

Founder effects and silvereyes

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Patterns of variation in nature have played a large role in the development of explanations for biological richness at the species level. One such influential pattern has been the morphological distinctiveness of small populations on islands at the periphery of a large continental land mass (1). If the island differs from the mainland in habitat or composition of the biological community, the morphological differences often can be explained in terms of adaptation by natural selection (2). But, if the environments are more or less the same, then an explanation has to be sought elsewhere. Fifty years ago, Ernst Mayr (3) suggested that the key to island evolution lies in the circumstances and immediate consequences of colonization. The model he proposed, called the “founder effects model,” postulated major changes in the genetic constitution of a newly established population that were set in motion by the reduced genetic variation carried by the few colonizing individuals in the founding event (4).

The model was a bold explanation, because nothing was known of the genetic basis of the morphological traits. It has been challenged repeatedly on theoretical grounds (refs. 5–7; but see refs. 8 and 9) and has fared little better empirically (10). The preferred method of testing has involved creating in the laboratory new populations with a few individuals of small organisms with short generation times (11–13). These experimental studies have yielded some (11, 13) but generally little or no support (10, 12). Adopting a different tactic, Sonya Clegg *et al.* (14) have returned to the source of the problem, bird populations on islands, and in this issue of PNAS, they report the results of some novel tests.

Silvereye is not the name of a *Drosophila* mutant but the name of a small, warbler-like bird that has colonized several islands from the mainland of Australia. Four colonizations occurred in historical times—from 1830 onwards—

and can be dated precisely. Three others took place much earlier, at times that have been estimated at 3,000–4,000 years for the most recent and more than a million years for the most ancient. Thus, the sequence of colonizations has been reliably established; taking advantage of it, Clegg *et al.* (14) have asked whether the genetic variation both within and between populations reflect substantial changes at the time of colonization, or whether changes have simply accumulated gradually over time. How could one distinguish between them?

It can be done as follows. After the establishment of a new population, alleles at selectively neutral loci will be lost by random genetic drift and gained by mutation. Drift can be expected to predominate in small populations, at least for some time until a new drift-mutation equilibrium is attained, and populations will gradually diverge. If drift and mutation are all that happen, the population does not rapidly increase in size, and gene flow from neighboring populations is negligible or nonexistent, then the magnitude of within- and between-population changes will be a function of time. In contrast, if

founder events have occurred, the effects may be so strong as to overwhelm the effects of long-term drift yet vary among populations in a manner unrelated to their

time of origin. Therefore, against the background of long-term drift, a signal of founder effects may stand out as sharp reductions in genetic variation within populations and large differences between neighboring populations. This pattern is what Clegg *et al.* (14) looked for.

They chose to work with allelic variation at six microsatellite loci because the alleles are likely to be selectively neutral (unless the loci happen to be closely linked to loci subject to selection). Their analyses failed to detect the signal of founder effects at any of the steps in the sequence of recent colonizations. Nevertheless, they found that allelic diversity

gradually declined with repeated colonizations of new islands. The individual reductions are small, but the cumulative changes are large. From first to last in the sequence of recent colonizations, the mean number of alleles per locus dropped by almost half. Because the last population in the sequence is the youngest, one cannot explain this result by long-term genetic drift. Instead, the pattern seems to reflect a small loss of alleles at each colonization, although hardly on the scale envisaged in the original formulation of the founder effects model; it is certainly not enough to kick-start a genetic revolution (1, 3).

Expected heterozygosity does not follow this pattern, as would be expected because it is less sensitive than allelic diversity to sampling effects (15). It remains roughly the same among the new populations regardless of their age but declines sharply as one proceeds from young to old ones, which is inconsistent with the pattern the authors expected from the founder effects model (3). Age-dependence hints at multiple bottlenecks over time. An additional factor (not analyzed in the paper) that might contribute to this pattern through its effect on demography and long-term effective population size is island size. Regardless of these causes, the conclusion drawn by the authors is that the patterns of variation at microsatellite loci principally reflect the effects of long-term genetic drift. Consistent with this conclusion, the oldest populations differ genetically the most from the presumed original source, and the newest populations differ the least. Other studies of bird populations have drawn similar conclusions (16–19) without being able to test for founder effects.

An important feature of this paper is the use of a model to supplement the empirical analysis by simulating colonization with and without genetic bottlenecks. By using a Bayesian approach, the authors sought to determine the sizes of the effective founder flocks, i.e., the number of individuals who bred. If the colonizing flocks were small, then founder effects may

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have been important. To estimate the sizes, they needed data on the known sizes of migrating flocks, generation times, and effective population sizes. These data are available from a detailed study on Heron Island initiated three decades ago by Jiro Kikkawa, one of the authors. Finally, they estimated mutation rates. The results indicate that one of the islands (Norfolk Island) may have been colonized by a couple of dozen silvereyes, but three other colonizations involved a minimum of 150–200 individuals. With effective numbers of this size, there is little reason to invoke founder effects. In fact, an exercise in fitting models to data showed the founder effects model (with a bottleneck) to be better than the gradual drift model (without a bottleneck) in only one (Norfolk Island) of four comparisons with the ultimate source population. None of the differences were statistically significant, however. The important point is that large numbers of colonists are identified here as the reason why founder effects did not occur, except perhaps on Norfolk Island.

