

Island hopping in *Drosophila*: patterns and processes

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SUMMARY

Radiation of *Drosophila* along the Hawaiian archipelago has resulted in an astounding array of diversity. The speciation in this group corresponds well to the geological history of the region and colonization events appear to have been a major contributing factor. Although much less impressive in terms of diversity, *Drosophila* have also radiated throughout the Caribbean islands. In contrast to the pattern exhibited in Hawaii, major changes that distinguish the species in the Caribbean are not always coupled to colonization events. The patterns of speciation for these two island groups are compared and contrasted in light of founder effect speciation models.

1. INTRODUCTION

Islands have always been attractive systems for the study of evolution – and in particular speciation – for a wide variety of reasons, the most obvious being that they tend to harbour numerous and splendidly diverse arrays of species not typically found in continental areas. These arrays are characterized by high levels of endemism and it follows therefore, that islands represent conditions that are extremely conducive to repeated speciation. If we can understand which evolutionary processes are important for speciation on islands, we may be able to define general principles that are applicable to a number of different biological situations.

Islands are also attractive because they define clear geographical boundaries that can be used as a natural framework for looking at patterns of diversification among assemblages of species. The geological formation of the islands themselves can suggest hypotheses about the evolution of the species that inhabit them, which adds an extra dimension for testing ideas about specific patterns and processes of speciation. In some cases, information about the geological formation of the islands can provide important corroborative evidence for timing different speciation events. Even if the formation of the islands predates speciation that has occurred on them, islands still serve as a natural sampling design that can be used for testing hypotheses about speciation mechanisms. To get the very most out of island studies of speciation, it is important to compare island systems with each other as well as with continental systems and thus develop a broad-based understanding of the relative importance of different evolutionary forces in speciation.

In this paper I will describe two island systems that have been used to study speciation patterns in *Drosophila*: the Hawaiian Islands and the Caribbean Islands. The Hawaiian system is probably the best known for studying *Drosophila* evolution. Although evolution on the Caribbean Islands is not as familiar, it too represents an active area in the research of *Drosophila* evolution and is the focus of my current

work. Although formation of these island archipelagos began at approximately the same time, the two are extremely different with respect to how they were formed, their proximity to the mainland, the number of endemic species that have evolved, and the pattern of speciation, and thus provide a good comparison with which to evaluate the importance of different speciation mechanisms for the evolution of *Drosophila* on islands in general.

2. THE HAWAIIAN DROSOPHILIDAE

The study of the evolution of Hawaiian Drosophilidae has had an enormous impact on ideas about speciation on island systems. Begun in 1963 as the Hawaiian Drosophilidae Project by W. S. Stone and D. E. Hardy, over the last three decades the study has involved several dozen researchers who have used a wide range of techniques to understand the biology and evolution of this diverse group. The summary that follows is by no means an exhaustive review of all the work carried out in this area, but serves rather as an overview of some of the major patterns and processes.

(a) *General patterns of speciation*

To understand the patterns of speciation on the Hawaiian islands, we must first briefly review the geology of the region. The present-day southeast corner of the Big Island of Hawaii sits over a stationary thermal plume of volcanic activity that is responsible for creating all the islands in the Hawaiian archipelago, past and present (McDougal 1979; reviewed in Carson & Clague 1995). Volcanic activity of this plume started 75–80 Ma BP. Lava was built up on the ocean floor, islands were formed, and then movement of the Pacific plate carried these newly formed islands in a north-westerly direction. Continuous volcanic and plate tectonic activity of this nature has built up the successive islands of the Hawaiian archipelago in a process analogous to a moving conveyor belt, with each new island progressively younger than the one immediately preceding it in the chain. Of the islands

existing today Kauai is the oldest, estimated to have been formed 5–6 Ma BP, and Hawaii the youngest, estimated to have been formed only 0.5 Ma BP. This pattern of the geological age of the islands decreasing towards the southeast holds true not only for the entire island chain, but also within the larger island of Hawaii, i.e. northern parts of the island are older than southern parts of the island.

