H.K. Lewis).
2. Williams, G.C. (1957). Pleiotropy, natural selection, and the evolution of senescence. Evolution 11, 398–411.
3. Wilson, A.J., Nussey, D.H., Pemberton, J.M., Pilkington, J.G., Morris, A., Pelletier, F., Clutton-Brock, T.H., and Kruuk, L.E.B. (2008). Evidence for a genetic basis of aging in two wild vertebrate populations. Curr. Biol. 17, 2136–2142.
4. Gavrilov, L.A., and Gavrilova, N.S. (1991). The Biology of Life Span: A Quantitative Approach (Harwood Academic Publishers).
5. Partridge, L., and Barton, N.H. (1993). Evolution of aging: testing the theory using Drosophila. Genetica 91, 89–98.
6. Ricklefs, R.E. (1998). Evolutionary theories of aging: confirmation of a fundamental prediction, with implications for the genetic basis and evolution of life span. Am. Nat. 152, 24–44.
7. Bennett, P.M., and Owens, I.P.F. (2002). Evolutionary Ecology of Birds. Life History, Mating Systems and Extinction (Oxford: Oxford Series in Ecology and Evolution).
8. Gaillard, J.M., Loison, A., Festa-Bianchet, M., Yoccoz, N.G., and Solberg, E. (2003). Ecological correlates of life span in populations of large herbivorous mammals. Population Dev. Rev. 29, 39–56.
9. Miller, J.K. (2001). Escaping senescence: demographic data from the three-toed box turtle (Terrapene Carolina triunguis). Exp. Geront. 36, 829–832.
10. Partridge, L., and Barton, N.H. (1996). On measuring the rate of ageing. Proc. R. Soc. Lond. B 263, 1365–1371.
11. Clutton-Brock, T.H. (1988). Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems (Chicago: Chicago University Press).
12. Clutton-Brock, T.H. (1984). Reproductive effort and terminal investment in iteroparous animals. Am. Nat. 123, 212–219.
13. Coulson, T., Benton, T.G., Lundberg, P., Dall, S.R.X., Kendall, B.E., and Gaillard, J.M. (2006). Estimating individual contributions to population growth: evolutionary fitness in ecological time. Proc. R. Soc. Lond. B 273, 547–555.
14. Hamilton, W.D. (1966). The moulding of senescence by natural selection. J. Theor. Biol. 12, 12–45.
15. Sozou, P.D., and Seymour, R.M. (2004). To age or not to age. Proc. R. Soc. Lond. B 271, 457–463.
16. Reznick, D., Ghalambor, C., and Nunney, L. (2002). The evolution of senescence in fish. Mechanisms Ageing Dev. 123, 773–789.
17. Kirkwood, T.B.C., and Holiday, F.R.S. (1979). The evolution of ageing and longevity. Proc. R. Soc. Lond. B 205, 531–546.
18. Orell, M., and Belda, E.J. (2002). Delayed cost of reproduction and senescence in the willow tit Parus montanus. J. Anim. Ecol. 71, 55–64.

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Insect Behaviour: Learning for the Future

Recent studies show that what, when and how a parasitic wasp learns is tailored to its specific ecological niche.

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Parasitic wasps specializing on particular hosts have evolved elaborate patterns of behaviour to breach their host's evasion strategies. Several recent studies [1–4] emphasise that smart adaptations of the learning behaviour of some of these wasps contribute to their success as parasites. The first set of studies [1,2] concerns locality learning in a parasitic wasp, which oviposits in butterfly eggs and learns the location of its host's eggs well before the eggs are mature enough to be exploited. The second set [3,4] examines subtle difference in the long-term memories of two closely related parasites that help these wasps adjust to their host's particular lifestyle.

Many bees and wasps learn the landmarks defining a place during elaborately choreographed flights (for example [5]). Such flights are seen in solitary wasps when they first leave their own nest — a valued resource that