# The neutralist, the fly and the selectionist

Jody Hey

**The neutralist–selectionist debate was a staple of molecular evolution and population genetic discourse in the 1970s and 1980s. It waned thereafter, without resolution, as it has taken time to understand what DNA data can reveal about the subject. Recent developments using DNA data from *Drosophila melanogaster* show that natural selection is pervasive to an extent that is surprising to some former neutralists. It is now known that natural selection acts on synonymous variation, and that linkage effects between selected sites are shaping patterns of variation over large pieces of the genome.**

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Imagine growing up a fan of a fierce rivalry, of two great teams persistently at loggerheads. And suppose that on the morning of the final test – the definitive encounter between the rivals – everyone involved lost interest and went home. That is partly what it seemed like to a graduate student reading avidly of the neutralist–selectionist debate in the early 1980s. There was hope that the ineffectual protein- and allozyme-based arguments of the 1970s (Ref. 1) were about to be superseded by new, far more powerful tests based on DNA sequence data. But I was wrong – at least about the timing of resolution – the debate quietly withered and came to some indeterminate demise in the mid to late 1980s. By the early 1990s, if the topic came up it was likely to receive an uninformative epitaph such as '… it is now recognized that any adequate theory of evolution must be consistent with both of these aspects of the evolutionary process at the molecular level'[2]. What caused the lively dialog – freshly innervated with new data – to move not to resolution, but to quiescence? And, if it has been more quiet than resolved, what is the current status of the original questions in the debate? This article tells some of the story, with a primary focus on *Drosophila melanogaster*. For both historical and practical reasons, the *D. melanogaster* model system, more than any other in recent decades, has been the focus of attempts to detect and measure natural selection[3,4].

## The old problem

The neutralist–selectionist debate had its roots in the classical–balance debate that preceded it[3] and in the nondarwinian (neutralist) proposal that natural selection does not contribute to most of molecular evolution[5] (Box 1). The dispute had two fronts, protein sequence divergence and protein allelic polymorphisms. At issue in the former was whether the amino acid differences found between species in homologous protein comparisons had occurred by positive natural selection, or by simple random drift. Most discussion revolved on the question of whether proteins evolved in a clock-like manner, as expected under a simple neutral model, or whether the rate of protein divergence exhibited too much variation for a simple model. The polymorphism argument was over the causes of the plethora of electrophoretically distinguishable enzyme alleles (allozymes) that had been found in a great many species. Were these polymorphic alleles maintained at intermediate frequencies by natural selection (the several candidates that can maintain alleles were lumped under 'balancing selection'); or were they actually just a transient phase in a slow process of genetic drift among functionally equivalent (i.e. neutral) alleles? Both aspects of the debate, divergence and polymorphism, centered on the proportion of mutations that were both perceived by natural selection and were not deleterious. Neither side of the debate had much interest in selection against the many deleterious mutations that occur, as these were expected to contribute to neither polymorphism nor divergence.

From the beginning, the selectionists held the more complicated and interesting position[6]. Natural selection is the creative force in evolution, but it can take myriad forms and the development of general, testable, mathematical models is not a simple task. In contrast, the neutral model was simple, elegant and highly predictive on both the divergence and the polymorphism fronts[7]. The simplicity and predictive nature of the neutral model had two very important implications that continue to give it considerable vitality, almost regardless of the evidence for natural selection. First, Kimura had identified a feature of evolution that must occur to some degree[5]. Regardless of the efficacy and frequency of natural selection, neutral evolution requires only neutral mutations, and so to the extent they occur (and presumably at least a few must) Kimura was correct. Second, and for these same reasons, the neutral model has been used as the null model for virtually every statistical test of natural selection that has been developed.

