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Original article

Hybridization between European and African-derived honeybee populations (*Apis mellifera*) at different altitudes in Perú

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Abstract – The current status of admixture between *Apis mellifera* of African and European origin was studied in populations from different altitudinal regions of Perú. Worker bees from 7 altitudinal regions were analysed by morphometrics and mtDNA RFLPs. Our results showed that the rates of admixture between African-derived and resident European populations have depended on the altitude of the region. Our finding of hybrid colonies at elevations above 2 500 m supports the hypothesis that climate alone may not restrain the northern limit of the distribution of African-derived honeybees in the Americas. We conclude that introgressive hybridization between African and European derived honeybees best explains the current patterns of distribution of morphotypes and mitotypes across the different regions of Peru.

Africanization / hybridization / *Apis mellifera* / mtDNA / morphometrics / Peru

1. INTRODUCTION

The genetic nature of the admixture between *Apis mellifera* L. of African and European origin in the neotropics remains controversial (Rinderer et al., 1993b; Clarke et al., 2001). Conflicting hypotheses of the process of Africanization seem to be the result of climatic and ecological conditions of the sampling region in various studies (Sheppard et al., 1991a; Sheppard et al., 1991b). Thus, extensive analysis of neotropical honeybee populations in regions with diverse biomes is necessary in order to better understand the nature of African-European honeybee genic exchange and propose more accurate models of Africanization for the Americas.

Peru owns some of the most diverse climates in South America as a result of the Andes dividing the country in altitudinal levels ranging from lowland rainforests to alpine regions located at 3 500 m above sea level. Predictions about the direction of movement of African-derived bees and the existence of African-European hybrid areas in Peru have been proposed by Kent (1991) based on information collected from beekeepers. African-derived honeybee swarms were first reported in Peru in the eastern tropical area of Pucallpa in 1974. This is 18 years after their accidental escape from an experimental apiary in Brazil (Kerr, 1967; Kerr et al., 1982). It was thought that the north-western and the Pacific coast of Peru would not be colonized by

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African-derived bees due to the geographic barrier of the Andes. However, by 1985 the eastern coast was already invaded by feral swarms (Kent, 1991). Presently, African-derived honeybees presumably occupy most of the Peruvian territory but the status of admixture with resident European populations, especially at high elevations (temperate climate) remains undocumented.

Its wide range of climates makes Peru a particularly interesting country to test hypotheses concerning the influence of climate on the admixture of African-derived bees with resident European ecotypes. Climatic differences between northern and southern Argentina have been invoked to explain the existence of a hybrid zone in which a diverse arrange of associations between nuclear and cytoplasmic markers of African and European origin was found in worker bees (Sheppard et al., 1991a). Altitudinal conditions in Peru may determine the existence of hybrid zones resulting from differences in climate similar to those found between northern and southern Argentina .

There is evidence that African-derived honeybees can successfully thrive at high altitudes in temperate climates of Argentina and Costa Rica (Dietz et al., 1985; Krell et al., 1985; Spivak, 1992). Studies on the population structure of honeybees in areas undergoing Africanization at elevations above 2 500 have not been conducted and Peru gives a unique opportunity to document such a situation. Moreover, the presence of diverse densities of resident European colonies prior to the invasion of African-derived honeybees may also influence the degree of admixture between both bee types depending on numerical competition (Quezada-Euán and Hinsull, 1995; Quezada-Euán and Medina, 1998).

In this paper we document the distribution and the extent of admixture between European- and African-derived honeybees in Peru using morphometric and mitotype polymorphisms. The outcome of the process of Africanization in Peru needs to be documented in order to develop future programs of selection and propagation of locally selected stock.

