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Hybridization between European and Africanized honeybees (*Apis mellifera* L.) in tropical Yucatan, Mexico. I. Morphometric changes in feral and managed colonies

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Abstract – Morphometrics of feral and managed honeybee colonies collected from tropical Yucatan, Mexico between 1986 and 1996, were analysed for changes in body size as an indicator of gene exchange between them. Twelve morphometric characters were analysed at the univariate level (ANOVA of single morphometric characters across years) and with a multivariate technique (principal component analysis, PCA). The results from both types of approach give evidence for: 1) an initial increase in body size of feral honeybees due to a flow of genes from the large resident European population; 2) a subsequent constant reduction in body size in both types of honeybees as Africanization has progressed probably due to a disappearance of colonies with European morphometrics in both populations; and 3) the existence of European genes in both the managed and feral populations of Yucatecan honeybees 10 years after the report of the first Africanized swarm in the area. Bi-directional gene flow resulting in a convergence in quantitative traits towards an intermediate body size seems to better explain the morphological changes that have occurred between managed and feral populations of honeybees during the process of Africanization in Yucatan. However, the persistence of European genes in both populations across time needs to be further studied.

***Apis mellifera* / Africanized honeybee / morphometrics / multivariate analysis / hybridization / Mexico**

1. INTRODUCTION

African honeybees (*Apis mellifera scutellata* Lepeletier) were first introduced in Brazil in 1956 for experimental purposes. After an accidental release, 26 African colonies swarmed and started interbreeding to an unknown extent with resident European honeybees (*Apis mellifera* L.) in apiaries [14, 33]; Sm. The resulting offspring, called Africanized honeybees, started a rapid spread throughout the Neotropics rapidly

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displacing European honeybees from apiaries and establishing feral populations [25].

Africanized honeybees were first reported in the tropical state of Yucatan, Mexico in September 1987 [2]. Initial predictions suggested a rapid takeover of apiaries and a collapse of local beekeeping as in other areas of tropical America. However, recent data suggested that there has not been either a complete and rapid takeover of Yucatecan apiaries by Africanized honeybees or a significant decrease in honey production in the state [23].

The genetic relationship of feral Africanized honeybees and managed European honeybees during the process of Africanization is still a matter of debate. Few long-term studies have been conducted on resident populations of honeybees during the process of Africanization [3, 23, 31]. Moreover, studies on the Africanization process have mainly followed changes of either managed or feral colonies separately. Since no long term study has been conducted on the changes that occur in both types of colonies at the same time it has been difficult to understand the genetic relationships between them [33].

Africanized honeybees have a smaller size compared to European honeybees and differences between their morphometric variables can be used to accurately classify them [7, 8, 27]. Honeybee morphometric characters are reported to be polygenic and nuclear [4, 21]. They have high heritabilities and are therefore suitable to study the process of Africanization, especially when combined in multivariate analyses [20].

Multivariate analyses have been used extensively when analysing patterns of hybridization [9, 19, 39]. Principal component analysis (PCA) is a multivariate analysis useful in elucidating relationships among variables (characters) measured on individuals when no a priori patterns or tendencies can be suggested or are suspected for different taxa [24]. PCA identifies a relatively small number of components (also called factors) that can be used to represent relationships among sets of many variables [38, 39]. An additional advantage of PCA is that it can be used to determine the most important size and shape components which separate individuals [13, 35, 36] and permits one to visualise groupings of these individuals by plotting pairs of scores for each individual in a dimensional space [1, 5, 13, 38].

In this paper, data collected on feral and managed populations of honeybees from Yucatan were analysed by means of univariate and multivariate techniques to answer the following questions. 1) Is there morphometric evidence of Africanization in Yucatan being a process of genetic admixture between Africanized and European honeybees? 2) Is there evidence of the high density of managed European colonies influencing the genetic make-up of the feral population? 3) Is there a persistence of European morphometric characters in the Africanized feral population? These honeybee types interbreed but the extent of their hybridization has not been well documented for Yucatan.

2. MATERIALS AND METHODS

2.1. Collection of honeybee samples

Samples of honeybees were collected from feral and managed colonies in the state of Yucatan, Mexico, in February and March every year, between 1992 and 1996. Samples from managed colonies were collected in the central and southern parts of the state in 1986 and 1987 before the report of the first Africanized swarm in the Yucatan Peninsula. Forty-five samples from feral colonies were also collected in 1988. The number of colonies sampled per year and their origin (managed or feral) are presented in *table I*.

In every locality, samples of honeybees included an average of 50 young worker honeybees collected from one colony. The honeybees were preserved in plastic jars (30 mL) containing ethanol (70 %).

2.2. Sample preparation and measurement

From each sample in ethanol, ten workers were chosen randomly and dissected. Four body parts were chosen for measurement: right forewing, right hindwing, right hindleg and third abdominal sternum (S3). Subsequently, the parts were placed onto glass photographic slide mounts. Twelve morphometric characters related to lengths and widths of the structures were measured on each worker bee. These characters are known to be highly correlated to general body size [6]. The list of morphometric characters used in this study is presented in *table II*.

