

Biogeographical correlates of population variance in the honeybees (*Apis mellifera* L) of Africa

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(Received 9 September 1996; accepted 5 March 1997)

Summary — Multivariate analyses of morphometric characteristics of worker honeybees from five transects through northwestern, northeastern, west central, southwestern and southeastern Africa yielded sequences of statistically defined morphoclusters (= subspecies) alternating with heterogeneous zones of introgression. All transects contain areas of significantly high variance. High intra-colonial variance indicates localised genetic variation and out-cross matings. Regions of high inter-colonial variance occur at and between subspecific boundaries. These are typical of transitions between, and rainfall-temperature discontinuities within, different ecological-climatological zones. They constitute areas of ecological instability amidst otherwise contiguous populations.

honeybee / populations / morphometrics / variance / phenology / Africa

INTRODUCTION

From a factor plot of a principal component analysis of morphometric characters Ruttner et al (1978) deduced that *Apis mellifera* comprises three lineages, a conclusion supported by mtDNA analyses (Cornuet and Garnery, 1991a, b; Garnery et al, 1992). Of these, honeybees of the African lineage are classified as several subspecies and/or ecotypes at a continental macrolevel (Ruttner, 1988, 1992; Kerr, 1992). More refined,

mesolevel sampling in a spatial context has begun to illuminate previously undetectable variations in honeybee populations (Lebdi-Grissa et al, 1991; Smith et al, 1991; El-Sarrag et al, 1992; Crewe et al, 1994; Hepburn et al, 1994, 1997; Moritz et al, 1994, 1997; Garnery et al, 1995).

While the discrimination of honeybee races (Ruttner et al, 1978; et alii), ecotypes (Louis and Lefebvre, 1968; Tomassone and Fresnaye, 1971) and genetic lines (Louis et

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al, 1968) can be achieved by principal component analysis, explanations of statistical inferences about honeybee populations should ultimately be interpreted in a context of topography and climate on the one hand and the phenologies of flowering and colony cycles on the other (Ruttner, 1988, 1992). For Africa, another layer of complexity comes with colony movements (reproductive swarming, but especially migrations and amalgamation) that alter the probability of gene flow within and between populations. In this report we define the variance distributions within and between the clusters of several African subspecies of honeybees and indicate probable zones of introgression. These data are then discussed with reference to the biogeographical contexts in which the bees actually live.

MATERIALS AND METHODS

Worker honeybees were sampled from the colonies of small scale, fixed-site beekeepers along five transects in northwestern, northeastern, west central, southwestern and southeastern Africa representing all major ecological-climatic zones of the continent (fig 1). Individual localities and inter-locality distances for each region are indicated in the tables for each transect.

Four to six colonies were sampled at each location along each of the transects. Anderson and van Schalkwyk (1977) and Ruttner (1988) demonstrated that between 10 and 20 bees would be a sufficient sample size for morphometric statistical analysis. Thus, morphometric measurements were made on samples of 20 worker bees/colony. Although Ruttner (1988) employed 36 morphometric characters in his global analysis of honeybees, he also indicated that as few as ten characters were adequate to resolve the honeybees of Africa using stepwise discriminant analysis. Crewe et al (1994) confirmed this result and showed that a suite of only 11 characters provided the same level of discrimination for African bees as had the original suite of 36 characters. Therefore, for all honeybee workers of all transects a standard suite of 11 morphometric characters was measured. Their Ruttner (1988) numbers are given in brackets [except the wing angle MJ1, see Ruttner (1988) fig 6.9, p 73) as

follows: length of cover hair on tergite 5 (1), length of proboscis (4), width of wax plate on sternite 3 (11), length of wax plate on sternite 3 (13), wing angle B4 (22), wing angle N23 (30), wing angle O26 (31), pigmentation of abdominal tergite 2 (32), pigmentation of scutellum (35) and pigmentation of scutellar plate (36).

The means and variances of each morphometric character were calculated for each colony. Multivariate statistical analysis of the colony mean data included principal component analysis (PCA), factor analysis (FA) and stepwise linear discriminant analysis (DA). The last procedure, however, may provide an overly optimistic estimate of the probability of correct classification. A jackknife procedure was therefore carried out which classified each colony into a group with the highest posterior probability according to the discrimination functions computed from all the data except the colony being classified. This is repeated for each colony left out in turn (Lachenbruch and Mickey, 1968).

