

## Dioecy as a specialization promoting sperm delivery – a correction

Priya Iyer and Joan Roughgarden

*Department of Biological Sciences, Stanford University, Stanford, California, USA*

---

In the appendix of our paper (2008, *Evol. Ecol. Res.*, **10**: 867–892), we claim that the local mate hypothesis is mistaken. But that is wrong. Fromhage and Kokko (2010, Spatial seed and pollen games: dispersal, sex allocation and the evolution of dioecy. *J. Evol. Biol.*, **23**: 1947–1956) pointed out this mistake and we apologize for it. We erroneously assumed a wrong group size of  $k$  rather than  $k + 1$  hermaphrodites. More seriously, we confused the local mating group of  $k + 1$  individuals with the entire population (consisting of infinitely many such groups) when carrying out the stability analysis.

Under Charnov’s assumptions (1982, *The Theory of Sex Allocation*. Princeton, NJ: Princeton University Press), in a population consisting of infinitely many clusters of  $k + 1$  hermaphrodites (called ‘local mate clusters’, LMCs), it is indeed the case that the evolutionarily stable sex allocation to sperm production is  $(k - 1)/(2k - 1)$ , and hence female biased. Hence, when the clusters consist of two hermaphrodites fertilizing each other’s eggs, the optimal sperm allocation is almost 0.

Fortunately, this error does not have a bearing on our model for the evolution of dioecy. Our model for the evolution of sperm concentration and sex allocation is a population genetic one, with no structure in the population. Hence we assume that the sperm produced by each individual can potentially fertilize the eggs produced by every other individual in the population; even selfing is allowed. Under these assumptions, the optimal sex allocation for a hermaphroditic population is indeed 1:1. Therefore, the argument that LMC is wrong is more an aside to the paper, and does not have any direct bearing on our model or its results. We use this opportunity to quote Charles Darwin from *The Descent of Man and Selection in Relation to Sex* (1871, London: John Murray):

p. 273: We are naturally led to enquire why the male in so many and such widely distinct classes has been rendered more eager than the female, so that he searches for her and plays the more active part in courtship. It would be no advantage and some loss of power if both sexes were mutually to search for each other; but why should the male be almost always the seeker?

p. 274: the male element is invariably brought to the female; and we can see the reason; for the ova, even if detached before being fertilized and not requiring subsequent nourishment of protection, would be, from their larger relative size, less easily transported than the male element.

---

Correspondence: P. Iyer, Department of Biological Sciences, Stanford University, Stanford, CA 94305, USA. e-mail: priya.iyer@gmail.com

Consult the copyright statement on the inside front cover for non-commercial copying policies.

---

pp. 274–275: It would, therefore, be a great advantage to such animals, as their organisation became perfected, if the males when ready to emit the fertilising element, were to acquire the habit of approaching the female as closely as possible . . . and in order that they should become more efficient seekers, they would have to be endowed with strong passions.

Hence Darwin may have viewed the issue of dioecy as being about mobility of males and transport of sperm rather than smaller investment in sperm. This is consistent with our view and model for dioecy, where males can be seen as evolving to offer ‘home delivery of sperm’ for females.