Behavioral Phylogenies and the Direction of Evolution

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Summary. A model for using mate preference data to deduce the direction of evolution between populations related by founder events or population bottlenecks is examined. Data from a wide range of organisms satisfying the necessary constraints of population structure are compatible with the model developed by K. Y. Kaneshiro from studies of Hawaiian *Drosophila*.

One of the principal tasks of the evolutionary biologist is the investigation of phylogenetic relationships. Paleontology has been admirably successful in this at a gross morphological level (*1, 2*) and modern techniques of DNA analyses promise to be useful at a more precise level (*3*) with much of the intervening territory covered by other methods. Data derived from the banding patterns of polytene chromosomes have been useful in sorting out the relationships within certain groups of Diptera (*4–10*). While these studies of polytene chromosomes have been among the most precise of any phylogenetic analyses to date they have almost always suffered by being incapable of defining a direction of evolution within the phylad of interest. Lemeunier and Ashburner have stated (*9*), "We can offer no evidence, from [polytene sequence] data alone of the direction of evolution within the group . . . the cytological evidence is quite neutral."

While related data are frequently useful, they are more often suggestive than compelling. This has not, however, been a problem in the studies of Hawaiian *Drosophila* (*4, 5*). Data from studies of these Diptera can be unambiguously correlated with data from studies of geology, and related disciplines (*11–15*) firmly to define a direction for the phylogenies established from polytene chromosome data. Kaneshiro has combined these directed phylogenies in turn with principles of population biology to provide a model that brings order to certain kinds of behavioral data and that promises to have, under the appropriate constraints, wide applicability for inferring phylogenetic directions.

The Kaneshiro model (*16, 17*) has been the subject of criticism, and alternatives to it have been proposed (*18–21*). It therefore seems appropriate to examine the model and the criticisms in an effort to clarify this area of inquiry.

The Kaneshiro Model

On the basis of principles of population biology (the founder effect) known to be important in the evolution of the biota of Hawaii (*22, 23*), Kaneshiro proposed a general model (*16*) to explain the asymmetrical patterns of courtship success observed in four closely related species of picture-winged *Drosophila*. The essential assumptions of this model are only two: that these populations are related by founder events with little or no subsequent gene flow, and that the ancestral populations have not been subjected to drastic population bottlenecks since these founder events.

The ontogeny of the Hawaiian Islands is well known from the data of oceanography, vulcanology, stratigraphy, paleomagnetism, and radiometric dating (*11–15*). Broadly speaking, the ages of the islands decrease from older to younger in a linear sequence from northwest to southeast (Fig. 1). If we juxtapose this information with data from biogeography, morphology, and cytogenetics, it is possible to assign ancestral or derived status to these four *Drosophila* species (*4, 5*). Two of them (*D. differens* from Molokai and *D. planitibia* from Maui) are thus judged to be ancestral while the other two (*D. heteroneura* and *D. silvestris*, both from the Big Island of Hawaii) are known to be derived. Kaneshiro found nonreciprocal isolation between the ancestral and derived species according to the following consistent pattern.

Males from ancestral populations are equally effective in courting females from either ancestral or derived populations, whereas males from derived populations are relatively ineffective at courting females from ancestral populations. Females from ancestral populations mate preferentially with males from ancestral populations, while females from derived populations mate either at random or else preferentially with males from ancestral populations. The two ancestral populations themselves showed a moderately asymmetrical pattern of reciprocal isolation while the two derived species were strongly and reciprocally isolated, although hybrids from nature are known (*24*), but are rare. From this broad amalgamation of information Kaneshiro proposed a mechanism to explain these asymmetries.

Spieth (*25, 26*) has shown that the courtship behavior of these flies is "always prolonged and often complex" in that it involves a series of stimuli (male) and evocative responses (female). Kaneshiro assumed that this courtship behavior is subject to at least a degree of genetic control. There is good supporting evidence for this assumption in *Drosophila* and in other organisms (*27*). With respect to Hawaiian *Drosophila*, recent preliminary studies demonstrate a rapid selective response of the differences in courtship success in these species (*28*) and imply that this assumption is valid. The second part of Kaneshiro's argument is based on the compelling evidence that founder effects have played a critical role in the evolution of the Hawaiian *Drosophila* (*29, 30*). Kaneshiro argued that the founder effect and subsequent explosive colonization that is believed to have been the common mode of speciation in these flies would likely result in a loss of some of the genetic determinants responsible for certain of the behavioral "elements" in the courtship repertoire of the ancestral species. Thus, a derived species would display a less complete courtship ritual than the ancestral. Given the "choosing female" (*31, 32*) mode of courtship common in *Drosophila*, the predicted pattern between ancestral and derived species would be precisely as observed by Kaneshiro in the four picture-winged species studied.