2. MATERIALS AND METHODS

Peru has an estimated surface of 1 285 215 km^2. It extends from 0°1’48’’ to 18°21’33’’ south of the Equator and from 68°39’27’’ on the Pacific and 81°19’34’’ on its border with Bolivia. The Peruvian landscape and climate is highly diverse, mainly as a consequence of extreme altitudinal regions ranging from the Pacific coasts at 0 m a.s.l. to the Huascarán peak on the white cordillera of the Andes at 6 746 m of elevation (Dávila et al., 1980). A total of 186 samples of worker honeybees were collected from the same number of colonies in all regions where beekeeping is practiced ranging between 0 and 3 500 m a.s.l. Samples came from beekeepers that conducted minimal management of the hives and these were allowed to requeen themselves. We divided the country in 7 altitudinal regions, the number of colonies that were collected in each region is presented in Table I. The samples were collected during the winter season from June through September of 2000. All samples were labeled and maintained in ethanol (95%) until further analyses were conducted.

2.1. Analysis of morphotypes

Ten worker bees were selected randomly from each colony sample and dissected under a microscope. Four body parts were mounted on projector slides and 25 morphometric characters were measured in accordance with the methods of Daly and Balling (Daly and Balling, 1978) and Rinderer et al. (1993a). The characters were measured using an inverted microscope which projected the images onto a digitizing pad. The points delimiting the 25 characters were marked using a mouse, the information was then transferred to a PC which converted the data into size and angle variables using the program AFUSDA (Rubink, unpublished). AFUSDA also calculated the probabilities of a sample being African- or European-derived. These probabilities were used to assign the samples to one of the four morphotype categories proposed by Rinderer et al. (1993a): Africanized (A), Africanized with evidence of European introgression (AE), European with evidence of Africanized introgression (EA) and European (E).

2.2. Analysis of mitotypes

For the analysis of mitotypes, the total DNA was extracted from the thoracic muscles of one bee per sample using the high salt extraction protocol by Paxton et al. (1999). The 1028 bp cytochrome oxidase I (COI) segment and the 964 bp region of the rRNA segment of the honeybee mtDNA (Crozier et al., 1993) were amplified using the protocol of Saiki et al. (1988). The PCR conditions were those of Nielsen et al. (1999, 2000). The amplified segments were digested with 3 IU of

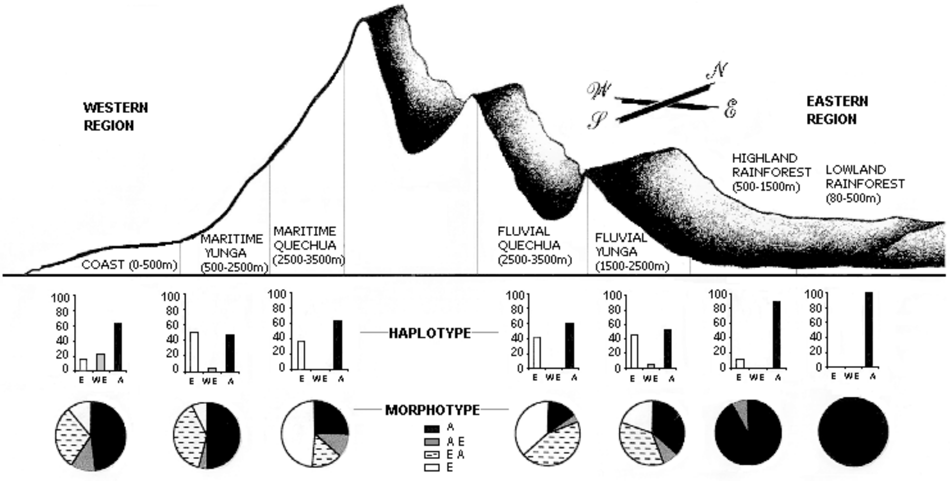

Figure 1. A map of the altitudinal regions of Peru where samples of honeybees were collected. The frequencies of haplotypes and morphotypes in each region are presented in bars and pies respectively. Abbreviations correspond to those for Table I.

either *Hinc* II or *Eco* RI. Three µL of the product were electrophoresed using 1.6–1.8% agarose gels and visualized after staining with ethidium bromide under a UV light. The presence of a *Hinc* II cleavage site at the COI fragment identified the bees with mitotype of west-European origin (lineage M). An *Eco* RI cleavage site on the rRNA segment identified the bees with mitotypes of east-European origin (lineage C). The bees that had no cleavage sites at either of the amplified fragments were identified as having mtDNA of African origin (lineage A) (Hall and Smith, 1991; Garnery, 1992).