## The new data

As DNA data became available, the neutralist–selectionist debate was sidetracked, primarily for three reasons. First was the finding that most DNA data simply did not relate to protein sequences (in which terms the debate had been cast). Much of the new data had either been sampled with restriction enzymes, and thus could not easily reveal the genotypic basis of protein polymorphisms, or they simply showed that most DNA sequence variation did not affect protein sequences. Synonymous site polymorphisms, intron and pseudogene variation were all more common than the amino acid replacement polymorphisms that affected protein sequences. This paucity of protein evolution was also, of course, the second major distraction. In

### Box 1. Kimura and the neutral model

In 1968 Motoo Kimura proposed that many mutations that change amino acids cause no effective change in protein function[5]. These 'neutral' mutations are subject only to random genetic drift so that some fraction of them is expected to become fixed in natural populations. In a diploid population with $2N$ gene copies, and neutral mutation rate $\mu$, there will be $2N\mu$ neutral mutations every generation. Most will be lost, but there is some chance $(1/2N)$ of fixation. Overall, the rate at which neutral mutations become fixed is equal to $2N\mu\ (1/2N)$, which is equal to the neutral mutation rate $\mu$. This simple result provided an elegant explanation for the observation that individual proteins evolve at a fairly constant rate. If most nondeleterious mutations are neutral, and if the mutation rate is constant, then a constant rate of evolution is expected.

Kimura was a brilliant mathematician, and he and colleagues (especially James Crow and Tomoko Ohta) developed a rich body of theory that shows how much variation in natural populations is expected under the neutral mode[l7,35]. The completeness of the neutral model (i.e. spanning both divergence and polymorphism) meant that it could be adapted for statistical tests of natural selection in almost any evolutionary genetic context.

 0169-5347/99/$ – see front matter  PII: S0169-5347(98)01497-9 

a sense – and in a way that was not very interesting to selectionists – the neutralists had won (at least for awhile). The finding that nonfunctional sequences evolved fastest and harbored lots of DNA sequence variation was definitely a neutralist prediction, and books written by neutralists in the middle 1980s proclaimed victory to varying degrees[8,9]. To a neutralist from this time (and I counted myself among them), it would not have seemed fair to label these findings a distraction from the debate, but that is what they seemed to selectionists. Even if one did accept that junk DNA could have neutral mutations, nonfunctional mutations in nonfunctional DNA did not bear on the original questions about natural selection on protein variation. The third distraction was that the new data typically came in the form of multiple polymorphisms, entangled in complex linkage relationships. In general, these haplotype data were much richer, with vastly higher information content than allozyme data; and the theory that had been constructed on the basis of allelic data were not up to the task of revealing the role of natural selection in shaping the pattern of this new kind of variation.

In summary, the data dictated a shift away from the broad protein-based debate to the minutiae of a new set of problems. The shift did not really mean that investigators were less concerned about the role of natural selection in shaping polymorphism and divergence, but the new data did not simply resolve the old issue, and figuring out what the new data did say proved to be difficult.

It was a paper by Kreitman that set the tone for the new DNA-based population genetics[10]. The study of 11 *D. melanogaster* sequences of the *Alcohol dehydrogenase* gene (*Adh*) revealed 44 polymorphisms, only one of which corresponded to an amino acid variant. It was another four years before Hudson, Kreitman and Aguadé[11] described a useful statistical test and revealed convincing evidence that natural selection had been maintaining the amino acid polymorphism for some time.

## Polymorphisms

With data and analyses from many genes, what can be said today about natural selection in general, and balancing selection in particular? For *D. melanogaster*, the *Adh* haplotype data, with the bubble of excess variation near the amino acid polymorphic site, remains the best case for balancing selection. So far, *D. melanogaster* has not revealed cases of very long-standing balanced polymorphisms, such as occur in mammalian immunological loci[12]. However, when we look more closely, many *D. melanogaster* loci have at least one region suggestive of balancing selection, including *G6pdh* (Ref. 13), *Esterase 6* (Ref. 14), *white* (Ref. 15), *Mst26A* (Ref. 16); and *Ref(2)P* (Ref. 17). Other loci show evidence of natural selection having removed variation, probably by the recent increase in frequency of a favored sequence. The *tra* locus revealed very little variation, significantly less than expected given the divergence between species and polymorphism levels observed at other genes[18]. At and near the *Sod* locus, there is a complicated pattern in which a large subset of the sampled gene copies are nearly identical, which suggests that natural selection has recently brought a previously low frequency haplotype to high frequency[19]. (Note that neither the *tra* nor the *Sod* study revealed much about the location of the site of selection, as can often be the case with selection that, via linkage, affects a long region of DNA.) It is also true that some studies have not found evidence of selection, but several of these are among the smaller data sets[20–22].

