Genetica (2005) 123: 39–47

Sex differences in recombination and mapping adaptations

Patrick D. Lorch
Zoology Department, University of Toronto, Ramsay Wright Labs, 25 Harbord St. Toronto, Ontario M5S 3G5, Canada (Phone: (919)843-2320; Fax: (919)962-1625; E-mail: plorch@email.unc.edu); Current address: Biology Department, University of North Carolina, CB 3280, Coker Hall, Chapel Hill, NC 27599-3280, USA

Received 15 April 2002 Accepted 15 September 2003

Key words: condition dependence, good genes, QTL mapping, sexual selection, sexual conflict

Abstract

Since the raw material of marker based mapping is recombination, understanding how and why recombination rates evolve, and how we can use variation in these rates will ultimately help to improve map resolution. For example, using this variation could help in discriminating between linkage and pleiotropy when QTL for several traits co-locate. It might also be used to improve QTL mapping algorithms. The goals of this chapter are: (1) to highlight differences in recombination rates between the sexes, (2) describe why we might expect these differences, and (3) explore how sex difference in recombination can be used to improve resolution in QTL mapping.

Sex differences in recombination

Sex differences in recombination rates generally are seen as differences in linkage maps (Figure 1). Since the physical size of chromosomes in each sex is assumed to be equal, sex differences in recombination result from different amounts of recombination during meiosis. These sex differences become apparent whenever mapping studies are conducted in such a way that recombination rates can be estimated separately for each sex. Taking a backcross design as an example (see Korol, Preygel & Preygel, 1994), the F1 generation produced by crossing two different inbred lines can be used as both sires and dams (pollen parent and seed parent) in the backcross to original inbred parentals. Sex difference in recombination can then be seen in the linkage maps produced from the two sets of backcross offspring. This is because inbred backcross parents should be homozygous at almost all loci, so any recombination occurs in the F1 parent. If half of your backcrosses use F1 dams and the other F1 sires, you can estimate linkage maps separately for each sex.

A survey of published literature shows that sex differences in recombination rates are widespread (for reviews see Callan & Perry, 1977; Trivers, 1988; Burt, Bell & Harvey, 1991; Singer et al., 2002). Table 1 and Figure 2 summarize all the data to date (The Appendix shows data collected since Burt, Bell & Harvey (1991) in a format similar to their appendix.). Where sex differences in recombination have been estimated, we can distinguish between species where both sexes experience some recombination (chiasmate species) and species where one sex has no recombination (achiasmate species). In chiasmate species 45 cases show more female than male recombination, 21 cases show more male than female recombination and 9 cases show no sex difference (Cano & Santos, 1990; Burt, Bell & Harvey, 1991; van Oorschot et al., 1992; Korol Preygel & Preygel, 1994; Lagercrantz & Lydiate, 1995; Kearsey et al., 1996). In achiasmate species 5 cases show female recombination, 8 cases show male recombination, and whenever there are heterogametic sex chromosomes, the heterogametic sex has no recombination (Burt, Bell & Harvey, 1991).

Whatever the causes of these sex differences, they provide a useful example of variation in recombination rates for two reasons. First, the

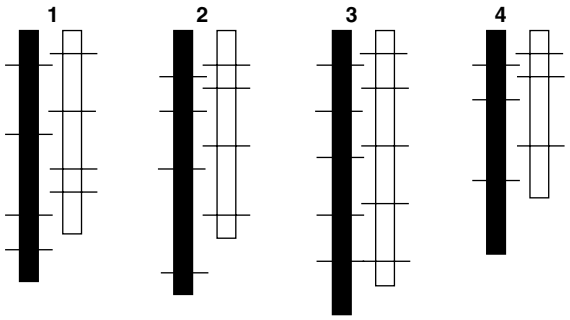

Figure 1. Typical pattern of sex-specific maps for four linkage groups in a hypothetical species. Male and female chromosomes should be of equal length, but maps often show sex differences. Bars show genetic marker loci. Distance between markers indicates larger numbers of recombination events between markers. Typically, female maps (black) are larger than male maps (white) due to more and/or less-localized recombination events.

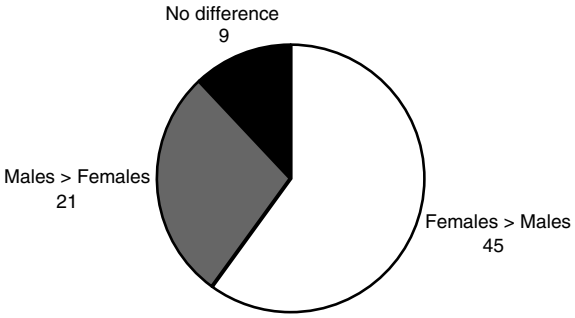

Figure 2. Summary of species where sex differences in recombination have been estimated. For chiasmate species, based on data in Burt, Bell and Harvey (1991) and the Appendix.

Table 1. Breakdown of sex differences in recombination for 75 species by taxon. Lists chiasmate species, based on data in Burt, Bell and Harvey (1991) and the Appendix

Taxon	F > M	M > F	F = M	Comments
Animals				
Platyhelminthes	2	1	0	
Insecta	2	9	3	All Orthoptera
Amphibia	4	2	0	
Mammalia	7	4	1	
Pisces	2	0	0	
Aves	2	0	0	
Plants				
Monocotyledonae	20	3	4	
Dicotyledonae	2	1	1	
Orchidaceae	4	1	0	
Total	45	21	9	

evolution of modifiers of recombination has been studied extensively in the context of the evolution of sex. This means that we have basic theory for understanding how recombination rates can be modified, albeit few specifics about how sex difference can arise. Second, by modifying breeding designs we may be able to exploit sex differences in recombination to improve map resolution and QTL discrimination (Singer et al., 2002). This is not to say that other forms of variation in recombination rates cannot also be used to improve maps, only that since QTL mapping involves crosses and algorithmic estimation of QTL location relative to a marker-based map, sex difference may provide a particularly useful form of variation in recombination rates. To make this second point clear we need to consider what we know about how recombination rates evolve.

How recombination rates can evolve

The evolution of recombination is difficult to study because recombination affects the way genes on the same chromosome interact. As evolution proceeds, recombination does three things, the first two of which directly conflict. It can bring together alleles on one chromosome with positive effects on fitness, allowing one parent to pass along sets of alleles that survived natural and sexual selection in the parents. Recombination can then break up these beneficial associations in the very next generation. It can also bring together deleterious alleles, allowing them to be more efficiently eliminated by selection. The complicated balance between these three processes will determine whether selection acts to increase or decrease recombination rates for a given region of a chromosome (Barton, 1995). Selection can act to increase recombination between some genes under some circumstances and to decrease recombination between another (possibly overlapping) set of genes under other circumstances.

Since the evolution of recombination rates depends on gene interactions, the nature of