Another possible mechanism is suggested by the work of Lande (*33*) on the "runaway" sexual selection processes

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first discussed by Fisher (*34*). These models consider the joint evolution of female mating preference and secondary sexual characters of males (including courtship behavior) and indicate that genetic drift (including founder events) can destabilize a previously stable mating system. As was discussed by Templeton (*35*), such destabilizations are particularly likely in organisms such as Hawaiian *Drosophila* that are characterized by extremely complex courtship rituals and displays. If such a destabilization is induced by alteration in a male signal or signals, the resulting selective forces are asymmetrical in the two sexes. The alteration of male signals induces selection on females to accept the new signals (which in turn feeds back onto selection in the males for the new signal) but not necessarily to reject the ancestral signals. Indeed, in the absence of ancestral males there is no direct selection of any kind upon the female's response to ancestral courtship signals. Any reduction in female responsiveness to the ancestral signals would be due to pleiotropy or other indirect effects.

The result of this process is to establish derived males with new courtship signals that are not accepted by ancestral females and derived females with at least some degree of acceptance (perhaps total) of ancestral males, that is, the Kaneshiro hypothesis. Thus, the asymmetry noted by Kaneshiro could simply be due to the asymmetry in selective forces associated with runaway sexual selection. Of course, the Kaneshiro and sexual selection mechanisms are not mutually incompatible, and elements of both could be manifest in any particular founder event. Under either mechanism, the specific constraints on this model are, then, that it is applicable only to cases of divergence involving founder events with virtually no subsequent gene flow, and that the ancestral and derived populations are directly related via the founder event.

Supporting Evidence

Support for the Kaneshiro model has come from numerous sources. Ohta (*36*) studied the Hawaiian picture-wings *D. grimshawi* (from Kauai, Oahu, Maui, Molokai, and Lanai) and the closely related homolog *D. pullipes* (from the island of Hawaii). From asymmetries of mate preference among his experimental populations, he drew conclusions that generally supported the Kaneshiro model. The single apparent exception aids in illuminating the constraints upon the model.

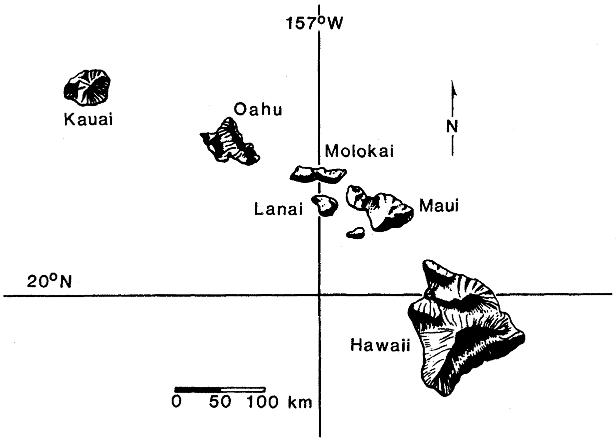

Fig. 1. The major islands in the Hawaiian archipelago. Their approximate ages [from (*14*)] are Kauai, 5.6 to 3.8 million years; Oahu, 3.4 to 2.2 million years; Molokai, 1.8 to 1.3 million years; Maui and Lanai, 1.3 to .8 million years; Hawaii, 0.8 million years to present (*88*). [Courtesy of Academic Press]

Ohta found the direction of evolution between these populations, inferred from the behavioral data, to be as predicted by the Kaneshiro model except in some tests involving flies from Maui, Molokai, and Lanai (the Maui Complex). Tests between populations within the Maui Complex showed the Lanai populations to be ancestral to Maui and Molokai, while the relation between these latter two was not resolvable. Flies from Lanai appeared, behaviorally, to be ancestral to *D. pullipes*, the Big Island homolog. Ohta speculated that specific factors related to the evolution of ovipositional generalism from specialist ancestors played a role in obscuring the relationships of the populations within the Maui Complex. In addition, however, it is known that the islands of the Maui Complex have been joined by land bridges formed as a result of sea-level fluctuations due to Plio-Pleistocene glaciation at least twice (*14, 15*). Craddock (*37*) believes that "it is probable that *Drosophila* populations were once coextensive across the lower-lying regions connecting the separate volcanoes" of the different islands. Furthermore, the distances separating the islands of the Maui Complex from each other (average minimum distance is approximately 9 miles or 14.5 kilometers) are small in comparison to the widths of the channels separating the other major islands (the average minimum distance, approximately 70.4 km). This implies a far more intricate, nonlinear series of founder events, or more likely "dumbbell" type splits involving large numbers of individuals in both subpopulations, and subsequent gene flow between the Maui Complex populations than is likely for the populations of the other major islands.