Samples were measured using an inverted microscope and a digitizer Tablet. Lengths and widths of characters were calculated by means of the software AFUSDA7 (W.L. Rubink, unpublished).

2.3. Univariate comparison of morphometric characters and principal component analysis of feral and managed honeybees

An assumption for this part of the study was that the Yucatecan feral population originally comprised Africanized colonies and the Yucatecan managed population originally comprised European colonies (European colonies have never built up a feral population in the Yucatan Peninsula). The speed of morphological changes towards a European or Africanized type of bee in the Yucatecan populations is not clear.

Changes in body size were used as an indication of genetic flow between both populations throughout the 10 year study. The morphometric data collected in section 2 were used in annual comparisons between managed and feral colonies of honeybees. Means and standard errors were calculated for each of 12 morphometric characters per population (feral or managed) per year. A comparison of single morphometric data amongst feral and managed groups across years was performed by means of ANOVA using the SAS statistical package.

Changes in size of two of the most important characters for classification of colonies, namely WL and FEL [6, 36], were visualized by plotting the mean values of each character across the years of study for both feral and managed colonies.

Linear regression analyses of the mean values for WL and FEL against years were used to have an indication of the speed of changes in both

Table I. Number of feral and managed colonies of honeybees sampled in the state of Yucatan during the 10 years of the study.

Year	Managed	Feral	Total
1986 and 1987	85	not sampled	85
1988	not sampled	45	45
1991	283	not sampled	283
1992	289	61	350
1993	300	63	363
1994	306	65	371
1996	283	30	313
Total	1 546	264	1 810

Table II. List of morphometric characters measured on worker honeybees. Within brackets are presented abbreviations used in the text and other tables.

1. Forewing length (WL)
2. Forewing width (WW)
3. Hindwing length (HWL)
4. Hindwing width (HWW)
5. Femur length on third leg (FEL)
6. Tibia length on third leg (TIL)
7. Basitarsus length on third leg (TAL)
8. Basitarsus width on third leg (TAW)
9. Length of sternum 3 (STL)
10. Length of wax mirror on S3 (WML)
11. Width of wax mirror on S3 (WMW)
12. Distance between wax mirrors on S3 (WMD)

populations. This approach could provide support for a general pattern of morphometric changes in both types of honeybee.

Additionally, changes in body size were analysed at the multivariate level. PCA was selected for this part of the study since the interest was to know the variability in the samples, assuming no previous information about group structure. For all PCAs, the mean values for each of the 12 morphometric characters in every colony were submitted (i.e. for each morphometric character, a colony had a single value).

Four different PCAs were carried out. They included samples of feral and managed colonies from 1986–1987 (managed) with 1988 (feral), 1992, 1993 and 1994.

In the first PCA (for 1986–1987 managed with 1988 feral colony data), a matrix in the array of 130 vectors (85 managed colonies and 45 feral colonies) by 12 morphometric characters was submitted. For 1992, 1993, 1994 and 1996 correlation matrices of 350 (289 managed colonies and 61 feral colonies), 363 (300 managed and 63 feral colonies), 371 (306 managed and 65 feral colonies) and 313 (283 managed and 30 feral colonies), respectively, were submitted to PCA.

After each PCA, component scores of colonies (CS) were calculated for each of the derived components. This was done by multiplying the mean value of each morphometric character in a given colony by the coefficient for that character in the component, then adding all these 12 products. Therefore, in the end each colony had a single value (i.e. one CS per component) as a measure of general body size.

The distribution of these indicators of body size (CS) for both feral and managed colonies was visualized by plotting them across component 1 which is the component related to the size of the body [39]. This approach can provide evidence of changes in general body size of both feral and managed honeybees across time as an indication of the process of gene flow between both populations and the speed of morphological changes.

Lastly, differences in CS between feral and managed colonies per year were also statistically analysed by means of univariate ANOVA [see 35]. Components 1 to 5 were used in this series of tests only since they include the largest amount of variation in the data. The factor procedure of the SAS statistical package was used to perform the PCA analyses.

3. RESULTS

3.1. Univariate comparison of feral and managed honeybees

The results of the univariate comparison of feral and managed colonies across 10 years are presented in *table III*.

All morphometric characters exhibited significant differences between both feral and managed colonies and across years (*table III*). However, a point to note is an increase in the values for all morphometric characters in the feral population in 1992 compared to those in the feral colonies from 1988. Presumably, 1988 samples could have been more Africanized-like since they have just recently arrived into Yucatan, assuming colonies at the colonizing front exhibit low frequencies of European genes [11]. Four years later, they seemed to have experienced an influx of genes from the managed population in accordance with the change towards larger values in single morphometric characters, presumably more European-like. Thus the analysis of single character morphometric data in this study, suggests that there was gene flow from Yucatecan managed colonies to the Africanized colonizing population. The plots of the mean values of WL and FEL across years also provide a clear view of this tendency (*figures 1* and *2*). Within the first 4 years of the arrival of Africanized honeybees, there was an initial increase in the size of both WL and FEL which suggests introgression of European genes into the feral population.