What can be made of these many patterns? There are some thorny statistical problems that would bedevil a more quantitative summary. On the side of selection, the statistical power of individual tests is weak, especially for recent balancing selection. Thus, one might argue that given lots of evidence of selection, and weak tests, there must be much more selection still not revealed. On the side of neutrality, however, several studies have drawn conclusions of selection based on just that portion of the data that seem most striking, and statistical conclusions from selected subsets of the data are easily wrong if the effect of prescreening the data is not properly accounted for. But one conclusion can be made from this polymorphism review: the pattern of variation in the *D. melanogaster* genome is itself quite variable, often over very short distances. It is not true that every region of the genome tells a new story, because some important themes have emerged, but one gets the impression that a fresh prospector could still jump in almost anywhere with a good chance of finding a new kind of history. Complexity *per se* was always a selectionist prediction, albeit a vague one.

An astute neutralist could still salvage a fair bit, primarily on two fronts: the statistical problems of multiple *a posteriori* tests for selection; and the issue of how local variation in recombination, or gene conversion, rates would contribute to the variation of polymorphism patterns found within and between loci.

## Divergence

From studies of divergence, the strongest evidence of natural selection come from *Adh* (Ref. 23) and *G6pdh* (Ref. 24), where the rate at which species diverge for synonymous and replacement sites is not in proportion to their respective polymorphism levels. In these cases, the favored explanation is that several amino acid substitutions have occurred by adaptive fixation. However, these two genes might be exceptions, as most do not show this pattern[25]. Also, in a detailed investigation of the molecular clock (24 genes compared among three *Drosophila* species) the data for amino acid substitution were consistent with a clock[26]. This study might be taken as strong support for the neutral model were it not for a second conflicting conclusion, that synonymous substitutions (which are expected to be under less selection than amino acid substitutions) did not fit the molecular clock[26].

## Two revolutions

So far this review has followed the mold of the debate cast in the 1970s and 1980s: at which loci, and how many of them, has natural selection shaped divergence and polymorphism? But, as can happen when lots of new data arrive, discoveries that bear on an old debate might not fit the mold of the old question. Two of the currently most active areas of theoretical and *Drosophila*-based population genetic research concern the tempo and mode of natural selection but not in ways anticipated by the traditional neutralist–selection debate.

### *The interaction of natural selection and linkage*

As the DNA haplotype data grew, population geneticists had to deal increasingly with an idea that had not seemed too relevant in the days of allozymes: the notion that natural selection on one base position will have a large effect not only on the history of that site, but also on all linked sites. It is a simple idea, but not a necessary one for dealing with allozyme loci that tended to show little evidence of linkage disequilibrium. The importance of linkage was brought home by Begun and Aquadro who showed a strong correlation between DNA sequence polymorphism levels and recombination rates[27]. Genes with more recombination had more polymorphism, but this was not due to the conventional neutralist explanation that they also had higher mutation rates – an independent check of rates of divergence between species showed no correlation with recombination rates[27]. Consistent with this, a gene on a tiny chromosome that lacks recombination showed no polymorphism in *D. melanogaster*[28]. These

results, and many more similar findings since then, clearly indicate an interaction between linkage and selection, although what kind of selection is not clear. The first idea was that selective sweeps – that is, directional positive selection and effects of genetic hitchhiking via linkage[29] – would remove variation from more genes in genomic regions of low recombination. However, Charlesworth *et al.*[30], realized that a quite different model would have similar effects. In their 'background selection' model, deleterious mutations are the cause of low variation in regions of low recombination. If the overall deleterious mutation rate is high for a genomic region with many genes and low recombination, then it is expected that many (perhaps most) of the copies of the region that are in the population are actually linked to one or more deleterious mutations. This large fraction cannot support other polymorphisms as it is steadily being purged by selection and rebuilt by deleterious mutation. Only the minority of copies that remain free of deleterious mutations can support other nondeleterious polymorphisms in appreciable frequency. This clever idea is actually quite consistent with the neutral model, at least in so far as it requires only deleterious mutations. One might even call the background selection model the neo-neoclassical position, given that the neutralist view in the 1970s was considered to be the 'neo' version of the classical view that most populations were relatively devoid of functional segregating variation[3].