The Hawaiian *Drosophilidae* is probably the most outstanding example of speciation known to have occurred in the family *Drosophilidae*. With over 500 extant species already named, and an additional 350 still to be described, estimates for the total number of species of *Drosophilidae* in the Hawaiian archipelago surpass 1000 (Kaneshiro 1993; Kaneshiro *et al.* 1995). But despite their morphological diversity, all the species are believed to be phylogenetically closely related, belonging to only two different genera, *Drosophila* and *Scaptomyza* (Throckmorton 1975; Kaneshiro *et al.* 1995). These genera represent sister taxa that began diverging from each other over 24 Ma BP (Thomas & Hunt 1991; DeSalle 1992, 1995), thus predating formation of the island currently thought to be the oldest in the chain, Kauai, and indicating that speciation has been occurring continuously along the Hawaiian archipelago involving islands that have long since subsided.

Most details of the patterns of speciation of the Hawaiian *Drosophila* come from studies of the picture-winged species group, which contains 111 species divided (on the basis of male genitalia) into approximately 12 subgroups (Kaneshiro *et al.* 1995). Initial analysis of polytene chromosomal inversions by Carson (1983) yielded a very detailed genetic phylogeny for the picture-winged subgroups. Because direction cannot be inferred from polytene inversion data alone, Carson (1983, 1987) then used information about the age of the different islands to assign a direction to the network of relationships and to produce a geographical phylogenetic scheme for the flies. In doing so, a general pattern of colonization from older to younger islands was revealed. A more recent reanalysis of the chromosomal data, in which the evolutionary direction was inferred by outgroup comparison and overlaid with the geographical data, showed that the ancestral species for a particular subgroup generally occurred on either Kauai or Oahu, with the oldest species of the entire picture-winged group concentrated on Kauai (Kaneshiro *et al.* 1995). DeSalle (1995) performed sequence and restriction fragment analysis on six subgroups and found evidence that corroborates this same general pattern of speciation from older islands to younger islands and even from older parts to younger parts within the island of Hawaii for different populations of *Drosophila silvestris*.

Together, these data show that the overall pattern of speciation in the Hawaiian picture-winged *Drosophila* is characterized by repeated colonization from older to younger islands. Because most species in this group are single island endemics, and sister taxa tend to occur on adjacent islands, it appears that the formation of new species of Hawaiian *Drosophila* is tightly coupled to colonization between islands. Congruent with this

pattern of colonization, shifts in mate recognition systems also appear to have been very important. Sister taxa on different islands tend to be remarkably similar in terms of their ecological niche, yet differ dramatically with respect to morphological and behavioural traits associated with mate recognition (Kaneshiro 1976; Carson & Templeton 1984).

(b) *Processes of speciation*

The central role of colonization events in the pattern of speciation for the Hawaiian picture-winged *Drosophila* was very influential in the formulation of founder effect speciation theory as elaborated by Carson & Templeton (Templeton 1980, 1981, 1982; Carson & Templeton 1984). The idea of founder effect speciation has its roots in earlier ideas expressed by Mayr. Greatly influenced by the views of Wright, Mayr felt that because organisms were balanced, integrated genetic systems characterized by high levels of fitness epistasis, natural selection would be slow and only marginally effective at bringing about speciation (Mayr 1963; Provine 1989). In expressing his view, Mayr wrote 'The real problem of speciation is not how to produce difference but rather to escape from the cohesion of the gene complex' (Mayr 1963, p. 518). For Mayr, founder events provided one such escape route. Because the response to selection of a particular allele in a population is a function of its complex interactions with alleles at other loci, then response to selection could change as a function of population structure. Mayr saw small founding populations as changing the genetic structure of a population in such a way as to set the stage for selection to act in directions previously blocked by the genetic structuring of the parental population. Mayr's model of 'genetic revolution' as he originally conceived it, involved high levels of inbreeding which would result in more and more recessive alleles being exposed to natural selection. Inbreeding could change the selective values of different alleles causing some alleles that were favoured in the original population to be lost, and as the population regained equilibrium with natural selection, new integrated gene systems could be eventually stabilized. Because Mayr's model required high levels of homozygosity which, in the long run, would actually not be conducive to rapid response to selection, Carson proposed his Founder-Flush model (1975) and Templeton proposed his Genetic Transilience model (1980), both of which relaxed the requirement for extended periods of inbreeding which would otherwise lead to the inevitable loss of genetic variability (Carson & Templeton 1984). In their models, genetic restructuring occurs during the initial stages of the founder event, followed by a period of rapid population recovery during which genes will change in response to either greatly relaxed selection in the new ecological environment (Carson 1975) or to selection in the new genetic environment triggered by the founding event (Templeton 1980). These models also differ from Mayr's original proposal in not requiring the genetic restructuring to involve the entire genome and, in fact, they predict that different genetic systems will respond

differently to the founder event. For example, neutral nuclear genes are not expected to change much at all under these models. On the other hand, because they are haploid and maternally inherited, mitochondrial genes are expected to be more sensitive to the founder event and show reduced variability. This predicted discrepancy between nuclear and mitochondrial genes was confirmed by DeSalle & Giddings (1986).

