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LETTERS

The Whitehead Institute and MIT

We are writing to correct misinformation in Michelle Hoffman's 3 April article (News & Comment, p. 25) regarding the relationship between the Whitehead Institute and the Massachusetts Institute of Technology Department of Biology. Although the article mentions many of the extremely positive features of the Whitehead Institute, it also presents comments by a faculty member that suggest incorrectly that the success of the Whitehead has somehow prevented the recruiting of young people in other parts of the Department of Biology, that Whitehead labs attract most of the graduate students, and that the Whitehead faculty do little teaching. Nothing could be further from the truth. In fact, in the past 2 years we have recruited six superb young faculty, who will certainly continue the "stellar" tradition of the department. Moreover, faculty in the Whitehead, who constitute 25% of the department, have attracted 26% (30/115) of the graduate students over the past 4 years and teach in 54% (20/37) of the undergraduate and graduate courses. The Whitehead faculty also serve actively on departmental and MIT committees, participate in all phases of community life, and do wonderful science. The relationship between the Whitehead and MIT has been a great success, the department is lively and vigorous, and we and most other faculty view the Whitehead as a highly valued partner.

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Out of Africa: Honey Bee Hybrids

In their report "Hybridization between European and Africanized honey bees in the neotropical Yucatan peninsula" (19 July 1991, p. 309), Thomas E. Rinderer *et al.* suggest that the population of Africanized bees (*Apis mellifera scutellata*) in Central America will be "Europeanized" before it enters the United States. Three major problems with the study undermine this conclusion.

The most fundamental problem is that only apiary bees, originally derived from European subspecies, were examined by Rinderer *et al.* However, it is feral (wild) bee populations, not those in apiaries, that are expanding their range, moving into new territory, and causing Africanization of European apiaries. Despite hybridization between European and Africanized bees in apiaries, the feral population in neotropical regions of the Americas still retains a high frequency of African genetic markers, including characteristic mitochondrial DNA (mtDNA) haplotypes (*1–3*), allozyme frequencies (*4, 5*), and nuclear restriction fragment length polymorphisms (RFLPs) (6). Recent studies (*7, 8*) conducted in temperate, southern Argentina document a hybrid zone between essentially African populations (as assessed by morphometrics and mitochondrial genetic markers) to the north and European populations to the south.

A second and related problem with the report by Rinderer *et al.* is their interpretation of data about the apiary colonies with "opposite" mtDNA and morphometric characters (as shown in their table 1). The 163 colonies they sampled were classified by mitochondrial genotype (African or European) and by their morphological similarity to reference bee population samples. Their discriminant analysis showed evidence that hybridization, followed by backcrossing to the paternal population, is taking place in both directions: bees of European maternal ancestry are backcrossing to the African paternal population, and bees of African maternal ancestry are backcrossing to the European paternal population.

Rinderer *et al.* conclude that this leads to Europeanization of the expanding feral Africanized bee population as well. However, because no samples were taken from the feral population, this conclusion is unwarranted. Colonies with European mtDNA and African nuclear-encoded characters are the expected outcome when apiary queens of European ancestry mate with African or Africanized drones over several generations. Colonies with African mtDNA and European morphometric

traits are attributed by Rinderer *et al.* to usurpation of apiary colonies by feral African swarms, followed by backcrossing to European drones. This is a possibility, but few cases of usurpation have been documented (9). On the other hand, wild African swarms looking for new nest sites readily colonize empty hives, and beekeepers often collect wild swarms to add to their apiary stock (*10*). These are more likely avenues for entry of African mtDNA into apiary populations.

A third problem is that the data Rinderer *et al.* present give only a static "snapshot" of the genetic composition of apiary populations. However, the spread of Africanized bees is a dynamic process. To interpret the data of Rinderer *et al.*, one needs to know if the "snapshot" was taken early in the invasion process, midway, or after the expanding feral African populations had stabilized in the region. The European character of feral and apiary populations is expected to be more pronounced early in the invasion, while African characters should become more common later on.