The proportions of morphotypes and mitotypes were obtained for the altitudinal regions and the association of both types of variable was studied using a χ^2 analysis. Due to the low frequency of west-European mitotypes, the data analyzed only considered African or European mitotypes without separating both types of European markers.

3. RESULTS

The number of colonies assigned to the morphotypes of Rinderer et al. (1993a) and to the different mitotypes in each of the 7 altitudinal regions is presented in Table I. Out of the 186 samples that were analysed, 52.7% (n = 98) were assigned to the African morphotype (A), 17.7% (n = 33) to the European morphotype and 29.5% to intermediate morphotypes (European with African gene introgression or African with European gene introgression). The A morphotype was predominant in the eastern and western regions at altitudes below 1 500 m. However, at higher altitudes the E and intermediate morphotypes were more abundant. The frequency and distribution of morphotypes and mitotypes per altitudinal region is presented in Figure 1.

The African mitotype was predominant: 67.74% (n = 126) of all colonies carried the African mitotype, 27.96% (n = 52) the east-European mitotype and 4.3% the western European mitotype (n = 8). However, the frequency of African mitotypes was lower on the western region (55%) compared to its eastern counterpart (75.5%) (Fisher's exact test = 0.0019). On the eastern region, no colonies from the lowland rainforest had European mitotypes, but on the coast from the western region, 37% of the colonies carried this mitotype. However, in the highland rainforest of the east, 11% of the colonies had east-European mitotype with African morphotype. In the coastal area, the frequency of colonies with African morphotype and mitotype was 44% and the frequency of bees with African mitotype and intermediate morphotype was 19%.

On the western region, we found a significant frequency of west-European morphotypes (9%) compared to the eastern

Table I. The number of colonies collected in each altitudinal region of Peru. The number of colonies in each morphotype (A = Africanized; AE = Africanized with evidence of European gene introgression; EA = European with evidence of African gene introgression; E = European) and mitotype (A = African; E = East European; WE = West European) category are also presented.

	MITOTYPE																				
MORPHOTYPE	Pacific Coast 0–500 m n = 27			Maritime Yunga 501–2500 m n = 26			Maritime Quechua 2501–3500 m n = 27			Fluvial Quechua 2501–3500 m n = 27			Fluvial Yunga 2501–3500 m n = 25			Highland Rainforest 501–1500 m n = 27			Lowland Rainforest 80–500 m n = 27		
	A	E	WE	A	E	WE	A	E	WE	A	E	WE	A	E	WE	A	E	WE	A	E	WE
A	12	1	0	12	1	0	5	0	0	4	0	0	8	1	0	22	3	0	27	0	0
AE	1	0	2	0	1	0	2	3	0	1	0	0	2	0	0	2	0	0	0	0	0
EA	4	1	3	0	9	1	3	1	0	8	4	0	2	6	1	0	0	0	0	0	0
E	0	2	1	0	2	0	5	8	0	3	7	0	1	4	0	0	0	0	0	0	0
TOTAL	17	4	6	12	13	1	15	12	0	16	11	0	13	11	1	24	3	0	27	0	0

region (1%), however, in both cases the presence of this mitotype was restricted to areas below 2 500 m. The overall association of morphotypes and mitotypes as indicated by the χ^2 analysis was significant ($\chi^2 = 71.028$; df = 3; $P < 0.01$). This result supports the fact that morphotypes tended to be associated with their respective mitotype.

4. DISCUSSION

The presence of honeybee colonies with diverse associations of morphotypes and mitotypes of European and African origin 18 years after the first report of African-derived honeybees in Peru, gives evidence for an extensive process of hybridization, especially at intermediate and high elevations. Our results are in agreement with the existence of climatic hybrid zones elsewhere but additional factors may also be evoked to explain the outcome of Africanization in Peruvian honeybees.