By 1996, morphometric data showed that seven morphometric characters in feral colonies were not statistically different from 1988 feral ones. This result suggests a return of feral colonies to the original Africanized morphotype as a consequence of European genes disappearing from the feral population. The same process seems to be true for the managed population (*table III*). Nevertheless, after 10 years of gene exchange between both populations a diverse array of morphotypes seems to exist in the managed

Table III. ANOVA of mean values (with SE) of 12 morphometric characters (in mm) for feral and managed Yucatecan colonies of honeybees between 1986 and 1996.

	Year						
	1986–1987	1988	1991	1992		1993	
Character	Managed ($n = 85$)	Feral ($n = 45$)	Managed ($n = 283$)	Managed ($n = 289$)	Feral ($n = 61$)	Managed ($n = 300$)	Feral ($n = 63$)
WL	9.034 ± 0.015^{a}	8.732 ± 0.012^{b}	8.997 ± 0.016^{c}	8.939 ± 0.019^{d}	8.891 ± 0.012^{e}	8.905 ± 0.028^{e}	8.858 ± 0.006^{f}
WW	3.045 ± 0.012^{a}	2.995 ± 0.012^{b}	3.035 ± 0.018^{a}	3.039 ± 0.013^{a}	3.035 ± 0.017^{a}	3.032 ± 0.023^{c}	2.909 ± 0.007^{d}
HWL	4.335 ± 0.015^{a}	3.998 ± 0.015^{b}	4.306 ± 0.012^{a}	4.257 ± 0.024^{c}	4.251 ± 0.010^{c}	4.256 ± 0.024^{c}	4.228 ± 0.009^{d}
HWW	1.784 ± 0.019^{a}	1.687 ± 0.011^{b}	1.774 ± 0.014^{a}	1.769 ± 0.007^{a}	1.762 ± 0.016^{a}	1.768 ± 0.012^{a}	1.727 ± 0.005^{c}
FEL	2.590 ± 0.018^{a}	2.492 ± 0.012^{b}	2.572 ± 0.012^{c}	2.564 ± 0.003^{c}	2.518 ± 0.017^{d}	2.531 ± 0.012^{d}	2.519 ± 0.012^{d}
TIL	3.173 ± 0.011^{a}	3.071 ± 0.011^{b}	3.153 ± 0.009^{c}	3.148 ± 0.013^{c}	3.164 ± 0.028^{a}	3.166 ± 0.013^{a}	$3.160 \pm 0.006^{a,c}$
TAL	2.100 ± 0.006^{a}	1.981 ± 0.014^{b}	1.996 ± 0.004^{b}	1.977 ± 0.005^{b}	1.959 ± 0.006^{c}	1.961 ± 0.013^{c}	1.946 ± 0.007^{d}
TAW	1.146 ± 0.004^{a}	1.122 ± 0.011^{b}	1.142 ± 0.005^{a}	1.135 ± 0.011^{a}	1.136 ± 0.013^{a}	1.139 ± 0.015^{a}	1.125 ± 0.010^{b}
STL	2.680 ± 0.005^{a}	2.571 ± 0.009^{b}	2.710 ± 0.006^{c}	2.703 ± 0.014^{c}	2.683 ± 0.018^{a}	2.693 ± 0.009^{a}	2.657 ± 0.007^{d}
WMW	2.295 ± 0.012^{a}	2.195 ± 0.011^{b}	2.300 ± 0.009^{a}	2.303 ± 0.003^{a}	2.295 ± 0.008^{a}	2.293 ± 0.016^{a}	$2.271 \pm 0.010c$
WML	1.482 ± 0.007^{a}	1.297 ± 0.007^{b}	1.402 ± 0.007^{c}	1.399 ± 0.006^{d}	1.365 ± 0.006^{d}	1.390 ± 0.008^{d}	1.356 ± 0.008^{d}
WMD	0.257 ± 0.011^{a}	0.331 ± 0.009^{b}	0.307 ± 0.008^{c}	0.314 ± 0.004^{c}	0.323 ± 0.014^{b}	0.321 ± 0.010^{b}	0.313 ± 0.008^{c}

