



## Pathological complexity and the evolution of sex differences

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### Abstract

Benenson et al. provide a compelling case for treating greater investment into self-protection among females as an adaptive strategy. Here, we wish to expand their proposed adaptive explanation by placing it squarely in modern state-based and behavioural life-history theory, drawing on Veit's *pathological complexity* framework. This allows us to make sense of alternative “lifestyle” strategies, rather than pathologizing them.

Benenson, Webb, and Wrangham (2022) provide an excellent empirical synthesis of data from different fields to support the idea that a greater investment into self-protection has evolved as a unique adaptive strategy in females. They draw on data that provide varying levels of support for the hypothesis that human females do produce stronger self-protective reactions than males, to a range of threats, which then suggests the presence of a general female self-protection strategy that may be adaptive rather than pathological. Nevertheless, the question then remains as to how best explain the results, and identify the adaptive function of domain-general self-protective behaviour. The authors locate this within Campbell's “staying alive” theory: That human females have a higher fitness value arising from self-protection than males do.

Here, we wish to expand their proposal by placing it squarely in modern state-based and behavioural life-history theory, which – despite a brief mention – was surprisingly not discussed within the target article. Life-history theory originated in simple models representing the necessity of a trade-off between longevity and the number of offspring created in a particular breeding period to maximize fitness (Stearns, 1992). Even this restricted approach to modelling life histories has demonstrated that greater offspring care leads to an investment into survival, rather than reproductive output (Hamilton, 1966; Williams, 1966). While Benenson et al. mention this part of the literature, they do not draw on the subsequent extension of this early work, which proceeded through the inclusion of behaviour and varying bodily states, to eventually lead to state-based behavioural and life-history theory (McNamara & Houston, 1996). This theory is not only important to understand the ecological lifestyles of different species, but also to assess the *teleonomic* complexity of different organisms in achieving their goal of reproduction – or rather, fitness-maximization – as it is only within such an ecological theory of the organism that we can distinguish pathological traits and behaviours from adaptive ones.

It is for this reason that one of us has used the term “pathological complexity” to refer to the complexity of this set of trade-offs, that is, the number of parameters and constraints in the teleonomic optimization problem, studied by modern state-based behavioural and life-history theory (see Veit, 2022a, 2022b). The term “pathological” here is not meant to imply that life-history complexity is inherently pathological; but rather that it is only in assessing this complexity of optimizing trade-offs to maximize fitness that we can determine which behaviours are pathological. This can be done by calculating the trade-offs inherent to different life-history strategies, with fitness serving as the common currency of organismal design, which a common example within life-history theory will help to illustrate. In Australian marsupials of the genus *Antechinus*, males typically die after a single breeding season. While such behaviour in males may be seen as strikingly pathological, through life-history theory we can see that it is not. Their best response to their species-specific pathological complexity is to invest all their resources into reproduction in a single breeding season, and hence this is not pathological.

Some life-history strategies will have higher pathological complexity than others, due to the higher number of parameters and constraints in their environment and evolutionary design. Again, this does not make their responses pathological, but it makes their design a more complex trade-off problem to be solved. If a life-history strategy puts all efforts into reproduction in a single period, there will inevitably be fewer complex trade-offs to be solved. Indeed, pathological complexity can be increased through external factors (e.g., the presence of predators) or internal ones (e.g., the need for a greater variety of nutrients), as well as the availability of more degrees of freedom of behaviour, which can greatly increase the computational problem of maximizing fitness both for the organism and for those modelling their life-history strategies. If we fail to account for one of those factors in our models, we will inevitably come to re-examine mistaken evaluations of some behaviours as pathological when we gain a greater understanding of species- and sex-specific life-history strategies.

It is thus hardly surprising that we urge the use of life-history theory in answering the question of whether females have a different optimal design solution to deal with their particular pathological complexity arising from the trade-off between survival and reproduction. It is *the* framework to assess the adaptive nature of diverse female traits and to challenge prevailing ideas about the pathological nature of differences between the sexes. In order to evaluate whether self-protection is sex-specific, life-history strategy requires investigation into the different social and ecological niches faced by human males and females, both currently and throughout our adaptive history, to identify possible factors – or sets of factors – that could serve to explain the observed difference in behaviour. For instance, it is possible that females face a greater range of potential threats to survival and reproduction, and hence require a more complex adaptive behavioural phenotype in response. If survival is more important for females than it is for human males, this may well suggest that their life-history complexity is higher with more threats to keep track of – demanding unique and more risk-averse adaptations, just as the authors suggest.

