

one review of Bell's book, many of the correlations reported by Bell could be explained in terms of the reproductive advantage enjoyed by asexual variants in low-density habitats<sup>7</sup>. Thus, this type of study may not shed much light on the nature of the forces that actively maintain recombination. Furthermore, a new theory for the advantage of sex and recombination, based on the maintenance of deleterious genes by mutation pressure, has since been proposed by Kondrashov<sup>8,9</sup>, and was not considered in Bell's original survey<sup>7</sup>.

If the somewhat arbitrary procedure of considering only the Red Queen and Tangled Bank models is discarded, then the interpretation of any real correlation between generation time and rate of recombination becomes hard. Theories of recombination that are in part dependent on the effects of finite population size, such as Muller's ratchet and the Fisher-Muller model of selection for favourable genes<sup>3</sup>, would often predict a higher advantage to increased recombination in populations with smaller effective sizes. Large mammals tend to have smaller numbers of individuals in the species, as well as larger generation times, consistent with the claimed correlation. Similarly, the Fisher-Muller model, the related model of Strobeck *et al.*<sup>3</sup>, and my own model of temporally fluctuating environments<sup>10</sup>, all predict a positive correlation between generation time and rate of recombination.

In summary, the claim by Burt and Bell to have found strong support for the Red Queen model of the evolutionary advantage of recombination is without firm theoretical or observational basis.

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SIR—Burt and Bell<sup>1</sup> showed a correlation between chiasma frequency and age at maturity in mammals. They interpret this as support for the Red Queen hypothesis, that high recombination is advantageous when there are large changes in the environment between generations, which change the phenotypic optimum. They assume that the extent of environmental change between generations is greatest in those species that have the longest generation intervals. I believe that this assumption is weak and that the

correlation could well have another explanation.

If parasites form the relevant part of the environment, as suggested<sup>1–3</sup>, then there may be a correlation between environmental change and generation length. However, because parasites with long generations tend to inhabit hosts with long generations, the mean generation length of parasites will be rather larger in those hosts that have long generations, so the rate of parasite evolution per unit of time will be lower than in parasites of hosts with short generations. If organisms other than parasites are important, the correlation will be weaker because animals tend to interact more with species of a similar size than with species of a dissimilar size and size is correlated with generation length. If the physical environment is the important component, the correlation between age at maturity and environmental change may be the opposite to that assumed. Physical factors change more markedly between seasons than from year to year, so species that have several generations per year suffer greater degrees of environmental change between generations than do species that have an annual cycle. Species with generation lengths of several years may tend to suffer higher levels of environmental change than those with annual cycles because of long-term changes, but the effects of such long-term changes will generally be overwhelmed by the law of large numbers: the mean environment in two successive years is likely to differ more than the mean in two successive spans of ten years.

The Tangled Bank hypothesis is that high recombination is advantageous when there is strong selective competition between sibs for survival, with some environmental change between generations. Burt and Bell state that if this hypothesis is true, one would expect to find a correlation between chiasma frequency and fecundity, which they did not find. But this rests on the view that sib-competition is stronger in species with high fecundity, which may be false. If animals produce litters that maximize the expected number of surviving offspring, litter size will reflect the resources available and inter-specific differences in the degree of sib competition will be unrelated to inter-specific differences in litter size.

Furthermore, so long as there is some environmental change between generations, recombination is favoured by any intense competition, not only sib-competition. Thus, an alternative explanation for the observed correlation is that competition is greater in longer-lived animals, which tend to be K-selected. This explanation, involving both environmental change and competition, reminds us that the Red Queen and the Tangled Bank are extremes of a continuum involving these two processes.

Correlations of this sort are valuable contributions to our understanding of selective forces moulding living organisms. However, the relationships between life history characteristics are complex, so most correlations will be explicable by more than one hypothesis. In the present case, the search for a general conclusion may never be successful: the way in which chiasma frequency is moulded may be different in different species; changes in the environment between generations may be more important for some, the strength of competition between individuals for others. To focus attention on one or the other may help to clarify ideas but must not constrain us into thinking that only one is important.

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SIR—In their recent letter (*Nature* **326**, 803–805, 1987) Burt and Bell may be too optimistic. The correlations they find between mammalian chiasma frequencies and various life history parameters do not necessarily support the Red Queen or reject the Tangled Bank theories for at least three reasons. First, the Tangled Bank has not yet been formulated as a theory of recombination, but as a theory concerning the maintenance of sexual reproduction. It thus does not predict any particular level of recombination, but only whether any level of recombination is favoured over clonal reproduction, that is, over no recombination. Hence the correlations with recombination rate to be expected for the Tangled Bank hypothesis are not clear. Second, even if it is assumed that the Tangled Bank is a theory of recombination, the correlations expected by Burt and Bell are not obvious. It could be argued that the organisms with short generation times and high litter sizes are not under severe competition. The Tangled Bank would then predict low recombination. On the other hand, organisms with long generation times may be selected by competitive effects, and are therefore predicted to have a higher rate of recombination. Hence the Tangled Bank would predict the positive correlation between recombination rate and generation time shown by Burt and Bell. Furthermore, it is well known that in host-parasite systems it is not the absolute generation time that affects the outcome of selection, but the differences in generation times of host and parasite. Thus if generation times of host and parasite themselves are correlated, the predictions of the Red Queen could range from positive to strongly negative correlations of recombination rate with generation time. Third, the