Although several restriction enzymes reveal informative polymorphisms among the mitochondrial genomes of honey bee subspecies (*1–3, 11–14*) Rinderer *et al.* used just one restriction enzyme (Eco RI) to identify mtDNA types and state that "[t]wo restriction patterns resulting from digestion with Eco RI are associated with sub-Saharan *A. mellifera* and two patterns with European subspecies." However, the Eco RI restriction fragment patterns typical of sub-Saharan *A. m. scutellata* are also found in bees from North Africa and in parts of Spain, where the North African *A. m. intermissa* appears to have hybridized with the Spanish honey bee, *A. m. iberica* (*13, 14*). Spanish honey bees may have been imported to Mexico by early Spanish settlers, so in order to use RFLPs generated by Eco RI alone as a marker for sub-Saharan African mtDNA, it would be desirable to have surveyed the feral honey bee population before the arrival of Africanized bees for evidence of relict populations descended from Spanish bees. The mitochondrial genomes of *A. m. scutellata* and *A. m. intermissa* could be distinguished by digestion with additional restriction enzymes (*13, 14*).

The available data thus do not support the hypothesis that the African bees will become Europeanized by mating with European bees in Mexico before they reach temperate regions of the United States. It seems more likely that a hybrid zone will form in those parts of the United States where the climate is favorable to both types of bees, with Africanized bees predominating south of the hybrid zone and European bees predominating to the north.

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Response: Smith seems to agree with us that previously postulated (*1*) barriers to hybridization between European and African bees [discussed in Marcia Barinaga's News & Comment article of 2 November 1990 (p. 628)] do not exist. However, we certainly do not wish to give the impression that we are unconcerned by the prospect of the Africanization of honey bees in some parts of the United States. We do believe that these bees are likely to have a biological, economic, and social impact in the United States. However, we believe that beekeepers and regulators can reduce the undesirable effects of Africanized bees by manipulating the hybridization.

Smith's criticisms of our paper are based on the fact that we collected bees from apiaries, not from hollow trees or swarm traps. We did not find feral bees in the Yucatan, which suggests that the feral population was quite small when we visited in October 1989 (some 2 years after Africanized bees arrived in the area). Also we know of no documented difference between the population genetics of feral colonies and those of commercial apiaries in which beekeepers do not practice queen management.

Smith suggests that the feral Africanized population has migrated northward from Brazil, unaffected by its contact with European bees (*2*). Our study about hybridization in the Yucatan was not intended to address this hypothesis directly. An area where Africanized bees have been introduced recently, such as the Yucatan, is not a good place to test this hypothesis because it is not possible to tell whether the sampled bees (from traps, trees, or managed colonies) are from the invading population, the extant population, or recent hybrids. Two studies (*1, 2*) that sampled bees from areas

where Africanization occurred long ago reported low but detectable levels of European genomic and mitochondrial markers in neotropical honey bees. Recent studies that used more markers, different techniques, and larger sample sizes suggest higher levels of racial mixtures occur (3–6).

We disagree with Smith's interpretation of the paper by Sheppard *et al.* (5), of which some of us are co-authors, that the morphology of Africanized bees in northern Argentina shows them to be "essentially African." To the contrary, both isozyme frequencies and morphology indicate that the bees have biracial origins (5). The American neotropical area that has had Africanized bees for the longest time is São Paulo, Brazil. A recent study of bees in this area (6) found appreciable levels of apparently stable European morphology and high levels of European mitochondrial polymorphisms in the Africanized population. One would expect to find higher population frequencies of selectively neutral African, rather than European, mitotypes because Africanized bees have higher reproductive rates.

The restriction enzyme we used does not distinguish some mitotypes that have been reported recently from some Spanish bee specimens (7). Therefore, as with earlier studies (*1*, *2*), we may have overestimated the introgression of African mitotypes into the Yucatan. This does not alter our basic conclusions: (i) there are no biological barriers to hybridization and (ii) requeening and drone production should help beekeepers mitigate problems caused by Africanized bees.

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