This solitary exception among the Hawaiian *Drosophila* to the model proposed by Kaneshiro is found only where there is excellent evidence to suggest a violation of the model's constraints. Set against the background of supporting data (the tests between the major islands, outside the Maui Complex), this "exception" is most conservatively viewed as supporting the Kaneshiro hypothesis via refinement of the necessary conditions.

There is also evidence to suggest that the Kaneshiro hypothesis holds true whenever its underlying assumptions are met and is not due simply to some singular feature limited to Hawaiian *Drosophila*. There are many examples of marginal populations that are isolated from the bulk of a more widespread species. In most cases, biogeographical arguments imply that the marginal population was derived from the more central populations. Moreover, founder events are often deemed likely in the establishment of the marginal population from biogeographical or other evidence. We recognize that the inferences of ancestral and derived status and of the occurrence of founder events are not nearly so compelling in these non-Hawaiian examples, and, as a result, such examples cannot provide critical tests of the Kaneshiro hypothesis. Nevertheless, they can legitimately be used to ascertain whether this hypothesis is applicable to organisms other than Hawaiian *Drosophila*.

An example of this type of evidence is provided by the work of Sperlich (*38*). He examined an extreme marginal population of *D. subobscura* in Norway and compared it to Central European populations. All matings among and between these populations were fertile; but when Central females were pair-mated to Norway males, only 52 percent of the crosses were successful as opposed to an 89 percent success rate in crossing Norway females with Central males (Norway by Norway had an 82 percent success rate and Central by Central had a 95 percent success rate). This asymmetry is exactly what is expected under the Kaneshiro hypothesis if the central population corresponds to the "ancestor" and the marginal population to the "derived"—a very likely situation in this case.

Another example is provided by the work of Bicudo (*39*) on *D. prosaltans*. The bulk of this species is found in South America, being distributed from northern South America to southern Brazil and Paraguay. However, a more limited portion of this species is found in Central America, and these Central American populations are not continuous with the South American populations. Bicudo discovered that the South American populations have extensive inversion polymorphisms in their polytene chromosomes, whereas the Central American populations are monomorphic. As described elsewhere (*40*), founder effects in *Drosophila* of the type that lead to reproductive isolation tend preferentially to lose inversion polymorphisms. Hence, both the biogeographical and the cytogenetic evidence indicate that the Central American populations are derived from the South American populations through a founder event. In crossing the Central American flies with South American flies, Bicudo found both hybrid sterility and sexual isolation. The sexual isolation was asymmetric in precisely the fashion predicted by the Kaneshiro hypothesis if we assume that the Central American populations were derived from South American flies.

Supporting evidence from organisms other than *Drosophila* is found in the work of McPhail (*41*) on behavioral isolation in the stickleback fish *Gasterosteus*. He reported on an isolated population in the Olympic Peninsula of Washington that has, in response to predation pressure, differentiated in pigmentation of the nuptial gular pouch from the ancestral red. His analysis of courtship behavior in the two populations reveals that the black (derived) population is asymmetrically isolated from the red (ancestral) precisely as the Kaneshiro model would predict.

Dwivedi *et al.* (*42*) performed "choosing female" tests on stocks of *D. takahashii* and *D. pseudotakahashii* and found asymmetrical mate preference favoring *takahashii* males. They interpreted biogeographical and cytological data to conclude that *takahashii* is the ancestral species, as predicted by the Kaneshiro model. Elsewhere (*43*) these same researchers tested mate preference in three species of the *D. bipectinata* complex. Here they reached conclusions contradictory to their interpretation of the Kaneshiro hypothesis in spite of strong cytological evidence repudiating their interpretations (*44*). Although such ambivalence is difficult to justify, it should also be noted that Bock (*44, 45*) also presents evidence that would lead one to question the applicability of the Kaneshiro model to these populations.

As mentioned earlier, the above examples cannot be regarded as tests of the Kaneshiro hypothesis, but rather they represent indicators that this model is applicable to organisms other than Hawaiian *Drosophila*. However, one of the strengths of the Kaneshiro hypothesis is that it makes explicit the underlying assumptions required for its applicability. As a consequence, this hypothesis can be directly tested by laboratory experimentation. The first such laboratory test is found in the work of Powell (*46*).