In the tropical areas of the east, next to the Amazon basin, beekeeping was never prosperous and the resident population of European honeybees prior to the arrival of African-derived swarms was practically zero (Dávila et al., 1980; CENAGRO, 1994). Therefore, the evidence of colonies from this area having almost fixed African morphotype and mitotype was expected since possibilities for hybridization with European colonies were numerically impossible. The African mitotype was probably more frequent in colonies from this area as a result of African-derived honeybees being able to colonize and outnumber European/derived honeybees in the tropical areas. However, in the highland rainforest we found colonies with east-European mitotype and African morphotype suggesting extensive introgression at this transition area where both ecotypes may be equally adapted.

In contrast with the tropical forest of the east (up to 500 m), on the coast we found colonies with evidence of mixed morphotypes/ mitotypes. On the coast, we found a comparatively lower frequency of bees with African morphotype and mitotype and a higher frequency of bees with African mitotype and intermediate morphotype. This is surprising since a better adaptation of African-derived honeybees to the tropical environments would, in theory, favour the colonization of the Pacific coast similar to what occurred on the eastern lowland rainforest. The reason for this result may be explained firstly, because beekeeping was practiced more intensely near the coast and therefore a higher density of colonies of European origin was present at the arrival of African-derived honeybees (Dávila et al., 1980). Secondly, there is a substantial difference with the tropical rainforests of the east. In the Pacific coast, the arrival of African-derived honeybees was not natural. The Andes act as a geographic barrier in the northern part of Peru which effectively stopped the natural westward movement of swarms. There is evidence that the presence of African-derived colonies in the Pacific coast is the result of the introduction of colonies by man from Africanized-saturated areas (the tropical rainforests) (Kent, 1991). Therefore, a continued natural migration of Africanized colonizing swarms from adjacent saturated areas to the coast is difficult, if not impossible (as opposed to what occurs in the eastern tropics from the adjacent Amazon forest). A rapid increase in the effective population size of African colonies in this area is therefore limited. In this way, European colonies, although not as well adapted to the tropical areas of the Pacific coast, would have a better numerical opportunity for admixture with artificially transported African-derived colonies. Therefore, hybridization between EHB-AHB in western Peru has probably occurred as a result of reduced numerical advantages of the latter, in this case, due to a geographic barrier limiting the continued influx of AHB swarms.

Beekeeping practices in the Pacific coast may also have contributed to the permanence of European genes in colonies. A similar situation has been observed in the neotropical Yucatan peninsula of Mexico. There, colonies of European origin were at high densities when African-derived swarms started colonization. As a consequence, Africanization in the Yucatan Peninsula occurred at a slow pace and resulted in an extensive hybridization with resident European colonies both in managed and feral populations (Quezada-Euán and May-Itzá, 1996; Quezada-Euán, 2000; Clarke et al., 2001).

On the other hand, European colonies have better adaptive opportunities in temperate climates than their African-derived counterparts and become dominant as documented in southern Argentina (Dietz et al., 1985). In our study, we sampled areas between 2 500 and 3 500 m and found that at these altitudes, the number of "pure" European-derived honeybees increased but did not become dominant. Surprisingly, we also found evidence of a great range of European-African hybrids. This finding may be a result of some beekeepers moving colonies to higher altitudes from the Africanized-saturated tropical areas or alternatively it may reflect the ability of African-derived honeybees to survive in temperate areas. In either situation, the daughter virgin queens (from African mothers) are more likely to mate with European- derived drones resident to these areas and thus, produce offspring with African mitotype and intermediate morphotype.

Since our samples came from managed colonies where relatively little management was conducted, we suggest that this result is likely a consequence of hybrid colonies surviving at high altitudes. Other studies have demonstrated the ability of European-African hybrid colonies to survive at altitudes above 1 500 m (Villa, 1987; Hall and McMichael, 1992; Spivak, 1992) and at low temperatures (Villa et al., 1991; Dietz and Vergara, 1995). Studies in Costa Rica at elevations in the range of the 1 500–2 500 m, have shown that both types of bee may survive and perform well (Spivak, 1992). As a result, Costa Rican honeybees at high altitudes show extensive hybridization (Hall and McMichael, 1992). This may be the reason why we found such an extensive number of colonies showing evidence of intermediate morphotypes with diverse array of mitotypes in the temperate areas of Peru.