Just as neutral traits are expected to be more or less sensitive to founder events depending on which part of the genome is considered, selected traits with different underlying genetic architectures are also expected to be differentially susceptible to changes brought about by founder events. Templeton (1980, 1982) continually stressed that the genetic architecture, i.e. the number and types of genes and their interaction, underlying a trait is very important in determining how that particular trait will respond to founder events, and suggested that traits governed by a few major genes with many epistatic modifiers were more likely to experience a genetic transience than additive polygenic traits. Evidence supporting the importance of a few major genes with epistatic modifiers in speciation comes from genetic analysis of the 'abnormal abdomen' system which was found to be responsible for isolation in artificial bottlenecks in *D. mercatorum* (Templeton & Rankin 1978; Templeton 1979*a*, 1982; Hollocher *et al.* 1992), and from the analysis of head shape differences between two picture-winged species, *D. heteroneura* and *D. silvestris* (Templeton 1977; Val 1977).

Although the idea of founder effect speciation has been very well received, it has not been universally accepted. The crux of the controversy involves the relative importance of random genetic drift versus natural selection in promoting speciation and how exactly these two evolutionary forces manifest their effects in founder populations. This controversy surrounding founder effect speciation is not new, and represents but one phase of a 'persistent controversy' that was started by Fisher and Wright back in the 1930s (Provine 1989) and will mostly likely persist until empirical studies provide new bases for useful model building. Opponents of founder effect speciation favour Fisher's genetic view over Wright's; they dismiss the idea that speciation is impeded by genetic cohesion of species, and favour instead natural selection operating in moderately sized populations as being most effective for promoting rapid speciation (Barton & Charlesworth 1984; Barton 1989; Provine 1989). These arguments are based on models that evaluate the effects of founder events on speciation, and assess the probability that genetic drift alone will cause a shift from one adaptive equilibrium or peak to a new adaptive peak, separated from the first by a valley of lower average fitness. Generally, these models show that the probability that a population will shift to a new adaptive peak during a founder event is relatively low, and that such a shift will not generate very high levels of reproductive isolation by itself. However the models fail to reflect accurately all the processes described in founder effect speciation, which involve not only drift but emphasise changes in the pattern of

pleiotropic effects between genes that could be shifting during a founder event. Such dynamic effects are never suitably analysed in these models, because they only deal in one phenotypic dimension (Carson & Templeton 1984; A. Templeton, personal communication).

Other work which comes closer to representing the genetic events that could be occurring during founder effect speciation has been done by Goodnight (1987, 1988) who has demonstrated that founder events can trigger epistatic genetic variance to be converted to additive genetic variance, thus allowing a renewed response to selection after a founder event. Additionally, Bryant & Meffert (1988, 1990) have shown that increases in additive genetic variance which affect morphological traits result from a bottleneck, indicating that complex genetic interactions between traits can be shifted during a founder event, promoting evolution along new trajectories. By incorporating changes in epistasis into their models, both these researchers have concluded that founder events may be important in promoting speciation, contradicting the results of models that largely dismiss the importance of epistatic effects. More recently Wagner *et al.* (1994) have taken Barton's original model (1989) and incorporated epistasis in a way which allows for gene effects to be context dependent rather than one dimensional and have found that this can increase the probability of the peak shift and result in much greater levels of reproductive isolation than the earlier additive models. Although Wagner *et al.* (1994) were modelling shifts in moderately sized populations rather than in extreme founder events, their results illustrate the large impact different assumptions about genetic architecture can have on the outcome of the same evolutionary model. Interestingly, the main effect of adding epistasis is to change the adaptive path that a population can follow as it shifts from one fitness optimum to another, allowing it to avoid having to traverse the point of lowest fitness (Wagner *et al.* 1994).