Powell (*46*) reported an experiment designed to test Carson's founder-flush speciation theory (*29, 30*) in the laboratory with populations of *D. pseudoobscura*. He demonstrated the rapid evolution of premating isolation in populations subjected to a series of founder-flush cycles (*47*). Recalculating Powell's data, Kaneshiro showed that of eight populations so derived, all three of those showing asymmetries of isolation did so precisely as predicted by the Kaneshiro model. As Powell wrote, "That [premating isolation] does not *always* evolve is not surprising. That it *can* evolve so rapidly, even in a minority of cases, is remarkable." Arita and Kaneshiro (*48*) reported on a similar phenomenon that was an accidental by-product of laboratory maintenance of two populations of *D. adiastola*. Two isofemale lines (an isofemale line consists of the offspring of a single female) were established in separate collections from the wild: the first in July of 1969 (stock M55G17) and the second in September of 1975 (stock T79B3), more than 6 years later. The only apparent differences between these two laboratory stocks were the length of time they had been kept in the laboratory and the exposure of the stock first established, M55G17, to four or five population crashes or bottlenecks, a fate that T79B3 escaped. Testing the mate preferences of these two populations, Arita and Kaneshiro found that a strong asymmetry had developed precisely as predicted by the Kaneshiro model—the stock exposed to the population bottlenecks (M55G17) appeared to be "derived" from the uncrashed stock representative of the ancestral population. Ahearn (*49*) observed similar results as an artifact of normal laboratory maintenance procedures. A stock of *D. silvestris* "which underwent several severe population reductions became partly ethologically isolated from the stock which is representative of the larger natural population of *D. silvestris* at Kilauea Forest Reserve."

The work of Ahearn (*49*) has recently been dismissed (*21*) as simply being due to inbreeding depression in male vigor caused by homozygosity induced by small population size. This inbreeding depression explanation is unlikely for three reasons. First, if the results were due to a depressed vigor in derived males, derived males should have as much trouble in mating with derived females as with ancestral females. There is no indication of this in Ahearn's data; rather, derived males only have difficulty in mating with ancestral females. Second, the experimental basis for the inbreeding depression explanation given by Charlesworth *et al.* (*21*) rests entirely on work done in *Drosophila* populations that were either intensely inbred for many generations or were maintained with very small population sizes for many generations. The experimental protocol used to test the Kaneshiro hypothesis involves a bottleneck or founding event followed by a rapid expansion of population size.

As explained by Templeton (*40*), the genetic consequences of a founder-flush event are not at all comparable to those associated with prolonged inbreeding or small population sizes. In particular, little genetic variation is lost during a founder-flush event (and hence, little increase in homozygosity), whereas considerable genetic variation is lost under prolonged small population sizes. Moreover, we know of no experimental work showing that founder-flush events can induce inbreeding depressions in *Drosophila*, and none were cited by Charlesworth *et al.* (*21*). Finally, as mentioned above, the experimental work of Powell (*46*) supported the Kaneshiro hypothesis. In a set of follow-up experiments, Powell and Morton (*50*) directly examined the impact of inbreeding upon mating behavior in *D. pseudoobscura*. Their results indicated that inbreeding induced no reproductive isolation whatsoever, and, therefore, of course, no mating asymmetries; a result in great contrast to what occurred under founder-flush cycles.

In summary, the available data satisfying the contraints made explicit by Kaneshiro (*16, 17*) support the Kaneshiro model. It is therefore appropriate to examine the proposed alternative and critiques.

Competing Perspectives

Watanabe and Kawanishi (*18*) analyzed data of the same form as that used by Kaneshiro, from "choosing female" tests (*31*) in the two species groups *D. melanogaster* and *D. virilis*. In an attempt to accommodate their behavioral data to prevailing ideas on the phylogenetics of these species groups, they propose that "it is the females of the new species which do not mate with the males of the ancestral species." They further assume that their data are compatible with a test of the Kaneshiro model and that, in testing it, they refute it. They thus overlook several crucial points.

First, there is an ambiguity in the behavioral data concerning *D. melanogaster* and its sibling species *D. simulans*. Watanabe and Kawanishi (*18*) present data from "choosing female" experiments that show *simulans* males are more likely to mate with *melanogaster* females than *melanogaster* males are with *simulans* females. This asymmetry, they argue, is inconsistent with the Kaneshiro hypothesis. Yet elsewhere Kawanishi and Watanabe (*51*) report on studies designed to elucidate the genetics of the mating preferences in these two species. In particular, they concluded that male mating preferences were controlled by a gene or genes on the X chromosome and that the degree of discrimination associated with the *melanogaster* X was weaker than that associated with the *simulans* X—an asymmetry that Watanabe and Kawanishi (*18*) say is consistent with the Kaneshiro hypothesis. Thus, the asymmetry with respect to "male choice" reported in Watanabe and Kawanishi (*18*) is reversed with respect to the "male mating discriminative abilities" reported in Kawanishi and Watanabe (*51*). Not resolving the relative importance of these conflicting asymmetries compounds the problem.

