Figure 1. Change in East Asian Ancestry
The change in East Asian ancestry in Polynesians for autosomal and Y chromosome loci for 50 generations of male gene flow from Melanesians followed by 50 generations of female gene flow from East Asians.

Polynesians has been reduced by genetic drift, making arithmetic average of mtDNA and Y ancestry before genetic drift higher and, therefore, the difference between this average and the estimated autosomal ancestry of 0.79 smaller. Overall, though, it appears that an estimated male Melanesian gene flow of 0.0251 per generation for 50 generations and a subsequent estimated female East Asian gene flow of 0.0318 per generation for 50 generations, or the equivalent, are necessary to result in the observed pattern of ancestry over the autosomal, mtDNA, and Y chromosome markers.

Philip Hedrick[1,*]
[1]School of Life Sciences, Arizona State University, Tempe, AZ 95287, USA
*Correspondence: philip.hedrick@asu.edu

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ancestry over the first 50 generations and then an increase in autosomal East Asian ancestry and no change in Y ancestry over the second 50 generations. Note that the mtDNA East Asian ancestry is 1.0 throughout the whole scenario (essentially the same as the estimated 0.94).

Several models of gene flow can be excluded as possible explanations for the observed pattern of ancestry. First, if gene flow is not sex-specific, then it cannot result in the observed pattern. Second, male gene flow must start before female gene flow (female gene flow from East Asians can influence the East Asian autosomal population ancestry only after it has some Melanesian ancestry). If the female gene flow and the male gene flow start at the same time, then the total amount of female gene flow must be even larger than that given in the above example.

In a more realistic model, the patterns of gene flow may differ somewhat from the above scenario and could vary over generations and still provide similar results. For example, gene flow from the two sexes from the different source populations could overlap; that is, the female gene flow from East Asians could start while male gene flow continues from Melanesians. Also, female gene flow from East Asians may not actually be from outside females with high East Asian ancestry but could occur because females of high East Asian ancestry had higher reproductive success in the population for some social or cultural reasons. Finally, it is possible that the Y ancestry in the

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Reply to Hedrick

To the Editor: Hedrick[1] proposed an interesting model to explain our previous observation that most of the Polynesian autosomal and mitochondrial gene pool is of East Asian origin whereas most of the Polynesian Y chromosomes originate from Melanesia.[2,3] We and others have previously interpreted the discrepancy between the geographic origins of Polynesian Y chromosomes and mitochondrial DNA by an episode of genetic admixture between Austronesian migrants from East Asia arriving in Melanesia and local non-Austronesians from Melanesia, according to the Slow Boat from East Asia hypothesis.[4] This admixture most likely occurred in a sex-biased way mainly between East Asian women and Melanesian men.[2,3,5] Hedrick's model also postulates sex-biased admixture between East Asians and Melanesians, but in two

separate events following the arrival of Austronesians from East Asia: first, Melanesian male gene flow into the Austronesians; and subsequently, East Asian female gene flow into the admixed group.[1] However, given our current knowledge of Polynesian history, this model includes a number of highly unrealistic aspects. First, this model assumes a period of genetic admixture of 100 generations, translating to a time period of 2000–2500 years (assuming a generation time of 20–25 years). If the admixture only occurred in Melanesia, then Hedrick's scenario is unrealistic given that archaeological evidence suggests that the incoming Austronesian-speaking people arrived in Northern Island Melanesia approximately 3400 years ago[6] and stayed for only about a few hundred years before further migration eastward toward Polynesia began.[7] Second, Hedrick's model raises the question of why the sex-biased admixture behavior changed from male-dominated toward female-dominated (and why it occurred after 50 generations). It appears unrealistic to assume that only a few East Asian women arrived in Melanesia as part of the initial Austronesian expansion, thereby first providing the basis of Melanesian male-biased gene flow, and later many more East Asian women arrived in a second migration event, causing an East Asian female-driven gene flow. If Austronesians arrived in Melanesia as a more or less single migration (favored by archaeological and linguistic evidence), then something must have caused a switch in the sex-biased admixture behavior after Austronesians arrived from East Asia in Melanesia in order to fulfill the assumptions of this model. The only scenario that we can think of that might explain such an admixture shift would be a change from a matrilineal and matrilocal society (favoring male Melanesian admixture) toward a patrilineal, patrilocal society (favoring female admixture, although not necessarily favoring East Asian females, which is then problematic in explaining the genetic data). However, this scenario is not supported by the fact that most Oceanic-speaking societies in Melanesia, as well as Polynesia, are matrilineal or at least matricentric.[5,8] In addition, previous studies have suggested that the pre-Polynesian society was indeed matrilineal and matrilocal.[9] Third, Hedrick's model assumes that the East Asian female-dominated admixture into the Polynesian gene pool occurred for the last 50 generations, which means either that East Asian women continuously migrated to Melanesia but also to Polynesia for the last 50 generations (for which there is no evidence whatsoever) or that the mixed population migrated (as we indeed proposed earlier) but the sex-specific admixture behavior changed before or during the move (which is difficult to explain, as discussed above).