There is now an energetic debate within the *Drosophila* population genetics community over just what kind of selection explains Begun and Aquadro's observation. The problem is difficult, however, because both the selective sweep and the background selection model are two extremes of a more general class of model in which multiple linked sites are under selection. Recently, there has been a reawakening of interest in some 30-year old theory that fits the problem quite nicely. Hill and Robertson studied the effect of linkage, between two sites each segregating two alleles under selection, on the probability of fixation of advantageous mutations[31]. They found that under linkage, selection at one locus reduced the probability of fixation at a second locus, and vice versa. The effect was analogous to an acceleration in the rate of random drift, or conversely a reduction of the effective population size experienced by each locus. This work did not play a large role in the neutralist–selectionist debate, although it was certainly relevant[3], and until recently it has been absent from the molecular evolution literature. Nevertheless, the implications are clear: for a given number of polymorphic sites under selection, the tighter the linkage the more interference and the greater the knockdown in effective population size. The smaller the effective population size experienced by a genomic region, the less polymorphism (neutral or balanced) will be maintained in that region. Furthermore, this Hill–Robertson effect will occur to some extent regardless of the selection coefficients on individual mutations – be they large or small, negative or positive – so long as there is linkage. Population geneticists will be grappling with this issue for some time to come.

### *Selection on synonymous sites*

The second revolution concerns the efficacy of natural selection in *D. melanogaster*, and whether natural selection can 'see' codon usage. In general, evolution at synonymous sites in *D. melanogaster* had been thought to be broadly consistent with the neutral model, as synonymous sites usually exhibit high levels of polymorphism and divergence relative to amino acid replacement sites. Therefore, I was surprised when, with Richard Kliman, we found strong evidence that natural selection does act on some synonymous site variation in *D. melanogaster*[32]. The reasoning behind our analysis proceeded in the following manner: (1) the correlation between recombination and polymorphism, observed by Begun and Aquadro[27], reveals some kind of Hill–Robertson effect; (2) this means that, overall, natural selection is not as effective in regions of low recombination because of conflicts under linkage; (3) consequently, we expected that if high codon bias was sometimes caused by natural selection, then codon bias should be lower on average where natural selection is less effective (i.e. regions of low recombination). This is exactly what we found. In a sample of 345 genes from high recombination areas, and 40 genes from low recombination areas, the codon bias was markedly, and highly significantly, reduced in the latter[32].

There is now a fairly rich theory on the effect of natural selection on codon usage in *D. melanogaster*, and on the interplay between natural selection, mutation and genetic drift[33]. The effect of these discoveries is that one of the major categories of 'neutral' mutations has been eliminated, at least for *D. melanogaster*. Instead, there is a large category of nearly neutral (or weakly selected) mutations. Ohta's extensive theoretical work on the evolution of these types of mutation has been prescient, but the theory is necessarily complex and cannot generate simple predictions in the way the strictly neutral model does[34].

## Conclusion

The neutral model has recently taken a beating from *D. melanogaster*, even as we continue to revere it for its clarity and statistical utility[4]. The findings on codon bias, the rediscovery and relevance of the Hill–Robertson effect and the fact that many loci reveal nonneutral local patterns of variation suggest that natural selection is highly pervasive at the DNA level.

To a scientist bred on neutrality, the discoveries of recent years present some daunting theoretical and empirical challenges. A rejection of neutrality is not the same thing as an understanding of natural selection, and the discoveries mean that evolutionary genetics has become more difficult than it once seemed.