Our findings suggest that colonization of temperate areas by African-derived honeybees is not restricted by temperature alone. Other conditions such as food availability and potential nesting sites may play a crucial role in the success of African-derived honeybees in temperate areas (Dietz and Vergara, 1995) and deserve further study. For instance, in the subtropical Yucatan Peninsula of Mexico, the lack of potential nesting sites has greatly reduced the opportunities for high densities of feral colonies to the extent that there are areas where only few feral African-derived colonies are found (Quezada-Euán, 2000). This fact has probably enhanced the probability of hybridization with resident European bees (Quezada-Euán, 2000; Clarke et al., 2001). Given the evidence, we suggest that the potential limits of African-derived honeybees in America may be further north than originally predicted (Taylor, 1977; Rinderer et al., 1993b; Dietz and Vergara, 1995).

The significant association between morphotype/mitotype is strongly influenced by bees from the lowland rainforest, highland rainforest and Pacific coast where African mitotype and morphotype predominate. However, in all other regions, the populations showed intermediate morphotypes associated with African or European mitotypes. These results give additional indication that hybridization has occured in all areas where European honeybees have either been able to compete in population numbers (Pacific coast) or have been climatically better adapted than their African counterparts (above 1 500 m). The fact that colonies with African morphology decreased from 100% in the tropical rainforest to ca. 20% in the temperate areas supports this hypothesis too.

Regarding a practical use of these results for beekeepers in Peru, the altitudes above 2 500 m may be selected for queen breeding if low levels of Africanization would be considered acceptable for national standards. We think that finding an African free zone for queen production may require further monitoring of the valleys between the higher peaks of the Andes or alternatively the use of instrumental insemination to produce European stock.

We conclude that the presence of intermediate morphotypes associated with European or African mitotypes at transition areas and temperate regions is the result of an extensive hybridization process due to a better opportunity of colonies of European origin to compete numerically or ecologically with their African counterparts. This finding also suggests that African-derived honeybees may successfully colonize temperate areas. Thus, altitudinal differences in Peru have produced areas where hybridization between European- and

African-derived honeybees has been extensive. We consider these areas to be hybrid zones where both ecotypes coexist and where there are no barriers to the production of viable offspring.

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Résumé – Hybridation entre les populations d'abeilles (*Apis mellifera*) issues d'Europe et d'Afrique à différentes altitudes au Pérou. L'état actuel du mélange entre les abeilles (*Apis mellifera* L.) d'origine africaine et d'origine européenne a été étudié au Pérou. Au total 186 échantillons d'ouvrières, issues de colonies appartenant à des apiculteurs et situées dans sept régions d'altitudes comprises entre 0 et 3 500 m (Tab. I), ont été analysés par morphométrie et RFPL de l'ADNmt. Quatre parties du corps de chacune des ouvrières, à raison de dix ouvrières par échantillon, ont été montées sur des diapositives et 25 caractères morphométriques ont été mesurés selon les méthodes de Daly et Bailing (1978) et de Rinderer et al. (1993a). Les probabilités d'africanisation ont été utilisées pour assigner les échantillons à l'une ou l'autre des quatre catégories de morphotypes proposées par Rinderer et al. (1993a) : africanisé (A), africanisé avec preuve d'introgression européenne (AE), européenne avec preuve d'introgression africanisée (EA) et européenne (E).

