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Letter

Integrated approaches to studying male and female thermal fertility limits

Benjamin S Walsh[1]*, Steven R Parratt[1], David Atkinson[1], Rhonda R Snook[2], Amanda Bretman[3], Tom A R Price[1]

[1]Institute of Integrative Biology, University of Liverpool, Liverpool, UK

[2] Department of Zoology, Stockholm University, Stockholm, Sweden

[3] Faculty of Biological Sciences, University of Leeds, Leeds, UK

Corresponding author:

Tom A R Price

T.Price@liverpool.ac.uk

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In Walsh & Parratt *et al* (2019) [1] we call for research into the thermal fertility limits (TFLs) of species to better predict the impact of climate change, especially the increased frequency of heatwaves, on biodiversity. In a response to this, Graziella Iossa outlined the need to consider sex-specificity of TFLs within this framework [2]. Broadly, we agree with this; sexual specificity may be common in TFLs, and understanding this may be crucial to predicting a species' vulnerability to temperature. Ascertaining the extent and prevalence of sex-specific differences should be an essential goal of TFL studies.

However, although we agree that the limited current evidence suggests males are more sensitive to fertility loss than females, outside the plant literature there are relatively few studies that directly measure both male and female fertility simultaneously, most of which are included in Iossa's response (see [2, 3, 4]). We caution that it is too early to assume that male fertility is universally more vulnerable to temperature. We think the literature is heavily biased towards male gamete thermal tolerance, probably due to the idea that with a smaller investment required, cheaper male gametes are less robust. There are also some obvious morphological adaptations in male homeotherms to prevent sperm from experiencing thermal stress, such as the presence of external testes in many mammals. But we caution that until more studies investigate the temperature sensitivity of female fertility, we cannot assume females are more robust than males. Ultimately, we need more studies that directly examine the fertility of both sexes under similar conditions. An interesting approach might be to study TFLs in monoecious (i.e. simultaneous hermaphrodite) species, such as mangrove killifish [5], many gastropods, and many flowering plants. This would provide excellent tests of which gametes are most vulnerable to temperature extremes. Moreover, we do not know a great deal about which stages of gamete production are most vulnerable to thermal stress. In many species oogenesis develops to a late stage early in a female's life, whereas males develop sperm from basal cells throughout their lives. If more mature gametes are vulnerable to thermal stress, thermally induced female sterility might be more likely to be permanent, while males may recover fertility over time. Again, we need more detailed studies, across a variety of taxa.

Where significant sex-specificity in TFLs exist, we need to consider how these differences manifest at the population level to understand species' vulnerability to climate change. For instance, in species where a few fertile males can fertilise large numbers of females, a small drop in thermally tolerant female fertility might have a similar effect as a catastrophic drop in male fertility at the same level of thermal stress. Theoretical methods that assess the contribution of each sex to population persistence may be invaluable in determining the relative importance of male and female TFLs**.** Analogous models on sex ratio [6] suggest that even a small loss in fertile females may have a greater impact on population persistence than losing the majority of fertile males. Therefore, even if female fertility is less vulnerable to temperature than male fertility, it may still be more important for many organisms.

Iossa makes the interesting point that the importance of sexual specificity in TFLs may depend greatly on the mating system of the species; monandrous species may be more at risk to low male fertility than polyandrous species. However, even populations of polyandrous species may be vulnerable, if sterile males or inviable male gametes act as inhibitors by blocking fertilisation opportunities for fertile males. Indeed, the application of sterile insect release techniques to control disease vectors is based on the principle that a loss in male fertility can leave populations vulnerable [7].

Ultimately, while laboratory data will reveal the underlying biology of sexual specificity in thermal fertility tolerance, field studies will highlight the relevance of these data to natural processes. One possibility might be to test variation in both male and female gamete viability in broadcast spawners, by taking samples from the water column as average water temperatures continue to rise or during extreme temperature events. Researchers could also examine the impact of natural heat waves on the population dynamics and demography in closely related species with different mating strategies. Paternity analysis may also allow researchers to detect the effects of heat-induced sterility in polyandrous species – low male fertility may result in fewer fathers within broods, whilst low clutch size or unhatched eggs might indicate both sexes are being affected.

Iossa’s comments highlight some of the inherent complexity within TFL research, but also the need for integrated approaches to these important questions. Ultimately, it will take field, laboratory, and modelling studies across a broad range of organisms to determine if, when and where TFLs matter.

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