3. THE CARIBBEAN DROSOPHILIDAE

Because so many of the specific characteristics displayed by the Hawaiian *Drosophila* went into formulating the model of founder effect speciation itself, it is important to move away from this system to dissect the different components of the model for their relative importance in speciation. Speciation of Drosophilidae in the Caribbean pales in comparison to that of the Hawaiian Islands. Although the numbers of species are decidedly less impressive, the Caribbean Island system nonetheless possesses some unique characteristics that make it particularly suitable for comparative studies of speciation with the Hawaiian Islands. As a point of comparison, the Caribbean is intermediate between the intense isolation of the Hawaiian Islands and the continuous distribution of species on continents. Because the Caribbean islands show an intermediate level of isolation with respect to their proximity to the mainland, we may be able to tease apart the effect of the actual founder event in promoting genetic reorganization, from the extreme geographical isolation that is invariably associated

with the founder event in the Hawaiian Islands. The Caribbean Drosophilidae also have very closely related continental groups that the Hawaiian Drosophilidae lack, and these can be used for comparison with the insular forms. For closely related Hawaiian species, only island versus island comparisons can be made; however with Caribbean species, comparisons of mating behaviour, reproductive isolation, and morphological traits can all be made between continental and insular forms, giving greater insight into those types of evolutionary changes which distinguish island species from mainland species. By using the same taxonomic group of organisms to investigate these two distinct island systems, we can begin to distinguish the relative role of different evolutionary processes in speciation on islands.

(a) *Patterns of speciation*

Unlike the comparatively simple geological formation of the Hawaiian islands, the formation of the Caribbean Islands is complex and still controversial (Donnelly 1988). Although situated rather close to continental areas, none of the Antillean islands is thought to be continental fragments. The Greater Antilles began forming ca. 80 Ma BP from a single independent Cretaceous island arc that was stretched and fragmented into a discontinuous series of islands during the Cenozoic period, as the Caribbean plate moved into its current location ca. 55 Ma BP. Formation of the Greater Antilles was not smooth, and at various points in its history parts of different islands were pushed together only to be pulled apart later. Early in the history of the Greater Antilles possible connections to the Central American mainland may have existed between Cuba and the Yucatán and between Honduras and Jamaica, although it is not known how important these connections were for the present-day biogeography. It is also not clear which island areas were submerged during much of the middle of the Cenozoic, although it is rather likely that Jamaica was completely underwater about 30 Ma BP (Donnelly 1988). In contrast to the ancient and chaotic formation of the Greater Antilles, the Lesser Antilles were built up by a gradual accumulation of volcanic material from 20 Ma BP to the present-day. Despite being built in part on fragments of the Greater Antilles arc, the Lesser Antilles were never subjected to elaborate plate tectonic movements and essentially developed where they are situated today. Water levels between islands of the Lesser Antilles are high and always have been, indicating that land connections never existed between these islands. In addition, no land bridges are thought to have linked South America with the Lesser Antilles. Therefore, just as with the Hawaiian archipelago, all colonization of the Lesser Antilles must have occurred by over-water dispersal (Donnelly 1988).

Fossil representatives of Caribbean Drosophilidae preserved in Dominican amber indicate that ancestral groups have existed in the Greater Antilles since the early Miocene, 23 Ma BP (Grimaldi 1987), before the formation of the Lesser Antilles. The endemic Carib-

bean Drosophilidae consists of a total of 58 Antillean species spread among nine different genera, of which only one – *Mayagueza* – is endemic to the region (Grimaldi 1988). All other species belong to groups that have representatives outside the immediate Caribbean Islands. Only two Caribbean *Drosophila* species groups are represented by more than a handful of species endemic to the Antilles: the *Drosophila repleta* group and the *Drosophila cardini* group (Grimaldi 1988). Because the *D. repleta* group has been described in detail recently (Grimaldi 1988), I will confine my attention to the patterns of speciation in the *D. cardini* group which consists of 16 species, eight of which are confined to the Greater and Lesser Antilles and eight of which have ranges in continental tropical America (Heed & Krishnamurthy 1959; Heed 1962).