	Year				
	1994		1996		
Character	Managed ($n = 306$)	Feral ($n = 65$)	Managed ($n = 283$)	Feral ($n = 30$)	F-value
WL	8.867 ± 0.037^{f}	8.751 ± 0.016^{b}	8.845 ± 0.038^{f}	8.762 ± 0.021^{b}	172.12**
WW	3.025 ± 0.024^{c}	3.031 ± 0.008^{c}	3.032 ± 0.024^{c}	2.971 ± 0.013^{b}	140.05**
HWL	4.229 ± 0.014^{d}	4.219 ± 0.019^{d}	4.233 ± 0.025^{d}	4.155 ± 0.013^{e}	149.02**
HWW	1.760 ± 0.012^{a}	1.720 ± 0.014^{c}	1.762 ± 0.013^{a}	1.709 ± 0.007^{d}	47.62**
FEL	2.533 ± 0.023^{d}	2.510 ± 0.009^{d}	2.526 ± 0.022^{d}	2.499 ± 0.016^{b}	155.24**
TIL	3.155 ± 0.013^{c}	3.129 ± 0.017^{d}	3.128 ± 0.023^{d}	3.092 ± 0.018^{b}	117.15**
TAL	1.981 ± 0.013^{b}	1.923 ± 0.006^{e}	1.973 ± 0.013^{b}	1.939 ± 0.007^{e}	118.19**
TAW	1.132 ± 0.014^{a}	1.123 ± 0.003^{b}	1.125 ± 0.021^{b}	1.121 ± 0.004^{b}	35.29**
STL	2.675 ± 0.013^{a}	2.630 ± 0.006^{d}	2.681 ± 0.023^{a}	2.620 ± 0.009^{d}	20.20**
WMW	2.262 ± 0.023^{c}	2.193 ± 0.008^{b}	2.273 ± 0.014^{c}	2.173 ± 0.010^{b}	119.06**
WML	1.382 ± 0.012^{e}	1.330 ± 0.005^{f}	1.383 ± 0.013^{e}	1.312 ± 0.008^{f}	83.10**
WMD	0.314 ± 0.012^{c}	0.347 ± 0.004^{b}	0.333 ± 0.012^{b}	0.328 ± 0.006^{b}	61.44**

Different letters in the same row indicate significant differences at $P < 0.01$.

population [see 23] and two morphometric characters (HWW and STL) were still not statistically different from the original European population in 1986–1987 *(table III)*.

The regression analyses for WL and FEL gave evidence that the reduction in size seemed to occur faster in the managed population than in the feral one. The value of the regression line for WL in the managed population was: $y = 11.05 - 0.023x$ ($r = -0.96$); and for the feral one the regression line was: $y = 8.49 - 0.003x$ ($r = -0.84$). For FEL the value of the regression line for the managed population was: $y = 3.28 - 0.007x$ ($r = -0.93$); and for the feral one the regression line was: $y = 2.99 - 0.005$ ($r = -0.96$). This result is in agreement with findings related to a decrease in European colonies and an increase in hybrid colonies in the managed population [23].

3.2. PCAs for feral and managed honeybee colonies

The distribution of CS frequencies from feral and managed colonies for component 1 from 1986 to 1996, are presented in *figures 3–5*. It is possible to observe that the means of CS in the feral and managed populations had separate distributions along component 1 across the years of the study. Statistical support for these differences in distribution comes from the results of ANOVA for CS per year between feral and managed colonies (*table IV*). Means of general body size between feral and managed honeybees were statistically different in all years compared.

The results of both plots for CS and of ANOVA of CS of feral and managed honeybees showed that there has also been great morphological variation in the body size within both groups of honeybees during the 10 years of study which indicates a diverse arrange of morphotypes in both of them. It is also evident that since European honeybees in Yucatan at the start of the Africanization seemed to be of smaller body size than other European populations elsewhere [28], a significant proportion of these European colonies overlapped with the distribution of Africanized colonies in *figure 3*.

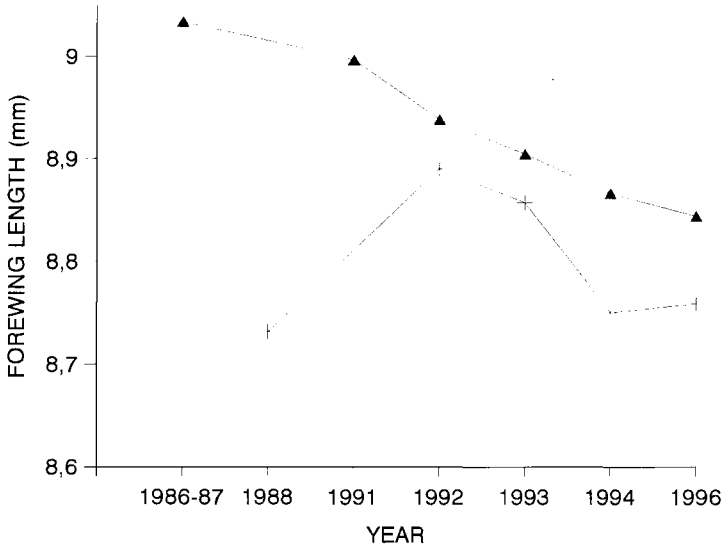

Figure 1. Distribution of mean values of forewing lengths for managed (▲) and feral (+) colonies across the years of study.

