

blood-meal sizes were also comparable for the resistant phenotype.

Artificially feeding insecticide-resistant and insecticide-susceptible mosquito colonies (PelRR and PelSS, respectively¹¹) with blood infected by *W. bancrofti* to an intermediate level of parasitaemia — which should result in the infection of mosquitoes without substantial insect mortality — produced stage-L3 infective parasite larvae after 12 days in 76% of PelSS females ($n=250$), but no larvae in any of the PelRR females ($n=200$). Our results indicate that an increase in esterase activity could affect the development of stage-L1 *W. bancrofti* larvae, which may be arrested in the gut cells of insecticide-resistant but not insecticide-susceptible mosquitoes.

Filarial infection severely damages the mosquito host, often killing it. The spread of esterase-based insecticide resistance in field populations of *C. quinquefasciatus* may therefore be influenced by selection pressures for both insecticide detoxification and reduction of the microfilarial burden. Similar esterase-based insecticide-resistance mechanisms have been selected in field populations of the malaria vectors *Anopheles albimanus*¹² and *A. culicifacies*¹³, which could directly affect the transmission of malaria.

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Second, does Doncaster *et al.*'s model aid our understanding of the patterns of sexuality observed in nature? Several theoretical problems have been pointed out with the tangled bank model, and empirical studies have tested its (identical) assumptions and predictions.

For example, the advantage of sex is reduced if asexual populations are made up of multiple clones that fill multiple portions of the niche space^{4,5}; coexistence of sexuals and asexuals is rarely observed⁴; plant and algae populations consisting of mixtures of genotypes have carrying capacities not much greater than that of the average of their component genotypes, and rarely greater than that of the best genotype⁸; and results from natural populations indicate that the ecological and demographic predictions of the tangled bank model are not met^{6,9}.

Third, does the model of Doncaster *et al.* provide new insights into the cost of sex (males)? The authors argue that the cost of males is ecology dependent, so there is not necessarily a twofold advantage to be recouped in adaptive payoffs. However, one of the model's implicit assumptions is that different genotypes use different niches (genotype-by-environment interactions), so the model is not purely ecological.

The way in which this type of model allows coexistence between sexuals and asexuals has already been discussed^{4,5}. Moreover, this mechanism is more appropriately viewed as an adaptive payoff in its own right, as in previous formulations^{1,3–5}. In this case, it may reduce the cost to be paid by other mechanisms, but such interactions between models have been discussed extensively¹⁰.

Nonetheless, Doncaster *et al.* remind us of the role that the tangled bank mechanism could play in a pluralist explanation of sex, possibly by interacting with deleterious mutations in a fashion analogous to the Red Queen¹⁰.

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Evolution

Paying for sex is not easy

Explaining the maintenance of sexual reproduction remains one of the greatest challenges for biology, with more than 20 hypotheses having been advanced so far¹. Doncaster *et al.*² have proposed another possible explanation, but we question the novelty and importance of their suggested mechanism.

First, does this model² provide a new mechanism to help explain sex? The model assumes that different genotypes exploit different parts of the environment, and that an asexual clone is not able to occupy all the environmental niches that are open to a sexual population. This provides an advantage to sex, and allows coexistence between sexuals and asexuals.

However, the assumptions are the same as those of the 'tangled bank' mechanism for the maintenance of sex^{1,3–5}. The message that has emerged from previous considerations of this mechanism is therefore the same as that proposed by Doncaster *et al.*² — namely, that competition within a fixed set of niches can provide an advantage to sex, with "the success of the clone [being] restrained by the narrowness of its ecological range" and leading to "a stable equi-

librium at which both sexual and clonal individuals persist"⁴.

Although the mechanisms favouring sex appear to be identical, the elegantly simple form of Doncaster *et al.*'s Lotka–Volterra model means that it requires implicit assumptions and is therefore hard to compare with previous tangled bank models, which were based on numerical simulations and which made more explicit assumptions^{4,5}. For example, does Doncaster *et al.*'s model require competition between siblings (as with some formulations of the tangled bank), or is it the special case in which sib competition is excluded³?

It is hard to test the implicit assumptions in the new model², but it may render some aspects of the tangled bank mechanism more testable by emphasizing two parameters: the maximum population growth rate, R_0 , and the degree of overlap between sexual and asexual niches, α . However, the importance of these parameters has been discussed previously — for example, it has been pointed out⁶ that, analogous to variation in R_0 , higher fecundity leads to greater sib competition and so increases the advantage of sex. It has also been shown⁴ how the advantage of sex varies with a 'competition coefficient', which is a version of α . Furthermore, such competition coefficients are notoriously difficult to measure⁷.