Second, the biogeography of these species groups is well known (*52–55*). The geological processes of formation and the ages of the relevant island masses are also well known (*56–58*). There is nothing in any of these data that indicates that founder events of the type required by the Kaneshiro model have been significant factors in the evolution of these groups. This point is critical in judging the relevance of the data presented by Watanabe and Kawanishi to the Kaneshiro hypothesis. There are many mechanisms by which reproductive isolation may evolve, and each has its own set of associated genetic and evolutionary implications (*40, 59*). Kaneshiro (*16, 17*) was careful to apply his hypothesis only to speciation processes in which founder events are strongly implicated. Kaneshiro never applied his hypothesis to speciation events not associated with founder events. Consequently, the Kaneshiro hypothesis can only be tested with data from species in which founder-event associated genetic change has occurred. As mentioned above, there is no evidence that founder events have been important to speciation in the species examined by Watanabe and Kawanishi and therefore both of their sets of data (*18, 51*) are inappropriate for testing the Kaneshiro hypothesis.

Third, an issue related to our second point above is the meaning of the words "ancestral" and "derived" as used by Kaneshiro (*16, 17*) in contrast to that used by Watanabe and Kawanishi (*18*). In Kaneshiro's model, ancestral and derived refer to species (or populations) separated by founder events such that the founders are "derived" from an "ancestral" population that is unaltered by subsequent severe bottleneck events. The new species arising from the founder population is the "derived" species. However, Watanabe and Kawanishi (*18*) use the words "ancestral" and "derived" to refer to karyotypic states in an intrinsically bidirectional chromosomal phylogeny. In these phylogenies, putatively ancestral inversions in present populations do not imply direct ancestral or founder relationships with extant populations that appear to be chromosomally derived. Chromosome evolution obviously can occur in *Drosophila* in the absence of founder events; and indeed founder-event associated speciation in the genus *Drosophila* seems to make chromosome evolution even more unlikely than in speciation not associated with founder events (*40*). Consequently, the "ancestral" and "derived" species of Watanabe and Kawanishi (*18*) do not bear any relationship to the ancestral and derived species of the Kaneshiro model. This disparity is further exacerbated when Watanabe and Kawanishi overlook the presence of chromosomal intermediates between tested populations (as many as four, for example, among the *D. virilis* phylad). We repeat that in the Kaneshiro formulation the ancestral species has undergone no founder-mediated speciation events during the time period in which the "derived" species was formed through a founder event, and the "derived" species has experienced only the one founder-associated speciation event.

It should be pointed out that the speciation model proposed by Watanabe and Kawanishi is a sympatric one. The concept of sympatric speciation has long been the subject of debate (*60, 61*) unresolved because of the difficulty in conceiving a mechanism that would provide the necessary limitations on gene flow. Although some possible mechanisms have been proposed (*61*), Watanabe and Kawanishi have not proposed a mechanism that could justify their model; thus it is difficult to make any testable predictions based on it; unlike the Kaneshiro hypothesis, theirs is unfalsifiable. Such propositions have been discussed at length elsewhere (*62, 63*).

A set of experiments performed by Markow (*20*) dealt with lines of *D. melanogaster* in which sexual isolation arose in conjunction with divergent artificial selection pressures in large subpopulations with no founder or bottleneck events. Consequently, Markow's experimental model of divergence does not correspond to speciation by a founder event, but rather to speciation via adaptive divergence [in the terminology of Templeton (*40*)]. Once again, we reiterate that the Kaneshiro hypothesis makes no predictions for this mode of speciation. Second, "derived" in Markow (*20*) means derived by an artificial selection experiment and does not refer to derivation through a founder event. Consequently, her "ancestral" and "derived" populations do not correspond to ancestral and derived populations in the framework of the Kaneshiro model. Markow (*20*) allows that the Kaneshiro hypothesis might hold true under some conditions, but her experimental design does not satisfy the conditions made explicit by Kaneshiro (*16*, p. 743). Consequently, her results cannot legitimately lead to a rejection of the Kaneshiro hypothesis.

Wasserman and Koepfer (*19*) used data (*64*) on character displacement for sexual isolation between *D. mojavensis* and *D. arizonensis* to examine both the Kaneshiro and the Watanabe and Kawanishi models. The distributions of these species are known (*65–67*) and their ecologies have been described (*68–70*). Johnson (*70*) concluded that the Gulf of California was a barrier critical to the differentiation of these species, and the geology of this region is complex and still subject to some controversy (*71, 72*) particularly with regard to the dating of Plio-Pleistocene events (*73*).