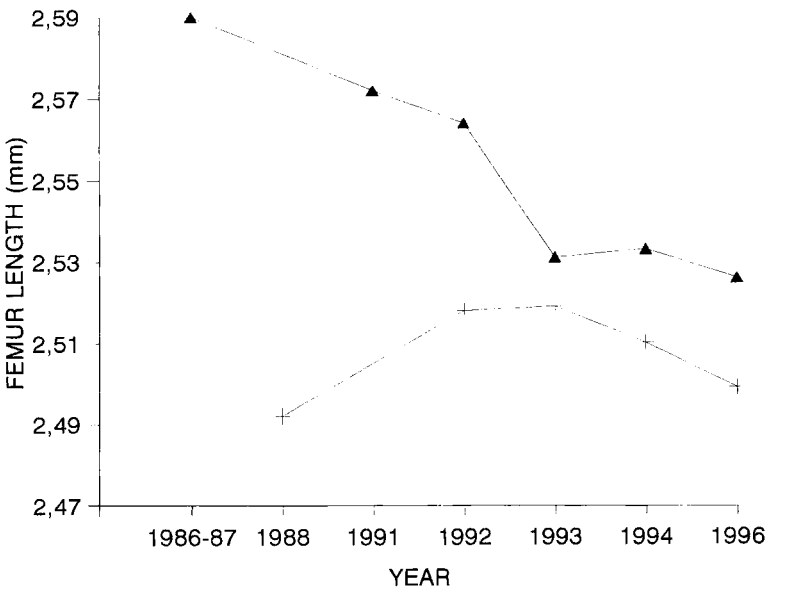

Figure 2. Distribution of mean values of femur lengths for managed (▲) and feral (+) colonies across the years of study.

The plots of CS values per year also revealed changes between the morphometrics of feral colonies collected in 1988 (a year after the first report of an Africanized swarm) compared with those in 1992 and afterwards. There was an initial increase in general body size of feral honeybees in accordance with the larger mean values of their CS (*figure 4* and *table IV*). This result is in agreement with the analyses of single morphometric characters in section 2. In a similar manner, in later years there has been a pattern of constant decline in body size in the feral and managed populations. However, the analysis of general body size by means of the distribution (*figures 3–5*) and statistical comparisons of CS (*table IV*) showed that the mean body size in feral honeybees after 10 years of the process is still larger than the initial body size of honeybees that first started colonizing Yucatan in 1988 (*table IV*, *figures 3* and *5*). These events probably indicate a loss of European genes in both the feral and managed populations as suggested in section 2 but that there has also been a continuing influence of European genes in the feral population after 10 years of interbreeding.

4. DISCUSSION

The results from both the univariate and multivariate analyses suggest that feral and managed Yucatecan honeybees, 10 years after the report of the first Africanized swarm, are the result of a bi-directional gene flow which has produced honeybees with body sizes between the European and the Africanized parental types.

Such an evidence supports the view of a flow of genes between the managed and feral populations at the start of the Africanization process which probably created the diverse array of morphotypes/haplotypes already reported in managed and feral colonies from Yucatan [22, 28]. Thus, it seems that densities of European colonies in an area where the Africanized colonizing front has recently arrived can in fact

Table IV. ANOVA of mean values of CS for the first five components of PCA for feral and managed Yucatecan colonies collected in 1986–1987, 1988, 1992, 1993, 1994 and 1996.

	Feral (n = 45) Mean SE	Managed (n = 85) Mean SE	F-value (d.f. = 1, 128)
Year 1986–1987 and 1988			
Component 1	−2.10 ± 0.13	1.15 ± 0.04	61.15**
Component 2	0.92 ± 0.06	−0.27 ± 0.072	3.11**
Component 3	0.46 ± 0.08	−0.11 ± 0.05	18.40**
Component 4	0.60 ± 0.06	−0.14 ± 0.06	13.41**
Component 5	−0.21 ± 0.07	0.39 ± 0.14	17.38**
	Feral (n = 61)	Managed (n = 289)	(d.f. = 1, 348)
Year 1992			
Component 1	−1.41 ± 0.07	0.10 ± 0.073	2.46**
Component 2	0.87 ± 0.09	−0.18 ± 0.07	25.44**
Component 3	0.16 ± 0.08	−0.03 ± 0.05	14.70**
Component 4	0.21 ± 0.06	−0.06 ± 0.23	5.54*
Component 5	−0.16 ± 0.07	0.16 ± 1.02	2.38 ns
	Feral (n = 63)	Managed (n = 300)	(d.f. = 1,361)
Year 1993			
Component 1	−1.47 ± 0.03	0.01 ± 0.06	21.15**
Component 2	0.53 ± 0.06	−0.12 ± 0.03	4.49*
Component 3	0.31 ± 0.03	−0.07 ± 0.04	8.33**
Component 4	−0.35 ± 0.03	0.08 ± 0.06	4.41*
Component 5	0.12 ± 0.03	−0.11 ± 0.05	1.01ns
	Feral (n = 65)	Managed (n = 306)	(d.f. = 1, 369)
Year 1994			
Component 1	−1.55 ± 0.02	−0.63 ± 0.08	14.12**
Component 2	−0.02 ± 0.03	0.01 ± 0.06	0.05 ns
Component 3	0.49 ± 0.02	−0.10 ± 0.06	5.18*
Component 4	−0.05 ± 0.03	0.02 ± 0.06	0.20 ns
Component 5	−0.28 ± 0.03	0.06 ± 0.06	1.97 ns
	Feral (n = 30)	Managed (n = 283)	(d.f. = 1, 311)
Year 1996			
Component 1	−1.31 ± 0.06	0.22 ± 0.04	25.11**
Component 2	−0.43 ± 0.03	0.07 ± 0.05	10.12**
Component 3	0.62 ± 0.03	−0.10 ± 0.04	6.15*
Component 4	−0.24 ± 0.03	0.04 ± 0.03	2.20 ns
Component 5	−0.12 ± 0.02	0.02 ± 0.02	1.88 ns