Despite these caveats, we nevertheless formally estimated whether the model suggested by Hedrick[1] would better explain the Polynesian genome-wide autosomal STR data we reported recently as compared with the model suggested by us.[3] We applied the Approximate Bayesian Computation (ABC) approach[10] used earlier[3] and estimated the posterior distributions of the parameters of the model proposed by Hedrick.[1] We computed 300,000 simulations using SIMCOAL 2.0[11] under the demographic scenario proposed by Hedrick[1] and the same summary statistics as reported by us earlier.[3] Prior distributions for the parameters of this alternative model were defined as follows: Ne of each population: logUniform(100, 40000), Ne ancestral population: logUniform(50, 5000), migration from East Asia to Polynesia: Uniform(0, 1), migration from Melanesia to Polynesia: Uniform(0, 1), time when the migration between Polynesia and Melanesia stops: logUniform(1, 1000), time split between East Asia and Polynesia: logUniform(1, 1000), time split between Melanesia and East Asia: logUniform(100, 100000). We then compared the posterior probability of Hedrick's model and of our previously suggested model by applying the approach suggested elsewhere[12] and implemented in the calmod package for R. We found that the genome-wide autosomal STR data we reported previously[3] provide small support for the model proposed by Hedrick ($p[Y = y \mid S = s] = 0.0003374238$) as compared with the model that we proposed earlier ($p[Y = y \mid S = s] = 0.9996626$).

However, Hedrick raises an interesting point in reconstructing the admixed population history of current Polynesians using genetic data. Although the previously proposed sex-biased admixture scenario between mostly East Asian women and mostly Melanesian men does explain why we see more Melanesian Y chromosomes together with more East Asian mtDNA in contemporary Polynesians,[2,5] it so far does not necessarily explain why the autosomal Melanesian component is so much smaller than the East Asian autosomal component in the Polynesian gene pool, as observed recently by us and others[3,13]. In contrast to the two-stage sex-biased admixture model proposed by Hedrick,[1] we suggest here an extension of the one-stage admixture model[2,4,5] between incoming Austronesians and local non-Austronesians in Melanesia, in which admixture was not only sex-biased but also biased in terms of the effective population size of the arriving Austronesian women and the local Melanesian men. According to this extended model, not only did Melanesian men preferentially mix with Austronesian women after the arrival of Austronesian-speaking East Asian migrants in Northern Island Melanesia, as we also described elsewhere,[14] but moreover, the total number of Melanesian men taking part in the initial genetic admixture process would have been considerably smaller than that of the participating East Asian women. This extended model can explain both the high East Asian component detected with genome-wide autosomal and mtDNA markers as well as the high Melanesian component identified by Y chromosome DNA markers. A scenario that would support this model is frequent polygyny of local Melanesians together with a matrilineal and matrilocal structure of the arriving Austronesians. Indeed, previous studies have shown that polygyny was very frequent in non-Austronesian societies of Melanesia at least before the influence of Christianity,[15,16] and pre-Polynesian Austronesians that initially

arrived in Melanesia are thought to have had a matrilocal and matrilineal society.[9] Thus, both factors are suggested to have played a role in the admixture procedure that occurred in Melanesia between early Austronesians and local non-Austronesians and gave rise to the people currently living on the many Pacific islands known as "Polynesia."

Manfred Kayser,[1,*] Oscar Lao,[1] and Mark Stoneking[2]
[1]Department of Forensic Molecular Biology, Erasmus University Medical Center Rotterdam, P.O. box 2040, 3000 CA Rotterdam, The Netherlands; [2]Department of Evolutionary Genetics, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany
*Correspondence: m.kayser@erasmusmc.nl

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The Crucial Role of Calibration in Molecular Date Estimates for the Peopling of the Americas

To the editor: In a recent study of Native American mitochondrial genomes, Fagundes et al.[1] claimed to have found molecular evidence that the colonization of the New World occurred well before the appearance of the Clovis cultural horizon (c. 12.6–13.2 thousand years [kyr] ago[2]). To support this claim, the authors performed a variety of phylogenetic analyses, including Bayesian date estimation and skyline-plot inference, using the software BEAST.[3] A very similar conclusion was reached in a recent study by Achilli et al.,[4] who estimated that each of the major Native American haplogroups coalesced around 19 kyr ago. A key failing of these studies, however, was an underappreciation of the importance of calibration choice. In fact, upon closer examination of the calibration techniques involved in the two studies, there appears to be little support for an American colonization event significantly antedating the earliest physical evidence of human occupation.[5,6]

Fagundes et al.[1] employed two approaches to calibrating their date estimates. The first, which was also used by Achilli et al.[4] in their study, assumed a global substitution rate of 1.26×10^{-8} subs/site/year, originally obtained by Mishmar et al.[7] with the use of a human-chimpanzee calibration at 6.5 Myr. The second method was to include a chimpanzee sequence in the phylogenetic analysis, again fixing the age of the human-chimpanzee split to 6.5 Myr. The date estimates produced under the two calibration methods were very similar, which is not surprising given that they were effectively based on the same calibration. However, using only a single calibration point makes date estimates sensitive to calibration choice, particularly