The *D. cardini* group has been subdivided into two subgroups, the *Drosophila dunni* subgroup which has species endemic to Puerto Rico, Jamaica and the islands of the Lesser Antilles, and the *Drosophila cardini* subgroup which has species which generally do not inhabit the islands (Heed 1962). These *Drosophila* are particularly interesting because the island species of the *D. dunni* subgroup show a more or less regular cline in abdominal pigmentation, a rare phenomenon in *Drosophila* that suggests the operation of natural selection (figure 1; Heed & Krishnamurthy 1959). In addition to the interesting biogeographical distribution of species within this group, hybridization studies show that the island species represent the entire range of possible genetic relationships from complete fertility in the F_2 generation to complete reproductive isolation (both pre- and postmating) (Heed & Krishnamurthy 1959; Futch 1962; Heed 1962). In addition to hybridization studies, relationships among the different species have been analysed through examination of male genitalia (Heed 1962), inversion polytene chromosome analysis (Heed & Krishnamurthy 1959; Heed & Russell 1971), and more recently in my laboratory, analysis of DNA sequence from the mitochondrial genome. Figure 2 shows how the different methods compare for assigning relationships between the different species in the group. Although the different data sets favour slightly different relationships, there are certain groupings that are strongly supported by all the data. The greatest discrepancy involves the inclusion of *D. belladunni* (the Jamaica species) in the *D. dunni* subgroup. This relationship was not supported by the mitochondrial tree, although the molecular data do pair this species with *D. acutilabella* and reveal them to be the sister taxa to all the other species in the *D. dunni* subgroup. In this sense, these two species form an insular bridge between the continental species of the *D. cardini* subgroup and the insular species of the *D. dunni* subgroup. This supports the idea that all the insular species are derived from a common ancestor and have not resulted from independent colonizations by different species on the mainland. Although physically close to the mainland, the Caribbean islands are sufficiently isolated to reduce gene flow significantly and allow for differentiation to occur between the different island and mainland species. The data also show that colonization by the insular forms has not