** $P < 0.01$; * $P < 0.05$; ns = not significantly different at $P > 0.05$.

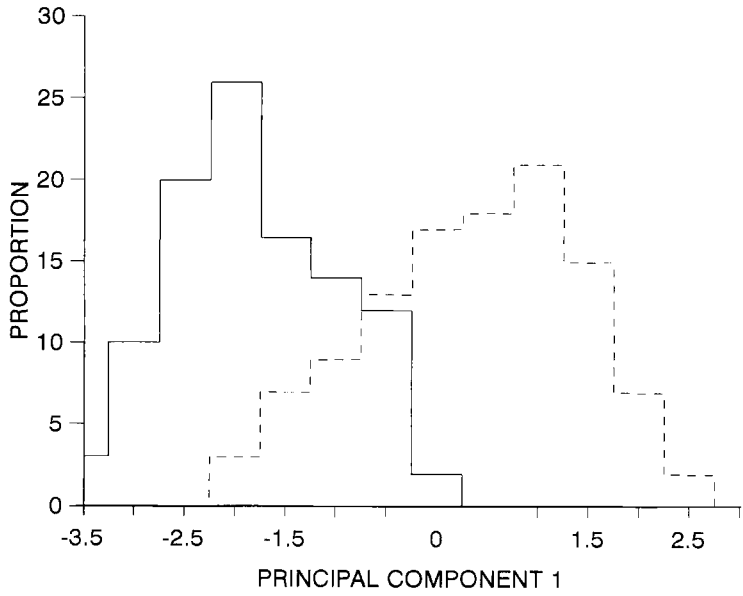

Figure 3. Distribution of CS values of feral (solid lines) and managed (dotted lines) colonies from 1986–1987 and 1988, across component 1.

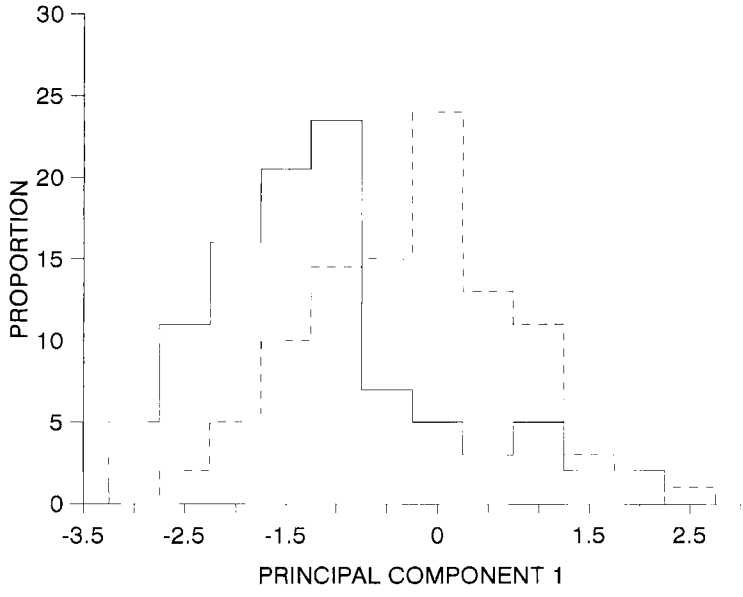

Figure 4. Distribution of CS values of feral (solid lines) and managed (dotted lines) colonies from 1992, across component 1.

have an influence on its genetic make-up and that there does not seem to be a restriction to gene flow between the populations. Similar conclusions were reached by Lobo et al. [17], Moritz and Meusel [18] and Lobo [15] when analysing morphometrics, isozymes and mitochondrial DNA of honeybees from Brazil and Costa Rica.

An inspection of the means for general body size of feral honeybees in 1996 revealed that this group exhibited a larger size than those at the start of the process in 1988. This result suggests the mutual sharing of European and African genes in honeybees from the feral population 10 years after the start of the process of Africanization. European genes in Yucatecan feral colonies very likely have originated through genetic introgression from managed colonies, since there does not seem to be evidence of European genes at the Africanized colonizing front [34]. However, a trend towards a continuous reduction in size is also evident probably due to natual selection favouring Africanized genes in feral colonies.

The results in this study contrast with those obtained in other areas than the Neotropics. In Panama, Boreham and Roubik [3] recorded the wing length values of feral colonies across 4 years at the start of the Africanization process. They found a steady decline in the size of the wings accompanied by a reduction in the variance for the character, which meant an eventual complete disappearance of larger honeybees (namely European) from the population of study. The authors concluded that given the small number of resident European colonies in the Panama canal compared with the Africanized population, the elimination of European characters was not an unexpected event.