Wasserman and Koepfer examined asymmetrical patterns of courtship behavior among populations of *D. arizonensis* from the mainland and *D. mojavensis* from both the mainland and Baja California. Assuming their data to be

Table 1. Mate preference data from six populations of *D. silvestris*; *I*, isolation index of Stalker (*81*); $I = (H_0 - H_e)/(H_0 + H_e)$ where H_0 represents homogamic matings, and H_e represents heterogamic matings. Values range from +1 (complete isolation) to −1 (complete heterogamy). *C*, represents test of significance. At a 5 percent level of significance, H_0 of random mating is not rejected if $-1.96 < C < +1.96$ (*80*). H, Hualalai; Ka, Kahuku; Ko, Kohala; Pa, Pauahi; Pi, Piihonua; O, Olaa. [Courtesy of *Pacific Science*]

Matings		*N*	Frequency of matings		*I*	*C*
♂	♀ ♀		Homogamic	Heterogamic		
H	H, Pa*	36	0.31	0.69	−0.38	−2.28
Pa	Pa, H	35	0.80	0.20	+0.60	+3.55
H	H, Ka	35	0.14	0.86	−0.72	−4.26
Ka	Ka, H	33	0.82	0.18	+0.64	+3.68
Pa	Pa, Ka	33	0.30	0.70	−0.40	−2.30
Ka	Ka, Pa	37	0.86	0.14	+0.72	+4.38
H	H, Ko	39	0.46	0.54	−0.08	−0.50
Ko	Ko, H	35	0.71	0.29	+0.42	+2.48
Ko	Ko, Pi	51	0.47	0.53	−0.06	−0.43
Pi	Pi, Ko	41	0.59	0.41	+0.18	+1.15
Ko	Ko, O	40	0.23	0.77	−0.54	−3.42
O	O, Ko	42	0.69	0.31	+0.38	+2.46
Pi	Pi, O	38	0.29	0.71	−0.42	−2.59
O	O, Pi	37	0.68	0.32	+0.36	+2.19

compatible with tests of both models they concluded that neither model led to a satisfactory explanation of their data and stated "that each model works under certain conditions but fails under others." In the absence of any proposed mechanism for the model of Watanabe and Kawanishi it is difficult to predict under what conditions it might be expected to work. But an examination of the data of Wasserman and Koepfer and background information on the species involved demonstrates that their data are not applicable to any test of the Kaneshiro model because they do not satisfy the critical constraints outside which the model would not be expected to function.

Investigating the evolution of the *D. mulleri* subgroup on cytological grounds, Wasserman (*7*) wrote, "The distribution of . . . gene rearrangements among the twelve species cannot be interpreted on the basis of the splitting of populations and subsequent divergence. One can assume that there has been a series of cycles in which populations became isolated, diverged as to gene orders, and then hybridized. Wasserman (1954) showed that three such secondary hybridizations could account for the cytological constitutions of the six species examined at that time: *arizonensis*, *mojavensis*," and four others. Although not accepting this as an ultimately sufficient explanation, Wasserman does accept (*7*) that there must have been at least two chromosomal intermediates between these two species. In view of these complex relationships between the two species involving several episodes of gene flow subsequent to the initial divergence, and no evidence for any founder events, the data of Wasserman and Koepfer are not at all applicable to any test of the Kaneshiro model. Therefore, the only possible test of the model with either of the two species might have been a test between the Cabo San Lucas (Baja) and mainland populations of *D. arizonensis*, a test that unfortunately was not performed.

In a general criticism of models that attempt to derive phylogenetic information from asymmetries of courtship success, Moodie (*74*) has said that they "ignore the fact that ethological isolating mechanisms may involve characters which are subject not only to reinforcing selection for reproductive isolation but in addition to other selective pressures unrelated to courtship and mate preference." He cites data from two stickleback (*Gasterosteus*) populations in the Queen Charlotte Islands where a purportedly "derived" population (Black) contains males that are more successful in courtship than those from the population (var. *leiurus*) that Moodie calls "ancestral" for the purposes of his argument. This is the opposite of what would be predicted by the Kaneshiro model. Moreover, Moodie invokes a discussion of "reinforcing selection for reproductive isolation" as if it were an integral part of the Kaneshiro model. In that the Kaneshiro model deals with allopatric speciation, it specifically excludes reinforcement. The mechanism proposed by Kaneshiro is a logical consequence of founder events, and their accompanying stochastic effects, which have been expanded upon by Templeton (*40*, *59*) and Lande (*33*) and which we have discussed above. It does not pertain to reinforcement, and, Watanabe and Kawanishi (*18*) argue that reinforcement would destroy the patterns predicted by the Kaneshiro model. In addition, Moodie provides a counterexample with two populations that are, by his own data (*75*, *76*) parapatric in distribution and occasionally sympatric. Not only is there no evidence for any founder events of the sort specified by Kaneshiro but we reiterate that the Kaneshiro model was inferred from and applied exclusively to allopatric populations. Parapatry or sympatry could easily violate the constraint of "little or no subsequent gene flow" that is fundamental to the Kaneshiro model. Finally, the Kaneshiro model requires "ancestral" and "derived" populations related through a founder event. Although Moodie (*74*) feels confident that the Black population is "derived," he admits "the ancestral species is uncertain." However, he then proceeds in testing the Kaneshiro model by assuming that *leiurus* is "ancestral." Elsewhere (*76*) Moodie states that "to suggest the Black stickleback evolved from *leiurus*, *trachurus*, or a predecessor of both would be gross speculation. A comparison of the similarities and differences among [them] leads to the conclusion that the Black stickleback is most like *trachurus*." And yet no tests are reported involving this third species, nor is it even mentioned in the critique in which Moodie assumes that the more distantly related var. *leiurus* population is ancestral (*74*).