The estimate of founding flock size is only the second of its kind. Vincek *et al.* (20) modeled the colonization of the Galápagos archipelago by ancestors of modern Darwin's finches. They used data from class II genes of the Mhc complex and alternative models of genetic bottlenecks to arrive at the conclusion that at least 30 individuals and probably many more founded the initial effective breeding population; in other words, the flock was large. These numbers are surprisingly high for the colonization of an archipelago almost 1,000 km from the mainland of South America, in view of the odds against such establishment. Consider, for example, the ship *Mayflower* and the founding of a colony at Plymouth Rock, Massachusetts in the United States. Approximately 100 pilgrims and “strangers” sailed from Plymouth, UK on September 6, 1620. One died at sea, some died shortly after arriving at the new continent less than 10 weeks later, and many more died in the first winter, with the result that out of an initial 27 women and girls, only 12 were alive the following spring (21). For bird populations, there is an additional loss in the failure of most of the breeders to contribute a single breeding offspring to the next generation (22). Thus, the effective founding size as calculated is likely to be a small fraction of

the original flock of would-be colonists, several hundred in the case of the silvereyes (14). The numbers estimated in both studies should not be taken literally; they could be too high and should be considered as a challenge to devise more realistic ways of reconstructing colonization.

It would be helpful to know from direct observations what happens in the founding of a new population. Colonizations of islands are rarely observed; they are usually known only after the event (16), and even more rarely are the genetic characteristics of the colonists studied. A good example comes from Hawaii. In 1967, 108 Laysan finches were translocated to a small island in the archipelago as a safeguard against the threat of extinction to the population on Laysan (19). Some dispersed naturally to nearby unoccupied islands, but less than half survived to breed. Sampling for DNA analysis began 20 years later. Comparisons with the source population on Laysan showed that alleles had been lost at nine microsatellite loci, and populations had diverged on a scale generally consistent with the results of the silvereye study.

The only direct study of natural colonization of an island has been done in the Galápagos. A breeding population of large ground finches was established on Daphne Major island by two females and three males in late 1982, and the fate of the population has been followed every year since (23). Only one male and one female produced offspring that formed the next generation, so the effective number of founders was just two. Several lessons can be drawn from this study that apply to attempts to infer the founding of populations hundreds, thousands, or even millions of years ago. First, the founders were unlikely to have been a random sample, genetically, from those that arrived on the island; they were unusually heterozygous. Second, inbreeding occurred, and loss of alleles was the consequence; this conforms to the founder effects model but is not specific to it. Third, the population increased in both numbers and allelic diversity at microsatellite loci, largely as a result of additional immigrants arriving and staying to breed. Finally, there was no major change in the assayed genetic or morphological characteristics of the popula-

tion in the first few generations following establishment and, therefore, no manifestation of founder effects.

The third lesson deserves special emphasis. The Plymouth Rock colony did not remain genetically impoverished because new waves of colonization took place, beginning in the year after its founding.

Why could not the same thing happen for the insular silvereye populations? After all, several new islands were colonized; therefore, the same island could have been invaded by immigrants several times. Perhaps, it is more parsimonious to invoke single-immigration events for each island, but I think this is likely to be wrong. If it is wrong, it carries an important implication: except for the most isolated islands, repeated immigration may obscure or obliterate any founder-effect changes that take place following the initial colonization. In the older populations on more isolated islands, founder effects may have been obscured by subsequent bottlenecks. Thus, rather than disposing of founder effects as unsupported, it would be more cautious to conclude the case is not proven (and indeed, it is very difficult to prove; refs. 7 and 10).

Despite the difficulties and lack of clear support from so many tests, the founder effects model and its derivatives (24, 25) continue to receive critical attention because of their relevance to two important research areas: speciation (8, 9, 25), and the conservation of small and potentially endangered populations (26, 27). For this broader context, it is necessary to consider crucial aspects of the model left out of the Clegg *et al.* paper (14) in their well justified focus on neutral loci. These are the generation of new epistatic gene complexes and natural selection (3, 28), together with the additional factor of sexual selection (25, 29, 30). The silvereyes could make an interesting contribution in this broader context. They have colonized some islands more than once, and the double or triple invasions have given rise to two or three species (1, 3), so it will be interesting to see what comes from a forthcoming analysis of their phenotypic divergence (14).

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