Wilks' lambda statistic was used to test for significant differences in the cluster vector of means of the characters entered into the discriminant functions. The distribution of the Λ statistic was approximated by the F distribution (Mardia et al, 1979). Mahalanobis distances were calculated between the clusters and $100(1-\alpha)\%$ confidence ellipses constructed for each cluster for various values of α (Cornuet, 1982).

A factor analysis procedure using the character measurements of each bee was carried out to determine the first factor scores of each bee. The intracolony variances were computed at each locality from the factor scores. The inter-colony variances were computed by the same method but this time the colony means were used to determine the first factor scores of each colony. Levene's F statistic was used to test for homogeneity of the intra- and intercolony variances. This test procedure is based on an analysis of variance using the absolute deviation of each case from its locality mean (Brown and Forsythe, 1974). Because of serious implications that may arise from small sample sizes when comparing variances, the localities with fewer than five colonies are indicated for each transect in tables I-V.

The relations of population morphological variation with environmental variables were investigated by canonical correlation analyses. The significance of each canonical variable was tested using Bartlett's statistic approximated by

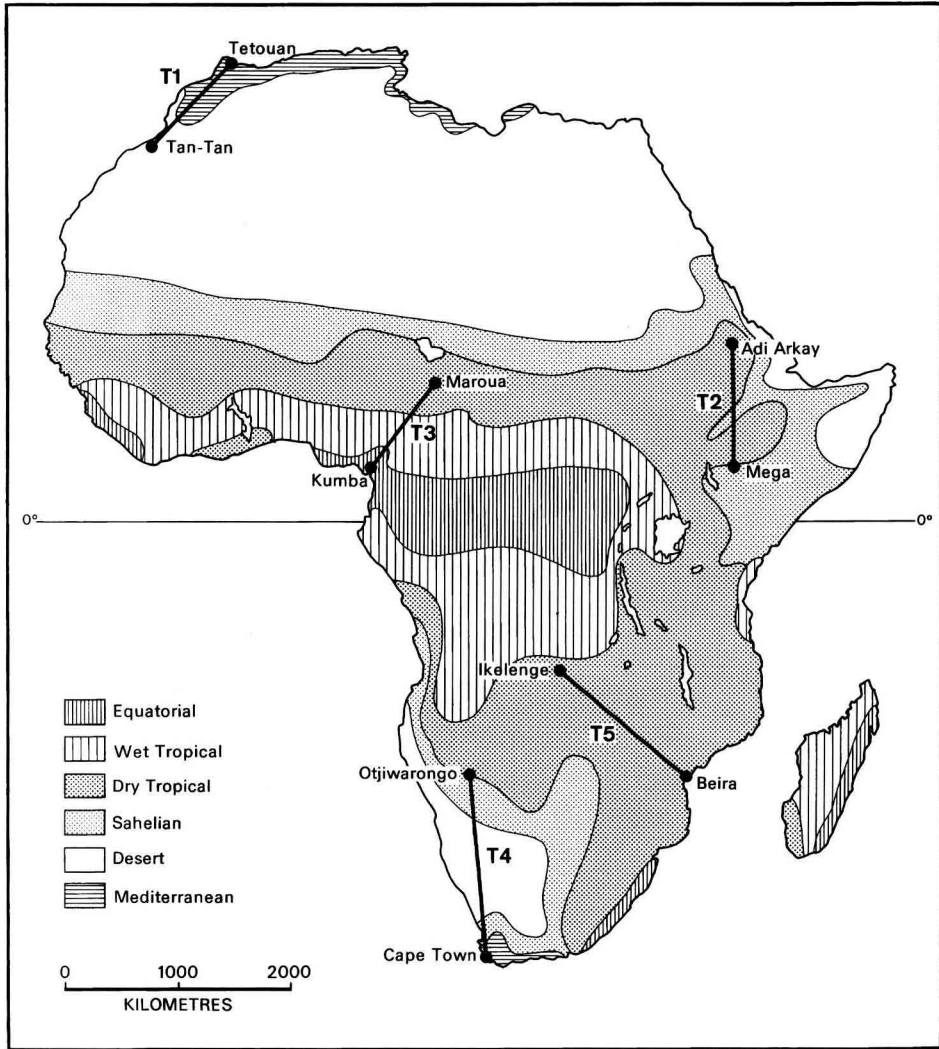


Fig 1. The major ecological-climatological zones of Africa (after van Chi-Bonnardel, 1973; Walter 1973, 1976). Transects sampled and their end-point localities are as follows: T_1 = Morocco; T_2 = Ethiopia; T_3 = Cameroon; T_4 = South Africa-Namibia; T_5 = Mozambique-Zimbabwe-Zambia.

a chi-square distribution. The environmental variables used were temperature, rainfall and altitude at each location. Rainfall and temperature data were taken from Jackson (1961) and Muller (1982). Data on swarming/migration were obtained from beekeepers at the different local-

ities and from the literature (Hepburn and Radloff, 1995). The basic data on morphometrics used in this analysis were obtained from Hepburn and Radloff (1996), Radloff and Hepburn (1997a, b), Radloff et al (1996, 1997).

