

results of Burt and Bell would be strengthened if a partial correlation of recombination rate with age at maturity and litter size were performed, and if the effects of common ancestry were considered. It seems that species within a family have fairly constant recombination rates, despite large differences in generation times. However, this latter point might not be very relevant, because the data on domestic animals and other, previously published, data show that recombination rates can change rapidly.

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**BURT AND BELL REPLY**—We have argued<sup>1</sup> that the positive correlation between excess chiasma frequency (EC) and age to maturity among mammals supports the Red Queen theory of recombination, according to which longer-lived hosts must have higher rates of genetic recombination per generation to escape from the counter-adaptations of their parasites. It was an implicit assumption of our test that the number of parasite generations per host generation, and therefore the relative rate of parasite evolution, is positively correlated with host generation time. Greenwood and Koella question this assumption, suggesting that the generation time of parasites may increase isometrically with that of their hosts. Unfortunately, neither author provides any data: we have therefore collated measurements of the prepatent period (time from infection of definitive host to release of first propagules into the external environment) of 37 parasitic species in four major taxa and the age to maturity of their mammalian hosts.

There is indeed a very highly significant positive association between parasite

prepatent period and host age to maturity ( $P < 0.001$ ), with no indication of heterogeneity of slopes among the four parasite taxa. However, the common slope of this association is much less than unity and so the number of parasite generations per host generation increases steeply with host generation time (Fig. 1). This result is completely consistent with our earlier interpretation and decisively refutes Greenwood's and Koella's conjectures.

We have further argued that the negative correlation between EC and litter size among mammals falsifies the Tangled Bank theory. Greenwood and Koella dispute our rejection, suggesting that longer-lived and less fecund species are subject to more intense competition. This claim, again made without empirical support, misses the basic proposition of the Tangled Bank: that the increased phenotypic variance created by recombination functions to reduce the level of competition within families. It is emphatically a theory of competition between siblings; claims that it does not predict a positive correlation with litter size contradict both common sense and conclusions from computer simulations<sup>2</sup>. Indeed, such a theory clearly does not predict that mammals with litter sizes of one will be among those with the highest levels of recombination, yet this is precisely what we observe. Furthermore, it would appear that litter size is not even a minor contributor to the observed variance in EC: the partial correlation, after removing the effects of age to maturity, is insignificant ( $r = -0.320$ , d.f. = 21,  $0.2 > P > 0.1$ ). This result seriously damages Greenwood's concluding plea for plurality.

Charlesworth is not interested in saving the Tangled Bank, but rather several theories not considered in our original paper. However, it is not clear why — he offers nothing to counter the well-

documented shortcomings of all but one of these theories<sup>3,4</sup>. The author of the remaining theory<sup>5</sup> concludes from simulations that his model cannot account for crossing over in organisms with many chromosomes; 70% of our mammals have haploid numbers greater than any of those used in his simulations ( $n > 16$ ).

Finally, Charlesworth claims that our treatment of each species' EC as statistically independent is likely to give spurious positive results. His argument conflates two separate issues. The first, common ancestry and phylogenetic inertia, is unimportant when there exists additive genetic variance for the character under investigation, for the response to selection will be instantaneous on a palaeontological timescale. Evidence for such variance in EC comes both from artificial selection and heritability studies<sup>3,4</sup> and from the twofold increase in EC among domesticated mammals<sup>1</sup>. Thus the EC of each species is an independent product of natural selection and should be analysed accordingly. Nevertheless, to allay any possible doubts, we have reanalysed our data at the family level; the correlation of family means is almost identical with that of species and the null hypothesis is rejected at the same level that we reported ( $r = +0.883$ , d.f. = 10,  $P < 0.001$ ).

The second issue is that of confounding selection pressures, for although EC is correlated with age to maturity, it is presumably also correlated with many other characters related to age to maturity. This problem motivated our partial correlation analysis of EC and age to maturity, keeping body weight constant. The latter is strongly correlated with age to maturity among mammals ( $r = +0.844$  in our data set), but when the three variables are analysed simultaneously, the partial correlation of EC and age to maturity remains large and significant ( $r = +0.689$ ,  $P < 0.001$ ), whereas that of EC and body weight becomes insignificant ( $r = +0.021$ ,  $P > 0.9$ ).

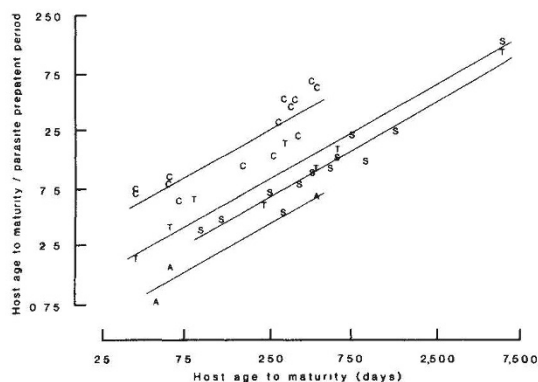
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**Fig. 1** The timescale of mammalian parasites. The ratio of host age to maturity to parasite prepatent period increases with host age to maturity in four parasite taxa with mammalian definitive hosts: A, Acanthocephala<sup>6</sup>; S, Schistosomatiidae<sup>7</sup>; T, Cestoda<sup>8</sup>; and C, Coccidia<sup>9</sup> (note logarithmic axes). When a parasite infests more than one species of host, or vice versa, means were used. To quantify the within-taxon association, the data set was transformed such that the four groups



had equal bivariate means. The transformed data set has Pearson correlation coefficient  $r = 0.948$  ( $n = 37$ ) and reduced major axis slope  $v_{y,x} = 0.867$ . This latter value is the common slope of the within-taxon association,  $\bar{v}$ , and has standard error about equal to that calculated by analysis of covariance:  $s_{\bar{v}} = 0.049$ . Both major axis regression and analysis of covariance showed the four slopes to be homogeneous ( $0.9 > P > 0.5$ ). The four solid lines are drawn with slope  $\bar{v}$  through the (untransformed) bivariate mean of each parasite taxon.