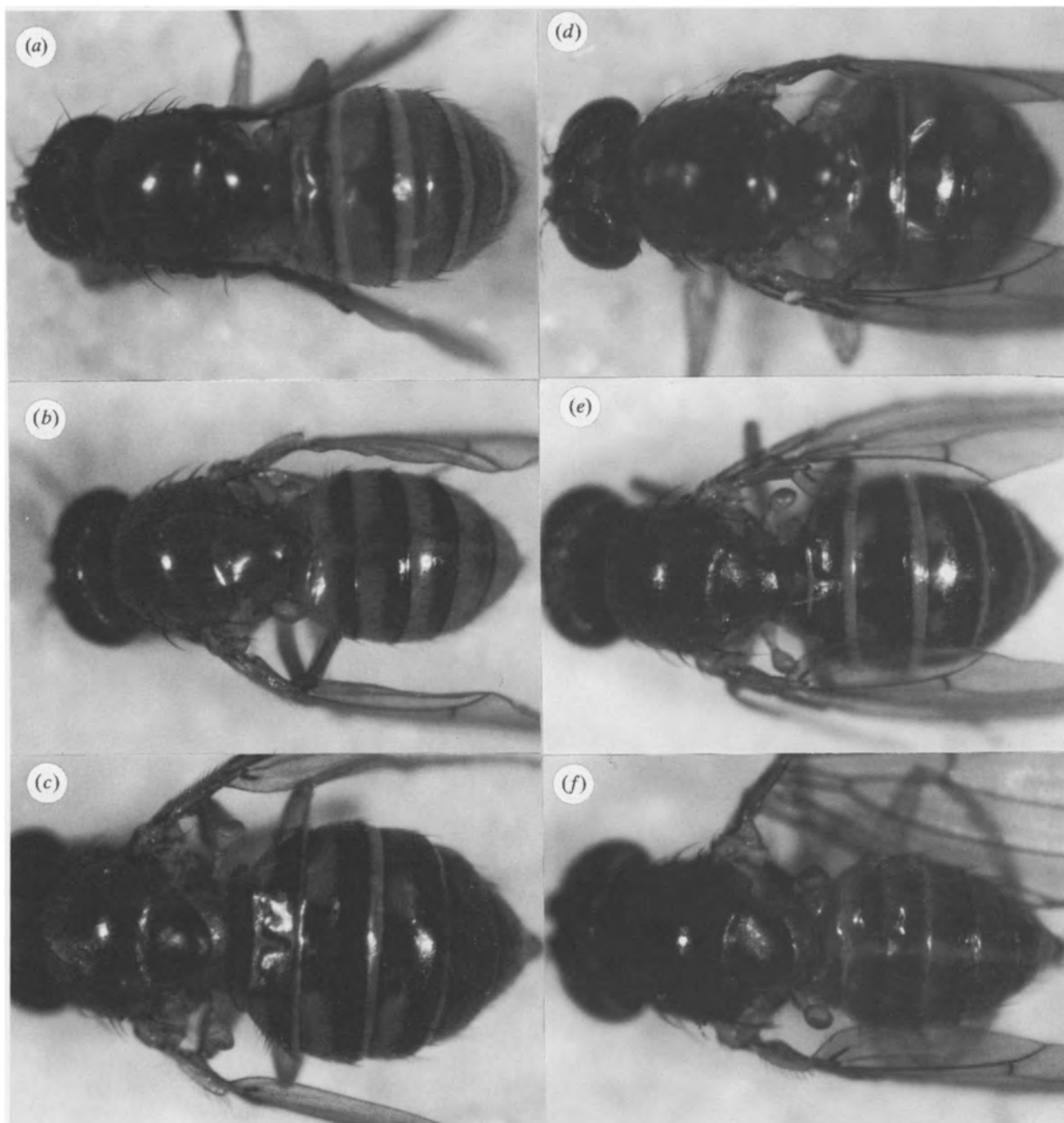


Figure 1. Female abdominal pigmentation patterns of the *dunni* subgroup. (a) *D. dunni dunni* (Puerto Rico); (b) *D. arawakana arawakana* (Montserrat); (c) *D. caribiana* (Martinique); (d) *D. antillea* (St. Lucia); (e) *D. nigrodunni* (Barbados); and (f) *D. similis* (Grenada).

followed a simple stepping-stone model from one end of the island chain to the other. Instead, species spread from Jamaica to the two ends of the islands chain (Puerto Rico and St. Thomas at one end and Grenada and St. Vincent at the other) and inward to Martinique in what appear to be at least two independent colonizations. Then from Martinique, the species have fanned out to Guadeloupe, St. Lucia and Barbados.

In general, the different traits that distinguish the species do not always couple tightly with the pattern of colonization. The pattern of island hopping in the *D. dunni* subgroup described above contrasts with the regular cline in abdominal pigmentation. Although colonizations have obviously played an important role in speciation in this group, natural selection has also worked on these species as shown by the changes in the

abdominal pigmentation. Light and dark species tend to be more closely related to each other than the dark species are to each other or the light species are to each other. Therefore, pigmentation pattern is not phylogenetically constrained, and selection on this trait may be separable from the initial effects of the founder event. At this point we are not able to determine whether the founder event itself may be able to facilitate changes in abdominal pigmentation, however a closer examination of the evolution of genes responsible for the differences in pigmentation may lead to an answer in the future.

Reproductive isolation follows the pattern of colonization more linearly, yet there are still inconsistencies that warrant closer inspection. For example, *D. caribiana* – which inhabits Martinique – shows greater

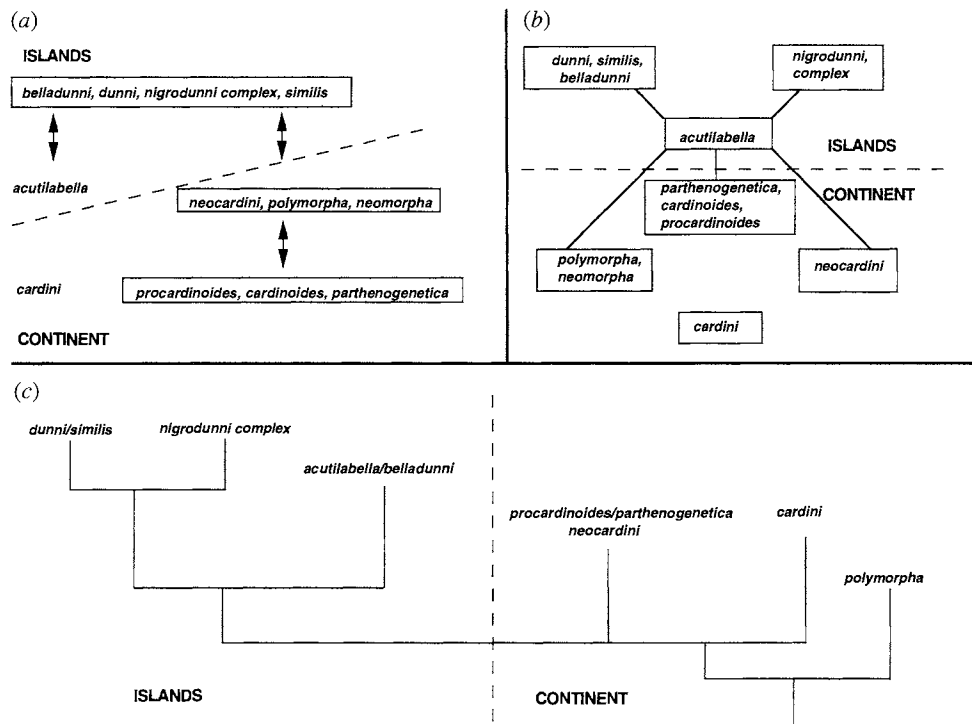


Figure 2. Groupings of the species in the *cardini* group based on: (a) male genitalia (Heed 1962); (b) cytology (Heed & Krishnamurthy 1959; Heed & Russell 1971); and (c) mitochondrial sequence analysis (H. Hollocher, A. N. Hibbs & D. P. Kutzler, unpublished data).