Table 1. Morphometric and mtDNA clusters, morphometric variances, and swarming for different subspecies of *Apis mellifera* in different climatic zones of northwestern Africa (Morocco) and southern Europe (Spain).

Localities	Coordinates	Distance (km) ^a	Morphometric clusters	mtDNA clusters ^c	Inter-colonial variance	Intra-colonial variance	Swarming and migration	Climatic zones	Remarks
<i>Spain</i>									
Montblanc	41.23N, 01.10E	148	}	}	1.81	6.09*	3-4	}	} T°Δ ^e } RΔ ^e
Benicarlo	40.25N, 00.25E	102			3.00	3.77	3-4 ^d		
Puerto de Sagunto	39.39N, 00.17W	120	} iberica	}	2.01	3.87	3-4 ^d	}	}
Callosa d'Ensania	38.40N, 00.18W	102			3.11	3.22	3-4		
Totana	37.46N, 01.30W	153	}	}	0.37	3.57	2-3	} mediter-ranean	}
Berja	36.57N, 02.56W	106			0.76	3.13	2-3 ^d		
Alhaurin el Grande	36.44N, 04.42W	143			3.73	5.21	2-3		
<i>Morocco</i>									
Tetouan ^f	35.34N, 05.22W	102	}	}	9.21	10.87*	3-5	}	} RΔ ^e
Ksar-el-Kebir	35.04N, 05.56W	190			5.15	10.44*	3-5		
Ez Zhliliga	33.18N, 06.30W	245	} intermissa	}	4.07	6.08	3-5	}	} RΔ ^e
Marrakech	31.49N, 08.00W	176			2.75	6.72	2-4		
S Rabat	31.02N, 06.51W	273	} sahariensis	}	2.19	11.25*	2-4	}	} T°Δ, RΔ ^e
Tan Tan	28.30N, 11.02W				6.45	9.43*	2-4		

^a The value next to a locality is the distance to the locality immediately below it; ^b biometric subgroups (unnamed) at the 90% confidence level; ^c significantly different heterogeneity groups (unnamed) derived from the data of Garnery et al. (1995) using the test of Oreenacre (1988); ^d altitude moderated; ^e area where there is a major shift in prevailing temperature, T°Δ, or rainfall, RΔ; ^f small sample size. * Significant ($P < 0.01$).

Table II. Morphometric clusters and variances, swarming and migration for different subspecies of *Apis mellifera* in different climatic zones of northeastern Africa (Ethiopia).

Localities	Coordinates	Distance (km) ^a	Morphometric clusters ^b	Inter-colonial variance	Intra-colonial variance	Swarming and migration ^c	Climatic zones	Remarks	
Adi Arkay	13.35N, 37.57E	116	} <i>jemenitica</i>	1.84	5.11**	5-6	} dry	} RΔ ^e	
Gonder	12.39N, 37.29E	117		5.30*	5.97**	9-11			} tropical
Bahir Dar	11.33N, 37.25E	124		2.49	4.85**	9-11			
Debre Markos	10.19N, 37.41E	141	} <i>bandasii</i>	1.44	2.71	9-11	} sahelian	} RΔ ^e	
Holeta	09.03N, 38.41E	209		4.46*	3.69	9-11			} dry
Shashemene	07.13N, 38.33E	181		3.52	3.50	5-6			
Agere Maryam	05.13N, 38.20E	186	} <i>sudanensis</i>	2.77	3.95	9-11	} tropical	} RΔ ^e	
Mega	04.02N, 38.19E			1.37	4.20	9-11			desert