Applications and Conclusions

The general applicability of the Kaneshiro model depends on whether it should be so narrowly defined as to be of limited use, or whether it is general enough to apply to previously unresolvable situations. In our opinion, the latter may be the more accurate view, and we urge consideration of several applications (both real and potential) that will serve to illustrate.

Drosophila silvestris is found in the high altitude mesic rain forests of the island of Hawaii. The present land area of this island was formed by a series of eruptions of five major volcanoes. In order of decreasing age they are Kohala, Mauna Kea, Hualalai, Mauna Loa, and Kilauea (Fig. 2). The rain forests are not continuously distributed, nor are the host plants within the rain forests, and these form "islands" of *Drosophila* habitat [see (*23*, *77*)] on the separate volcanoes. On the basis of these geological data alone, one might predict that *Drosophila* colonization would probably have followed a similar pattern, and early research was based on this tentative assumption. However, Carson and Bryant (*78*) reported data that called this assumption into question. They examined populations of *D. silvestris* for variation in a secondary sexual characteristic, large modified bristles (cilia) on the tibiae of males of this species. These cilia are very important at a critical point in the complex courtship ritual of these flies (*26*), and the variation reported in this character indicates that the trait is still subject to natural selection and suggests incipient speciation.

In related species on adjacent, older islands, males have only two rows of tibial bristles. Males of *D. silvestris* from the south and west side of the Big Island (Hualalai and Mauna Loa, the volcanoes intermediate in age) share this ancestral characteristic. Those from the north and east side of the island, however (Kohala, Mauna Kea, and Kilauea, including both the oldest and youngest volcanoes), show variation for cilia number in a third, intermediate row of tibial bristles. On the basis of these bristle data alone (*78, 79*), we can make tentative inferences about the relationships of the windward (north and east) populations, but the situation in the leeward (south and west) side of the island is unresolvable. Kaneshiro and Kurihara (*80*) studied the mate preference behavior of these populations in order to resolve these relationships, and they achieved enlightening results.

Kaneshiro and Kurihara gave females from each of these populations a choice between males of their own and one foreign population. Results of these trio tests were then analyzed according to the method of Stalker (*81*), which permits a quantification of the degree of ethological isolation (Table 1). It is important that isolation coefficients are thus calculated for each individual test, rather than for pooled data from reciprocal tests to produce a joint isolation index, as some researchers have done (*45, 82*). Calculation of joint isolation indices can mask a substantial degree of isolation if it is asymmetrical, and thus obscure important information. These mate preference data led Kaneshiro and Kurihara to conclude "that the population of Hualalai is the oldest population, and from there two separate lineages gave rise to the remaining five populations (tested). One lineage provided progenitors for the south and west populaions, that is, at Pauahi and Kahuku. The econd lineage involved an introduction from Hualalai to the Kohala Mountains and subsequent colonizations of the Piihonua and Olaa populations" (Fig. 2). Spieth has suggested (*26*) that the prevailing wind patterns over the archipelago are more likely to result in propagules landing on Hualalai than the older Kohalas. This is also in accord with other biogeographical data (*83*).