In the northeastern part of Mexico, Rubink et al. [30, 31] studied the morphometric changes of a long-resident feral European population across the entire Africanization process from the first arrival of Africanized honeybees to the total elimination of European honeybees. They found a rapid increase in Africanization rates regardless of the high European honeybee density

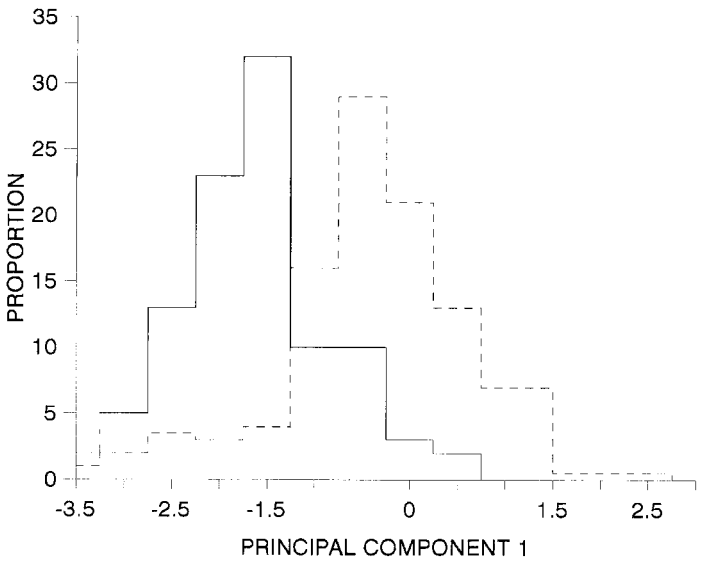

Figure 5. Distribution of CS values of feral (solid lines) and managed (dotted lines) colonies from 1996, across component 1.

in the study area, with accompanying morphometric changes of the resident population to a more African-like type of honeybee in a period of 3 years. Although densities of both types of colonies were not mentioned in their work, Rubink et al. [31] concluded that the high density of the feral European population had little mitigating effect on Africanization. In a similar way, Hall and Muralidharan [11] and Smith et al. [34] found no evidence that European honeybees have genetically contributed to the pool of the colonizing front of Africanization. However, the hybrid status of honeybee populations in other parts of South America has been demonstrated [18, 32]

In the present study, the size of the resident European managed population seems to have had an effect on the genetic make-up of feral Africanized honeybees, although a gradual decline in size is also evident in the managed and feral populations. In accordance with this evidence, it is possible to suggest a scenario for Yucatan where at the start of the Africanization, a large number of colonies with intermediate morphotypes (hybrids) might have arisen in both the feral and the managed population as a consequence of the large numbers of resident European honeybees whose queens and drones mated largely with gynes from feral Africanized colonies. Nevertheless, the eventual reduction in body size indicates a loss in the numbers of colonies with predominantly European genes and a constant tendency towards a smaller type of honeybee, probably due to selective advantages of Africanized honeybees in the tropics.

The present data cannot provide conclusive evidence on the mechanism by which colonies with European morphometric characters seem to be eliminated from the feral and managed Yucatecan populations. However, since introgressive hybridization between Africanized and European honeybees seemed to have occurred in Yucatan, it might be possible that reproductive differences between both types of bees (higher swarming rates and parasitism by reproductives) and possibly a constant migration of Africanized colonies from other areas of Mexico and Central America have acted as a source of African genes and diluted the European gene pool [21, 26, 37]. Human contributions to this process could also have played an important role by increasing the numbers of African genes in apiaries through the capture and incorporation of feral colonies [33].

Within a period of 10 years, morphometric characters in the Yucatecan populations of honeybees seem to have changed as a result of: 1) an initial gene exchange between feral Africanized and European managed colonies due to a large population effect of the latter; and 2) a subsequent reduction in the frequencies of European genes from both populations. However, to date there is still morphometric evidence of the presence of European genes in both the managed and the feral populations from Yucatan. Such evidence seems to be in accordance with the hypothesis of racial admixture proposed by Lobo and Krieger [16] to explain the genetic nature of Africanized honeybees in Costa Rica. It seems that the size of the resident European population in an area determines the contribution of European genes to the process of hybridization of both bee types.

It is difficult at the present time to predict if there is going to be a complete disappearance of European genes in the Yucatecan populations. Further studies including the use of genetic markers need to be conducted to determine the persistence of European alleles in feral and managed Yucatecan honeybees.