^a The value next to a locality is the distance to the locality immediately below it; ^b subspecific names for this region *sensu* Mogga (1988); in Ruttner (1988) system, all would be *Am. jemenitica*; ^c swarming periods inferred from Kassaye (1990); ^d altitude moderated; ^e area where there is a major shift in prevailing rainfall, RΔ. * Significant ($P < 0.05$), ** ($P < 0.01$).

Table III. Morphometric clusters and variances, swarming and migration for different subspecies of *Apis mellifera* in different climatic zones of west central Africa (Cameroon).

Localities	Coordinates	Distance (km) ^a	Morphometric clusters	Inter-colonial variance	Intra-colonial variance	Swarming and migration	Climatic zones	Remarks
Maroua	10.36N, 14.20E	176	} <i>jemenitica</i>	2.22	3.57	9-10, 4-5	} dry	} T°Δ, RΔ ^c
Garoua	09.18N, 13.24E	56		6.14*	5.61**	9-10, 4-5		
Gouna	08.32N, 13.34E	116	} <i>adansonii</i>	4.74	4.79	9-10, 4-5	} wet	} T°Δ ^c
Lewa ^d	07.19N, 13.35E	160		1.78	3.94	11-12, 2-3, 3-5		
Banyo ^d	06.45N, 11.49E	120	2.37	3.83	8-9, 2-3	} b	} equatorial	
Kumbo ^d	06.12N, 10.40E	60	1.54	3.18	8-9, 2-3			} T°Δ ^c
Bamenda	05.56N, 10.10E	76	} 'monticola-like'	6.36*	5.43**	8-9, 2-3	} T°Δ ^c	
Mamfe	05.46N, 09.17E	24		1.86	2.87	9-10, 2-3		
Kumba ^d	04.38N, 09.25E	24	} <i>adansonii</i>	4.62	4.42	9-10, 2-3	} equatorial	

^a The value next to a locality is the distance to the locality immediately below it; ^b altitude moderated; ^c area where there is a major shift in prevailing temperature, T°Δ, or rainfall, RΔ; ^d small sample size. * Significant ($P < 0.05$), ** ($P < 0.01$).

Table IV. Morphometric clusters and variances, swarming and migration for different subspecies of *Apis mellifera* in different climatic zones of southwestern Africa (South Africa and Namibia).

Localities	Coordinates	Distance (km) ^a	Morphometric clusters	Inter-colonial variance	Intra-colonial variance	Swarming and migration	Climatic zones	Remarks
<i>Namibia</i>								
Otiwarongo	20.29S, 16.36E	152	} <i>adansonii</i>	1.74	7.78	8-9	} dry tropical } sahelian	} RΔ ^b
Okahandja	21.59S, 16.58E	62		3.69	6.00	8-9		
Windhoek	22.43S, 17.06E	207		9.92	11.16*	9-10		RΔ ^b
Mariental	24.36S, 17.59E	200		9.86	9.80	9-10	} desert	} T°Δ ^b
Keetmanshoop	26.36S, 18.08E	145		2.43	5.81	9-10		
Karasburg	28.00S, 18.43E	169		2.50	6.81	9-10		
<i>South Africa</i>								
Nababeep	29.36S, 17.46E	148	} <i>scutellata</i>	6.45	7.95	7-8	} sahelian	} RΔ ^b
Bitterfontein	31.03S, 18.16E	159		6.26	10.48*	8-9		
Citrusdal	32.36S, 19.00E	145		9.72	9.98	9-10		T°Δ ^b
Cape Town	33.56S, 18.28E		} <i>capensis</i>	3.32	7.66	9-12	} mediterranean	

^a The value next to a locality is the distance to the locality immediately below it; ^b area where there is a major shift in prevailing temperature, T°Δ, or rainfall, RΔ. * Significant ($P < 0.10$), ** ($P < 0.01$).

