

Commentary

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e e y . . . l e l .  
e . . . y e e i c e  
a d a c . . . e a e f  
e e d . b d e**

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population divergence; see Jennings & Edwards 2005, Bowie *et al.* 2009). The CHD1-Z intron is a common nuclear marker used for such studies (Peters *et al.* 2005) and should be carefully evaluated for evidence of selection. Although requiring population-level sampling, one way to test for selection is to make use of several different neutrality tests such as Tajima's D (Tajima 1989), Fu's  $F_s$  (Fu 1996) and Hudson-Kreitman-Aguadé (Hudson *et al.* 1987), carefully evaluating their underlying assumptions in light of the specific research question being addressed (reviewed in Nielsen 2005, Nielsen & Beaumont 2009). All of these tests can be applied to intron data and are readily implemented in widely used software (reviewed by Excoffier & Heckel 2006).

The finding that the CHD1 intron is affected by selection may be most problematic for studies of avian relationships above the level of species. Selection may not be a problem for phylogeneticists if it is occurring in a consistent manner across the species studied. Problems will start to appear, however, when selection is limited to a specific set of branches within the tree. In this case, one may observe a slowdown or an acceleration of the substitution rate for this branch and eventually all of its descendants. Such biases may result in spurious phylogenetic trees with very different branch-lengths at the tips and should be carefully evaluated. Several tests exist to detect selection in a phylogenetic context, but such tests only apply to protein-coding genes and hence are of no use when the sequence data are from introns (McDonald & Kreitman 1991, Yang 2006).

Studies such as that of Schroeder *et al.* have important implications not only for researchers using CHD1 for phylogenetics, but also for phylogeneticists in general, as selection is not likely to be restricted to the CHD1 intron. However, we maintain that introns should continue to be used in phylogenetic studies, as data from a genomic dataset of mammals (Pollard *et al.*