En outre, le segment de cytochrome oxydase I (COI) de 1028 pb et la région de 964 pb du segment d'ARNr de l'ADNmt de l'Abeille (Crozier et al., 1993) ont été amplifiés. Les segments amplifiés ont été digérés avec 3 IU soit de *Hinc* II soit de *Eco* RI. Les abeilles qui ne présentaient pas de sites de reconnaissance à aucun des fragments amplifiés ont été identifiées comme ayant un ADNmt d'origine africaine (lignée A) (Hall and Smith, 1991 ; Garnery et al., 1992). La proportion de morphotypes et de mitotypes a été obtenue pour chaque région d'altitude et l'association des deux types de variables a été analysée par le χ^2.

L'analyse morphométrique montre que 53 % des colonies sont du morphotype africanisé, 17 % du morphotype européen et 30 % appartiennent aux catégories intermédiaires. L'analyse des mitotypes montre que 64 % des colonies appartiennent à la lignée A, 28 % à la lignée C et 4 % à la lignée M. La Figure 1 donne la fréquence et la répartition des morphotypes et des mitotypes par région d'altitude. L'association des morphotypes et des mitotypes est significative ($\chi^2 = 71{,}0285$; df = 3 ; $P < 0{,}01$). Excepté dans les régions tropicales et subtropicales, la population d'abeilles montraient des morphotypes intermédiaires associés à des mitotypes africain ou européeen à des taux allant de 26 % dans le Quechua occidental à plus de 35 % dans le Quechua oriental. Nos résultats montrent que les abeilles d'origine africaine se sont dispersées à travers le Pérou mais que les taux de mélange avec les populations européennes présentes dépendent de l'altitude de la région. Dans les régions tropicales basses, les abeilles d'origine africaine prédominent. Au contraire, dans les régions de haute altitude les hybrides d'origine africaine-européenne représentent le type le plus courant.

Nos résultats sont en accord avec l'existence de zones hybrides climatiques en d'autres endroits, mais des facteurs supplémentaires peuvent aussi être invoqués pour expliquer le résultat de l'africanisation chez les abeilles du Pérou. D'autres conditions, telles que la disponibilité alimentaire et les sites potentiels de nidification, peuvent jouer un rôle crucial dans le succès des abeilles d'origine africaine dans les zones tempérées (Dietz et Vergara, 1995) et méritent une étude complémentaire. Nous concluons que la présence de morphotypes intermédiaires associés aux mitotypes européen ou africain dans les zones de transition et les zones tempérées fournit la preuve d'un processus d'hybridation extensive dû à une meilleure opportunité des colonies d'origine européenne dans la compétition numérique ou écologique avec les homologues africains. Ce résultat signifie aussi que les abeilles d'origine africaine peuvent coloniser avec succès les régions tempérées. Les différences d'altitude au Pérou ont déterminé l'existence de zones où l'hybridation entre abeilles d'origine européenne et d'origine africaine a eu lieu de façon extensive . Ces zones peuvent être considérées comme des zones hybrides où les deux écoptypes coexistent et où les barrières pour la production de descendance viable sont absentes.

***Apis mellifera* / africanisation / hybridation / ADNmt / morphométrie / Pérou**

Zusammenfassung – Hybridisierung zwischen Populationen der Honigbiene (*Apis mellifera*) europäischen und afrikanischen Ursprungs in unterschiedlichen Höhenlagen in Peru. In Peru wurde der jetzige Stand der Vermischung von *Apis mellifera* afrikanischer und europäischer Abstammung bei Populationen in verschiedenen Höhenlagen untersucht. Insgesamt wurden 186 Proben mit Arbeiterinnen aus von Imkern betreuten Völkern in 7 Höhen zwischen 0 und 3 500 m über dem Meeresspiegel mit Hilfe der Morphometrie und von mtDNA RFLPs analysiert.

Vier Körperteile von jeweils 10 Arbeiterinnen wurden in Diarahmen montiert und 25 morphometrische Eigenschaften nach den Methoden von Daly and Balling (1978) and Rinderer et al. (1993a) gemessen. Die Proben wurden nach dem Afrikanisierungsgrad 4 von Rinderer et al. (1993a) vorgeschlagenen Kategorien zugeordnet: afrikanisiert (A), afrikanisiert mit Befunden einer europäischen Introgression (AE), europäisch mit Befunden einer afrikanisierten Introgression (EA) und europäisch (E).