However, it should be emphasized that none of the discoveries regarding natural selection would have been possible without the neutral model in the role of statistical null model. Indeed, neutrality continues to be the baseline limiting case for virtually all evolutionary genetic theory, and Kimura's theoretical discoveries are continuously drawn upon by evolutionary geneticists for all manner of applied and basic research questions. For both historical and continuing relevance it is probably fair to say that Kimura deserves to be placed with the trinity of great mathematical biologists: R.A. Fisher, S. Wright and J.B.S. Haldane.

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# A showcase for shrews

## The Evolution of Shrews

*edited by Jan M. Wojcik and Mieczyslaw Wolsan*

Polish Academy of Sciences, 1998.
$38.00 (+ postage) hbk (xi + 458 pages)
ISBN 83 9075210 7

If one is looking for up-to-date information on what is known about the shrew world, this book certainly has it. Wojcik and Wolsan have succeeded in promoting shrews as a fascinating model for evolutionary studies from diverse fields of research, such as paleontology, systematics, cytogenetics, metabolism and social systems. The remarkable traits of this group of morphologically uniform insectivores are (1) the number of species (335) widely distributed in diverse habitats, and (2) the existence of two main lineages (Soricinae and Crocidurinae) that are the most speciose and differ in metabolic rates, ecological and dental adaptations as well as in social structure. One of the main attractive features of this book is the number of lists including fossil and extant species, as well as diploid numbers and chromosome races, which altogether provide a highly valuable source of information.

One-third of this volume is devoted to the systematics of shrews (J.W.F. Reumer) and to their paleontological history over large areas: Europe (B. Rzebikk-Kowalska), Asia (G. Storch, Zh. Qiu, V.S. Zazhigin), Africa (P.M. Butler) and North America (A.H. Harris). Reumer recounts the conceptual development of shrew systematics and argues for the existence of two sister-families within shrews: the Heterosoricidae (mainly fossils) and the Soricidae. Heterosoricidae remain rare in the Holarctic and are unknown elsewhere. Current data show that this family appears during the Middle Eocene of Wyoming and disappears during the Lower (North America) or Higher (Europe and Asia) Miocene. The presence of Soricidae, documented on all continents except Australia and South America south of Colombia, is discreet from the Lower Oligocene (Europe) or Miocene (North America, Asia, Africa) up to the Pliocene when major diversification occurred. In Africa, the genus *Crocidura* shows a remarkable adaptive radiation. For each geographical area, all fossil and extant shrew species are indicated along with geographical (country or state), chronological (levels), and stratigraphic (geological formation) indications as well as exhaustive references.

Shrews of the genus *Sorex* have been one of the outstanding models of chromosomal evolution, which is extensively reviewed by J.B. Searle and J.M. Wojcik, who provide an up-to-date and critical account of the extent, patterns and processes involved in karyotypic change. Attempts to uncover general trends of chromosomal modifications at a higher taxonomic level (J. Zima, L. Lukacova and M. Macholan) have met with difficulties owing to the scarcity of G-band data for many species and to the diversity of patterns. J.R.E. Taylor thoroughly examines the contrasting metabolic patterns between Crocidurinae and Soricinae. Through correlations between metabolic rates and life history traits, Taylor provides an environmental and adaptive background for the differences in energetic strategies. Predictions are made on correlated social structures which are then explored in an impressive review on the social systems that occur in shrews (L. Rychlik).

A recurrent point made by several authors is the need for multidisciplinary studies on shrews. The value of such an approach is particularly evident in the case of phylogenetic reconstructions in the genus *Sorex*, which provide discordant patterns between chromosome and allozyme (M. Ruedi) or mtDNA (J. Hausser, L. Fumagalli and P. Taberlet) derived trees, suggesting varying modes of differentiation for these markers. Such studies, particularly on population structure, are missing in this review, and would have led to better predictions on rates of change and speciation (which sometimes appear contradictory between chapters). This gap is now being filled[1].

Wojcik and Wolsan have succeeded in combining a valuable synthesis of systematic data with a stimulating overview of the evolutionary biology of shrews. If one of the aims of this book is to interest researchers in this group of insectivores, I believe this goal has been achieved.

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