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Résumé – Hybridation entre abeilles européennes et abeilles africanisées (*Apis mellifera* L.) dans le Yucatan tropical, Mexique. I. Modifications morphométriques dans les colonies sauvages et les colonies domestiques. Les modifications de la taille corporelle des abeilles ont été étudiées sur des échantillons prélevés dans des colonies sauvages et des colonies domestiques au Yucatan entre 1986 et 1996. Puisque la morphologie des abeilles est supposée être héritée des deux parents et présenter une variabilité élevée, son utilisation se justifie pour étudier les changements de la taille corporelle comme indicateur des échanges de gènes entre populations. Douze caractères morphométriques relatifs à la longueur du corps et à la largeur de quatre structures anatomiques (aile antérieure, aile postérieure, 3^{e} patte et 3^{e} sternite abdominal) ont été mesurés. Les données ont été analysées au niveau d'une variable (ANOVA des caractères morphologiques pris individuellement au cours des années) et avec une méthode multivariée (ACP : analyse en composantes principales). Cinq ACP ont été réalisées ; elles portaient sur des échantillons de colonies domestiques prélevés en 1986–1987 (avant l'arrivée des abeilles africanisées au Yucatan) et des échantillons de colonies sauvages prélevés en 1988 (date de l'arrivée des premières colonies africanisées) et sur des échantillons issus des deux types de colonies prélevés en 1992, 1993, 1994 et 1996. Pour chaque ACP on a calculé les scores des colonies pour la première composante qui était liée à la taille. On a visualisé ces indicateurs de la taille en les reportant sur un diagramme avec les valeurs de la première composante par année. Les comparaisons statistiques des scores ont été faites entre colonies sauvages et domestiques au moyen d'ANOVA. Les résultats des deux types d'approche montrent : 1) que l'accroissement initial de la taille des abeilles sauvages est due à un flux de gènes provenant de la forte population européenne résidente, 2) que la réduction constante subséquente de la taille des deux types d'abeilles au fur et à mesure que l'africanisation progressait est due à la disparition dans les deux populations des colonies à morphométrie européenne et 3) que les gènes européens persistent dans les populations sauvages aussi bien que domestiques dix ans après la première mention d'essaims africanisés. Le flux de gènes bidirectionnel, qui aboutit à une convergence dans les caractères quantitatifs vers une taille intermédiaire, semble mieux expliquer les changements morphologiques qui sont survenus entre les colonies domestiques et les colonies sauvages au cours du processus d'africanisation dans le Yucatan. Néanmoins la persistance de gènes européens dans les deux populations nécessite d'être étudiée plus à fond.

***Apis mellifera* / abeille africanisée / hybridation / morphométrie / analyse multivariée / Mexique**

Zusammenfassung – Vermischung von europäischen und afrikanisierten Honigbienen (*Apis mellifera* L.) im tropischen Yucatan. Im tropischen Yucatan, Mexiko wurden zwischen 1986 und 1996 Bienenproben (*Apis mellifera* L.) von verwilderten und von durch Imker betreuten Völkern gesammelt und die Änderungen der Körpergröβe der Bienen untersucht. Da allgemein angenommen wird, daβ morphometrische Merkmale der Bienen mit hoher Heritabilität von beiden Eltern vererbt werden, ist die Verwendung der Änderungen von Merkmalen der Köpergröβe als Indikator von Genaustausch zwischen Populationen gerechtfertigt. Bei jeweils 10 Arbeiterinnen aus jedem Volk wurden jeweils 12 mit Länge und Breite der Biene im Zusammenhang stehende morphometrische Merkmale anatomischer Strukturen (Vorder-

und Hinterflügel, 3. Bein und 3. abdominaler Brustring) vermessen. Die Daten wurden auf der univariaten Ebenen (ANOVA von einzelnen morphometrischen Eigenschaften über Jahre) und mit einer multivariaten Technik (Principal Component Analyse, PCA) ausgewertet. Fünf separate PCAs wurden durchgeführt, diese enthielten Proben aus Imkerbetrieben von 1986–1987 (vor Ankunft der afrikanisierten Völker in Yucatan) und von verwilderten Völkern aus dem Jahr 1988 (es gab die ersten afrikanisierten Völker in der Gegend); weiter wurden Proben von beiden Volkstypen 1992,1993,1994 und 1996 gesammelt. Von jeder PCA wurden Meβgröβen der Völker (CS) für die erste Komponente berechnet, die mit der Körpergröβe im Zusammenhang steht. Die Verteilung dieser Indikatoren für allgemeine Körpergröβe wurde visualisiert, indem man sie pro Jahr gegen die Werte der Komponente 1 auftrug. Statistische Vergleiche der CS wurden zwischen verwilderten und betreuten Völkern mit Mittelwerten aus der ANOVA durchgeführt. Aus den Ergebnissen von beiden Methoden wird ersichtlich: 1) eine anfängliche Zunahme der Körpergröβe der verwilderten Honigbienen erfolgte durch den Genfluβ aus der groβen angesiedelten europäischen Population; 2) es erfolgte anschlieβend eine konstante Verminderung der Körpergröβe bei beiden Bienentypen während der Zunahme der Afrikanisierung, wahrscheinlich infolge des Verlustes von Völkern mit europäischen Merkmalen in beiden Populationen und 3) Europäische Gene kommen 10 Jahre nach dem Fund des ersten afrikanisierten Schwarms in dieser Gegend in beiden, den betreuten und den verwilderten Populationen der Yucatan Honigbienen vor. Zweiseitiger Genfluβ, der zu einer Konvergenz der quantitativen Merkmale in Richtung einer intermediären Körpergröβe führt, scheint die morphologischen Änderungen besser zu erklären, die zwischen den von Imkern betreuten und verwilderten Populationen der Honigbienen während des Prozesses der Afrikanisierung in Yukatan aufgetreten sind. Der Erhalt der europäischen Gene in beiden Populationen über die Jahre sollte jedoch weiterhin untersucht werden.

***Apis mellifera* / afrikanisierte Hoigbiene / morphometrische Merkmale / Hybridierung / multivariate Analyse / Mexiko**

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