


Letter

Williams' Intuition about Extrinsic Mortality Is Irrelevant

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Williams' [1] model is presented as a general description of how selection favours age-specific survival in an age-structured population, but it has been falsified soundly on theoretical grounds. As a better model, namely Hamilton's [2], exists, there is no legitimate scientific reason to test Williams' model further. If Williams' predictions are supported empirically, then these results are coincidental and not for the reasons imagined by Williams [3]. da Silva [4] appears willing to consider coincidence as intuition. The crux of his argument appears to rest on two claims, but these are based upon misrepresentations of Williams' model and the findings of later models of ageing that explore the effects of density dependence.

da Silva [4] claims that Williams' model examines the effects of adult mortality and because subsequent models used to falsify Williams' invoke extrinsic mortality (age-independent mortality in this context) instead, the latter do not faithfully test the former. However, the relevant section in Williams [1] (p. 405) states: 'According to the theory, death rates prior to maturation have no influence on the evolution of

senescence.' We know from Hamilton [2] that this evolutionary inference is incorrect, but more to the point, Williams' is telling us that his model does not recognise a difference between adult mortality and extrinsic mortality. This is because we are free to increase juvenile mortality to the point that the two definitions converge with no effects on evolutionary outcomes (at least as predicted by Williams [3]). da Silva's argument is undermined by Williams' own insights into his model.

He also claims that Williams' intuitions are correct if 'biologically reasonable assumptions are made', even if the extrinsic mortality case applies. These assumptions are represented by density-dependent population regulation 'through changes in fertility, adult mortality, or the age of maturity'; da Silva's suggestion is that the simple presence of density dependence is a sufficient condition to make Williams' prediction hold true. This is a biased and oversimplified representation of the proper theory (in the sense that it is compatible with Hamilton's) that da Silva references [5]. The truth is that the relevant theory recognises that extrinsic mortality combined with different kinds of density dependence can make qualitatively different predictions regarding the evolution of senescence: some predict accelerated senescence (consistent with Williams' prediction), but some conditions predict no change or even suppressed senescence (the opposite of Williams' prediction) [6]. Unfortunately, da Silva does not attempt to discriminate amongst these

conditions and implies inaccurately that all forms of density dependence lead to predictions that agree with Williams.

We do not find da Silva's [4] arguments to be compelling. If others feel that a modern investigation into the evolution of senescence should be motivated by Williams' [1] model, they should be prepared to articulate carefully what purpose this perspective serves and why such a study would not be improved by using Hamilton's perspective [2] instead. If biologists truly wish to honour Williams' insights into the evolution of senescence, they should emulate his own decision to subscribe to Hamilton's perspective [7].

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