postmating isolation with all the species in the *D. dunni* subgroup than is expected though chromosome analysis (Heed & Russell 1971), and mitochondrial sequence analysis (H. Hollocher, A. M. Hibbs & D. P. Kutzler, unpublished data), indicating that the evolution of postmating isolation may have been faster in this particular species. In addition, the two species that show the closest affinities in terms of mitochondrial sequence data, *D. dunni* and *D. similis*, show the greatest amount of premating isolation seen between all the species pairs in the *D. dunni* subgroup (H. Hollocher, A. M. Hibbs & D. P. Kutzler, unpublished results), although they occur on islands that are more than 725 miles apart. Many models of the evolution of premating isolation require contact between the two species diverging, and in this case it is not immediately obvious what may be driving the sexual isolation, although it is interesting to note that these two species do represent two extremes in abdominal pigmentation (Heed & Krishnamurthy 1959; H. Hollocher & A. M. Hibbs, personal observations).

(b) Processes of speciation

Carson & Templeton (1984) make a point that not all species are equally prone to founder effect speciation. Even within *Drosophila*, different groups are not equally susceptible to speciation via founder events due to differences in population structure, system of mating, and even their chromosomal constitution. Therefore, it is important to determine whether the insular species in the *D. cardini* group meet the criteria that suggest they would be susceptible to genetic change via a founder event. Cosmopolitan species or generalists are

not expected to be able to respond readily to a founder event (Carson & Templeton 1984). Species that are particularly good at invading new habitats usually have a 'general purpose genotype' characterized by a balanced system of heterosis. Because of the balancing selection involved in maintaining these systems, they can be easily carried through the founder event without much change and would be, therefore, least likely to experience a genetic shift. The species of the *D. dunni* subgroup are not considered generalists. Although specific details of the breeding sites of the different species are not known, the flies have not been found in areas which commonly attract other cosmopolitan species. They are confined to middle elevation, native and secondary growth forests (Heed & Krishnamurthy 1959; H. Hollocher personal observation). Carson & Templeton also hypothesized that founder effect speciation is more effective if crossover suppressors are eliminated or fixed so that recombination is free to establish new gene complexes (Carson 1975; Templeton 1980, 1982; Carson & Templeton 1984). As positive evidence that free recombination may be important, they cite how inversion polymorphisms are not carried over during speciation in the Hawaiian *Drosophila*. Examination of the species in the *D. dunni* subgroup show them to have the same low level of inversion polymorphism relative to the continental species as seen in the Hawaiian *Drosophila* (Heed 1971). Therefore, if founder effect speciation is important, it would not be inhibited by blocked recombination in the insular species of the *D. cardini* group. It is possible that founder effect speciation may be operating within the *D. dunni* subgroup; however, its role in this group cannot be properly evaluated without analysis of the

underlying genetic architecture of the traits that distinguish the different species.