Zusätzlich wurden die 1028 bp des Segments der Cytochrome Oxidase I (COI) und die 964 bp der Region des rRNA Segments der Honigbienen mtDNA (Crozier et al., 1993) amplifiziert. Diese amplifizierten Segmente wurden mit 3 IU von *Hinc* II oder *Eco* RI verdaut. Die Bienen, bei denen in keinem Bereich der amplifizierten Fragmente eine Auftrennung erfolgte, wurden als Bienen mit afrikanischer mtDNA (Linie A) identifiziert (Hall and Smith, 1991; Garnery et al., 1992).

Die Verhältnisse von Morphotypen und Mitotypen wurden für die Höhenlagen bestimmt und die Variabilität in der Assoziation beider Typen wurde mit einer χ^2 Analyse bestimmt. Die morphometrische Analyse ergab, dass 53 % der Völker dem afrikanisierten und 17 % zu dem europäischen Morphotyp angehörten, während 30 % zu einer intermediären Kategorie zugeordnet wurden. Die Analyse der Mitotypen ergab, dass 64 % der Völker zur Linie A, 28 % zur Linie C und 4 % zur Linie M gehörten. Frequenz und Verteilung der Morphotypen und Mitotypen nach der Höhenlage ist in Abbildung 1 gezeigt.

Insgesamt war die Assoziation von Morphotypen und Mitotypen signifikant ($\chi^2 = 71{,}0285$; df = 3; $P < 0{,}01$). Abgesehen von den tropischen und subtropischen Bereichen zeigten die Populationen der anderen Bereiche intermediäre Morphotypen assoziiert mit afrikanischen oder europäischen Mitotypen, die von 26 % in der westlichen Quechua bis über 35 % in der östlichen variierte.

Unsere Ergebnisse zeigen, dass sich Honigbienen mit afrikanischen Eigenschaften über ganz Peru verbreitet haben, aber die Rate der Vermischung mit den ansässigen europäischen Populationen war abhängig von der Höhenlage. In den tropischen Gebieten im Tiefland überwogen die afrikanischen Eigenschaften. Im Gegensatz dazu waren in den höheren Lagen Hybriden mit afrikanisch-europäischen Eigenschaften der häufigste Typ.

Unsere Befunde stehen im Einklang mit dem Vorkommen von klimatischen Hybridzonen an anderen Orten, es könnten aber zusätzliche Faktoren für die Erklärung des Verlaufs der Afrikanisierung der Honigbienen in Peru herangezogen werden. Andere Bedingungen wie Nahrungsangebot und mögliche Nistgelegenheiten könnten eine entscheidende Rolle beim Erfolg der Honigbienen mit afrikanischer Abstammung in gemäßigten Bereichen spielen (Dietz und Vergara, 1995) und sollten weiter untersucht werden. Wir folgern, dass die Präsenz von intermediären Morphotypen assoziiert mit europäischen oder afrikanischen Mitotypen in Übergangsbereichen und in gemäßigten Zonen auf einen extensiven Hybridisierungsprozess hinweisen. Dies hängt mit günstigeren zahlenmäßigen Möglichkeiten der Völker mit europäischer Abstammung zusammen, durch die sie mit den afrikanischen Gegenstücken konkurrieren können. Diese Ergebnisse bedeuten auch, dass Honigbienen afrikanischen Ursprungs erfolgreich gemäßigte Zonen besiedeln können. Dementsprechend bestimmen die Höhenunterschiede in Peru das Vorkommen von Bereichen, in denen die Hybridisierung von Bienen mit europäischer und afrikanischer Herkunft besonders häufig sind und die als Hybridzonen betrachtet werden können, in denen beide Ökotypen vorkommen und es keine Barrieren für die Erzeugung lebensfähiger Nachkommen gibt.

Afrikanisierung / Hybridisierung / *Apis mellifera* / mtDNA / Morphometrie / Peru

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