RESULTS

Northwestern Africa and southern Europe

Comprehensive multivariate analyses of the worker honeybees along a transect from the Sahara to the Pyrénées (fig 1) unequivocally established the occurrence of three major morphoclusters that are classified as *sahariensis*, *intermissa* and *iberica* (table I). In addition, the *iberica* cluster could be further resolved into three biometric subgroups. Moreover, when the original mtDNA data of Garnery et al (1995), obtained from different localities but in the same region, was subjected to Greenacre's (1988) method of analysis, six distinct and significantly different mtDNA subgroups were obtained (table I).

When the variances of the morphometric characters were tested for homogeneity, a significant difference was found between the intracolony variances over all localities (table I, Levene's test $F = 4.54$ with 12,730 df, $P < 0.0001$). In pair-wise tests between localities the variances obtained for Tan Tan, S Rabat, Ksar-El-Kebir, Tetouan (small sample) and Montblanc were significantly different from the other localities along this transect (table I). There were no significant differences in the intercolony variances between localities (table I, $F = 1.57$ with 12,60 df, $P = 0.1239$); however, large values of variance were obtained for Tan Tan, Tetouan (small sample) and Ksar-El-Kebir (Hepburn and Radloff, 1996).

A canonical correlation analysis revealed a significant correlation ($R = 0.97$) between the set of morphological characters and the set of environmental variables (table VI). The largest squared multiple correlation was found between temperature and the set of morphometric variables ($R^2 = 0.93$, $P < 0.0001$).

Northeastern Africa

Multivariate analyses of worker honeybees along a north-south transect through the highlands of Ethiopia (fig 1) yielded three morphometrically distinct clusters, which are classified as *jemenitica*, *bandasii* and *sudanensis* (table II). This represents a subdivision of *jemenitica* (Ruttner, 1988) subsequent to the availability of considerably enhanced data bases for this region (Mogga, 1988; El-Sarrag et al, 1992; Radloff and Hepburn, 1997a). The variances of the first factor scores of the morphometric characters were used to test for homogeneity of the intracolony variances at each locality. A significant difference was found between the variances (Levene's test $F = 15.00$ with 7,825 df, $P < 0.0001$) and concentrated between Adi Arkay and Gonder (table II). The intercolony variances were computed for each locality and Levene's test used to test for heteroscedasticity. A significant difference at the 10% level of significance was established between the intercolony variances ($F = 2.10$ with 7,34 df, $P = 0.0704$). Large values of variance were noted for Gonder and Holeta (table II).

A significant canonical correlation ($R = 0.83$) was established between the set of morphological characters and the set of environmental variables (table VI). The largest squared multiple correlation was found between rainfall and the set of morphometric variables ($R^2 = 0.69$, $P = 0.0026$).

West central Africa

Multivariate analyses of worker honeybees along a transect from southwestern to northeastern Cameroon (fig 1) showed that these honeybees resolved into three distinct morphoclusters. The honeybees of southern and central Cameroon are classified as *adansonii* whose distribution is intruded in the southern Bambouto mountains by a large, *monticola*-like bee, while those in the north

consist of a discrete population of the smaller *jemenitica* (table III).

In tests for homogeneity of the variances of the morphometric characters at each locality significant differences were found for all intracolony variances (table III, Levene's test $F = 8.38$ with 8,771 df, $P < 0.0001$). Intercolony variances computed by the same method resulted in significant differences between localities, notably Bamenda and Garoua (table III, $F = 2.22$ with 8,31 df, $P = 0.0529$).

A canonical correlation analysis was used to assess the environmental variability in honeybees along the transect. A significant canonical correlation ($R = 0.83$) was obtained between the set of morphological characters and the set of environmental variables (table VI). Larger squared multiple correlations were determined between rainfall and temperature and the set of morphometric variables (rainfall: $R^2 = 0.85$, $P < 0.0001$; temperature: $R^2 = 0.75$, $P < 0.0001$).

Southwestern Africa

Multivariate analyses of worker honeybees along a transect from the Cape peninsula in South Africa to northern Namibia (fig 1) established the occurrence of three distinct and homogeneous morphoclusters. These are classified as *capensis* in the southernmost Cape, *scutellata* in northern South Africa and southern Namibia, and *adansonii* in the far north (table IV).