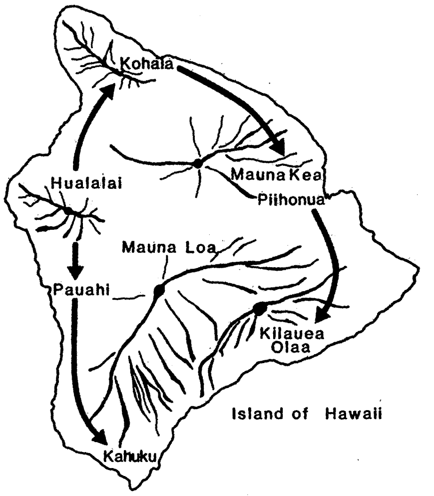

Fig. 2. Probable colonization route for *Drosophila silvestris* on Hawaii (*80*). [Courtesy of *Pacific Science*]

While *D. silvestris* is the only species to have been extensively studied with these methods to date, there is good reason to expect they might be profitably applied to other of the Hawaiian picture-winged species that have so far been incompletely understood, notably *D. crucigera* (*84*). However, there is no reason to limit future studies to Hawaiian *Drosophila*. For example, the species *D. mercatorum* is subdivided into two subspecies, *D. m. mercatorum* and *D. m. pararepleta*. The subspecies *pararepleta* is found in South America east of the Andes, while the *mercatorum* subspecies is found west of the Andes, Central and North America, and, more recently, has been globally distributed by human activities. The *pararepleta* subspecies has extensive inversion polymorphism, whereas the *mercatorum* subspecies is almost chromosomally monomorphic (*85*). The biogeographical and cytogenetic evidence implies that this species originated in the lowlands east of the Andes and that a small number of individuals crossed the Andes to establish the chromosomally monomorphic subspecies *D. m. mercatorum*, which subsequently spread to the north. Obviously, the Kaneshiro hypothesis can be used to test the validity of this reconstruction, and we intend to do so once the appropriate stocks can be obtained.

The model need not be restricted to *Drosophila* populations. In view of the constraints articulated by Kaneshiro it seems that the model could be applied to almost any situation where populations are separated by founder events although success will vary with the precise nature of such events as well as the genetic architecture of the populations involved (*40*). Many insular populations of a variety of organisms should be susceptible to these sorts of analyses, as well as populations of continental organisms that are somewhat insular in their distributions. Certain fossorial rodents may lend themselves well to such analyses (*86, 87*), and some workers have already noted this potential (*87*). Indeed, the range of possible applications, although somewhat restricted by the critical constraints, seems to be broad and far reaching.

Recently, there has been a growing awareness that speciation is not a monolithic process, but rather a collection of variable processes yielding diverse outcomes (*40, 59*). Accordingly, universal truths concerning speciation should not be expected. This is not to say that predictions cannot be made, only that predictions will be valid under a limited range of conditions. In this sense, the studies of Watanabe and Kawanishi (*18*), Wasserman and Koepfer (*19*), and Markow (*20*) do not disprove the Kaneshiro hypothesis; rather, they refine it by showing the conditions sufficient for the Kaneshiro hypothesis (*16, 17*) also appear to be necessary. The Kaneshiro hypothesis has been extensively tested. A number of experimental and natural situations which satisfy its constraints all yield the expected mating asymmetries whereas a number of experimental and natural situations which violate its conditions can yield discordant results. All these results are compatible with the Kaneshiro hypothesis. Application of this model in the future should expand our ability to resolve phylogenetic relationships.

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The Nature of Technological Hazard

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Summary. Technological hazards are evaluated in terms of quantitatively expressed physical, biological, and social descriptors. For each hazard a profile is constructed that considerably extends the conventional definition of risk. The profile, which is termed hazardousness, was understood in pilot experiments on perception and appeared to capture a large fraction of lay people's concern with hazard. It also suggests an orderly method for establishing priorities for the management of hazards.

Each year the hazards associated with technology lead to illness and death, as well as varying environmental, social, and economic impacts; these effects correspond to a significant fraction of the gross national product (*1, 2*). Despite the burden imposed by technological hazards and the broad regulatory effort devoted to their control, there have been few studies comparing the nature of technological hazards in terms of generic characteristics. Most investigators have produced case studies (*3*), comparative risk assessments of alternative technologies (*4, 5*), comparative lists of hazard consequences (*6, 7*), or comparative costs of reducing loss (*8–10*).

A first step in ordering the domain of hazards should be classification. Today technological hazards are classified by the source (automotive emissions), use (medical x-rays), potential for harm (explosions), population exposed (asbestos workers), environmental pathways (air pollution), or varied consequences (cancer, property loss). One scheme is chosen, usually as a function of historical or professional choice and the relevant regulatory organizations, even though most technological hazards fall into several categories. For example, a specific chemical may be a toxic substance, a consumer product, an air or land pollutant, a threat to worker health, or a prescription drug. Indeed, a major achievement has been the cross-listing of several of these domains of hazardous substances by their environmental pathways (*11*).

We have sought to identify common differentiating characteristics of technological hazards in order to simplify analysis and management of them. Technological hazards may be thought of a involving potentially harmful releases energy and materials. We characterize the stages of hazard causation by