Finally, we applaud the application of this work, in demonstrating that the distinctive female responses to threat are an adaptive reaction to their differential niche, and should thus not be pathologized. For too long, deviations from the male

“norm” have been seen as problematic, rather than simply different acceptable strategies. As the authors suggest, this can enhance understanding of female health and well-being with reference to what is normal for this group. Experiences and conditions that are more common in females – such as pain disorders, anxiety, and autoimmune diseases – can be examined and treated accordingly. A deeper understanding of the environmental challenges that have shaped these sex differences, and where they currently still do or do not apply, could also assist in determining when there is a normal reaction or a pathological maladaptation to modern social and living conditions.

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## Sex differences in longevity are relative, not independent

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### Abstract

I ask three questions related to the claims made within the staying alive theory (SAT): Is survival more fitness-enhancing for females than for males? Does the historical record on sex differences in mortality support the SAT? Is it possible to talk about “independent selective pressures on both male and female traits” when all we have are sex/gender comparisons?

A central tenet of the target paper is that “survival is more fitness-enhancing for females than for males.” There is something odd about this claim, since survival is a necessary condition for reproductive fitness. Without survival there is no reproduction. Without further specification it thus becomes meaningless to talk about sex-differences in fitness linked to survival. A favorable

reading of the paper says that the authors are really aiming not at survival but longevity. In other words: survival beyond a certain point. One crucial time point is obviously mating. Before mating survival is infinitely fitness-enhancing for both sexes.

Beyond mating, the mother’s reproductive fitness relies on her survival during pregnancy as well and this is where the paths of the two sexes diverge. The fitness of the father no longer depends on his own survival, but solely on the survival of the mother and the fetus. One may therefore argue that after this time point there is a stronger evolutionary pressure on the survival of the mother than on the father. After the child is born, the reproductive fitness of both parents depends on the survival of the child. The authors convincingly argue that mothers spend more time than fathers looking after their children and that her survival thus may be more important for the survival of the child than that of the father. This seems to be the evolutionary account behind females’ longer life expectancies, according to the staying alive theory (SAT). However, it misses one crucial point. Males are fertile throughout their lives, and their fitness is not tied to one individual pregnancy. It is therefore difficult to see why longevity would not also increase male fitness equally, given that longer life would provide opportunities for additional mating. Data exist to support a correlation between parity (i.e., reproductive fitness) and longevity in both sexes (Barclay & Kolk, 2019; McArdle et al., 2006). Within this naive evolutionary framework for human reproduction, which disregards culture, family, and parental collaboration, longevity thus appears to be an advantage for both sexes. More effort is needed to flesh out why the evolutionary advantage of longevity would be greater for females than for males.

Does the historical record on sex differences in mortality support the SAT? Following the link to parental care, the authors predict “increased magnitudes of sex differences following puberty.” However, when making a detailed investigation of differences in mortality, the picture is not clear. Excess male deaths in reproductive years (between 15 and 40), where the evolutionary pressure would occur according to the SAT, account for less than 25% of the life expectancy gap, both presently and historically (Zarulli, Kashnitsky, & Vaupel, 2021). The sex difference in life expectancy is also to some extent a recent phenomenon (Beltrán-Sánchez, Finch, & Crimmins, 2015; Thorslund, Wastesson, Agahi, Lagergren, & Parker, 2013; Wilmoth, 2007). The growth of the gap in mortality in the twentieth century (Fig. 1) can to a large extent be explained by differences in smoking habits (Preston & Wang, 2006) and lung cancer is still one of the most significant predictors of sex differences in age of death (main article, Fig. 2). However, historically, most excess male death occurred during the pre-mating stage of life (0–14 years) (Zarulli et al., 2021), with infant deaths carrying the majority of the burden (Fig. 1). Doesn’t both the historical variability of sex/gender differences in life expectancy and the changing distribution of excess deaths in males across age-spans yield an explanatory challenge for the SAT which proposes that the difference is due to an independently adapted female trait linked to “parental investment”?

Furthermore, is it possible to talk about “Independent selective pressures on both male and female traits” when all we have are sex/gender comparisons? The claim in SAT that lower levels of aggression forms “a positive female adaptation driven by the critical importance of the mother’s survival for her own reproductive success” (Campbell, 1999) has an important flaw. If less is more, then having nothing may be even better. One could argue that not having antlers or peacock feathers are positive