In two important respects, the *D. dunni* subgroup does show distinct differences from the Hawaiian *Drosophila*, differences that may affect how the two species groups have responded to colonization. First, the species in the Antilles are not as isolated from each other as are the Hawaiian species. Therefore, some speciation in the *D. dunni* subgroup may not have involved complete isolation from the source population during the entire process of differentiation. Of course, recurring gene flow would counteract the genetic effects resulting from the founding event. However, because the species of the Lesser Antilles are single island endemics, colonization is rare relative to the formation of new species on each island. If the genetic reorganization triggered by a founder event is rapid enough, then subsequent gene flow may have little impact on the system. In general, other species of the *D. cardini* group do not occur on the Lesser Antilles, except for *D. cardini*, which is unable to crossbreed with any of the other species in the group and therefore would not be able to contribute to gene flow. Because species from adjacent islands are sometimes able to produce fertile offspring in the laboratory, there exists the formal possibility that gene flow between more distant islands could result from island intermediaries. However if this was the case, laboratory crosses performed to test how effective this mechanism of gene flow would show that there was strong selection against the formation of genetic combinations from more distant islands. Only a very small subset of the possible genetic combinations could be produced through a series of crosses, indicating that there are strong incompatibilities between these species at several levels, making it unlikely that continuous gene flow had occurred during their formation (Heed 1962). A second important distinction between the Hawaiian *Drosophila* and the Caribbean *Drosophila* is how responsive the mating behaviour has been to speciation. Although differences in male genitalia have occurred in both groups, the elaboration and diversification of courtship in the Hawaiian picture-winged *Drosophila* is not paralleled in the Caribbean *Drosophila*. Founder effect speciation can be very effective when coupled with sexual selection (Kaneshiro 1980, 1983, 1989), and once elaborate mating behaviour first evolved in the Hawaiian *Drosophila*, that system was more susceptible to founder effects (Ringo 1977; Templeton 1979*b*; Giddings & Templeton 1983). It is necessary to determine how tightly founder effect speciation needs to be coupled both to complete allotropy and to sexual selection to determine how generally it can be applied to other systems outside of Hawaii.

4. CONCLUSIONS

Inferring process from pattern is and always will be challenging. It is clear from the above discussion that a final decision regarding the importance of founder effect speciation cannot yet be made. The formulation

of the model relied principally on characteristics of the Hawaiian *Drosophila*. How general the process is outside this system has not been adequately explored to decide which elements must co-occur for founder effect speciation to be plausible. However there are important concepts contained in the model which do not only apply to founder effects, and need to be addressed in all aspects of speciation. Reducing the controversy to the relative importance of drift versus selection under-values the genetic issues of speciation that the founder effect model of speciation was originally formulated to address. It is becoming increasingly obvious that the genetic architecture of traits involved in speciation is a central issue which begs for more empirical work. The genetics of species divergence in general is still a little-understood area of research, although some headway is being made recently with respect to the genetic basis of reproductive isolation in *Drosophila* (Coyne 1992; Coyne *et al.* 1994; Wu & Palopoli 1994; Wu *et al.* 1995). Not only does genetic architecture play a role in determining the effectiveness of different evolutionary processes, but it also appears that different traits considered important in speciation, such as postmating reproductive isolation, sexual isolation, and morphological differences are all differently susceptible to different evolutionary processes as well, because of the nature of the traits themselves. Postmating reproductive isolation is never directly selected during speciation, but rather evolves as a pleiotropic consequence of divergence being caused by some other evolutionary process. Therefore it consistently shows an entirely different genetic patterning than premating isolation, which is more likely to be directly selected during speciation, even when both these traits occur in the same species pair (Coyne *et al.* 1994; Wu & Palopoli 1994). Similarly, hybrid sterility has been shown to have evolved quite differently from hybrid inviability. They are fundamentally different physiologically, even though they are often grouped together under the rubric of postmating reproductive isolation (Orr 1993; Wu & Davis 1993). Therefore, what are truly needed are more systematic analyses of the genetic architecture of several different traits simultaneously for different related species, in both the Hawaiian and the Caribbean species groups, to help resolve the genetic issues tackled by founder effect speciation, issues which need to be confronted for all aspects of speciation.

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Discussion

M. WILLIAMSON (*Department of Biology, University of York, York YO15DD, U.K.*) Would Professor Hollocher accept that Professor Carson's emphasis on major interisland jumps is somewhat misleading? If you map Professor Carson's inversion phylogeny onto the islands (Williamson 1981, figure 8.3) you will find 90 intrainland speciation events against about 40 interisland events. This ratio of about 2:1 is normal for Hawaiian jumps (Wagner 1995). The intrainland speciation may well still be allopatric, between neighbouring volcanoes etc.

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H. HOLLOCHER I do not think that Carson's emphasis on interisland colonization is misleading at all. Based on inversion polymorphism which has limited resolution, Carson (1983) was able to infer 45 founders for 97 single-island, endemic species of the Hawaiian picture-winged *Drosophila*. Considering all the possible speciation mechanisms that exist, to be able to account for about half the picture-winged species via colonization is remarkable and indicates that colonization was a major contributing factor to speciation in this group. Molecular techniques have offered greater resolution for some of these sister groups and speciation has consistently progressed from older to younger islands across the island chain, in addition to there being a pattern of speciation from older to younger parts of an island when that information is available (DeSalle 1995).

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