In tests of homogeneity of the variances of the morphometric characters, intracolony variances for all localities differed significantly (table IV, Levene's test $F = 1.89$ with 6,553 df, $P = 0.0808$). While there were no significant differences between the intercolony variances, notably high values were associated with Citrusdal, Mariental and Windhoek (table IV, $F = 1.29$ with 6,21 df, $P = 0.3052$).

A canonical correlation analysis showed no significant correlation between the set of morphological characters and the set of environmental variables (table VI).

Southeastern Africa

Multivariate analyses of worker honeybees along a transect from coastal Mozambique through the highlands of Zimbabwe and on to northwestern Zambia (fig 1) indicate that these honeybees morphometrically resolve into three distinct populations. These groups are respectively classified as *litorea*, *scutellata* and *adansonii* and are distributed as shown in table V.

When homogeneity of the variances was assessed a significant difference was found between the intracolony variances over all the localities (table V, Levene's test $F = 2.30$ with 7,752 df, $P = 0.0251$). Larger variances were found at Karoi and Kitwe. While, no significant difference was found in the intercolony variances between localities (table V, $F = 1.40$ with 7,30 df, $P = 0.2415$), the intercolony variation was again higher between the Karoi and Kitwe regions.

A significant canonical correlation ($R = 0.89$) was found between the set of morphological characters and the set of environmental variables (table VI). The largest squared multiple correlation was between temperature and the set of morphometric variables ($R^2 = 0.76$, $P = 0.0008$).

Inter-transect correlations and variances

A canonical correlation analysis performed on all five transects (fig 1) yielded a significant correlation between the full set of morphological characters and the full set of environmental variables (table VI). In these comparisons, temperature variation was the most significant factor in the relationship ($R^2 = 0.62$, $P < 0.0001$). Similarly, Levene's

Table V. Morphometric clusters and variances, swarming and migration for different subspecies of *Apis mellifera* in the woodland savanna of south-eastern Africa (Mozambique, Zimbabwe and Zambia).

Localities	Coordinates	Distance (km) ^a	Morphometric clusters	Inter-colonial variance	Intra-colonial variance	Swarming and migration	Climatic zones	Remarks
Zambia								
Ikelenge	11.30S, 24.05E	200	} <i>adansonii</i>	2.79	4.90	8-9	} dry } T°Δ, RΔ ^c	}
Solwezi	11.28S, 26.23E	172		3.33	5.02	8-9		
Kitwe	12.48S, 28.14E	202		3.36	5.85	8-9, 3-4		
Lusaka ^d	15.26S, 28.20E	286		3.45	4.77	8-10, 3-4		
Zimbabwe								
Karoi	16.46S, 29.45E	162	} <i>scutellata</i>	4.73	6.17*	8-10, 3-4 ^b	} tropical } T°Δ ^c	}
Harare	17.43S, 24.13E	124		2.22	5.64	8-10		
Mutare	19.00S, 32.40E	238		2.72	5.27	9-11		
Mozambique								
Beira ^d	19.49S, 34.52E		} <i>litorea</i>	1.02	4.92	9-11		

^a The value next to a locality is the distance to the locality immediately below it; ^b facultative swarming associated with development of *Eucalyptus* plantations in recent decades; ^c area where there is a major shift in prevailing temperature, T°Δ, or rainfall, RΔ; ^d small sample size. * Significant ($P < 0.05$), ** ($P < 0.01$).

Table VI. Canonical correlations between the full set of morphological characters and the set of environmental variables (temperature, rainfall and altitude) for each transect.

<i>Transect</i>	<i>Canonical correlation</i>	χ^2 - <i>statistic</i>	<i>df</i>	<i>P-value</i>
Northwestern	0.97	285.6	33	$P < 0.0001$
Northeastern	0.83	75.4	33	$P < 0.0001$
West central	0.94	113.9	33	$P < 0.0001$
Southwestern	0.83	44.6	33	$P = 0.0862$
Southeastern	0.89	80.6	33	$P < 0.0001$
Combined	0.91	610.6	33	$P < 0.0001$

test was used to test for significant differences in the variations in temperature, rainfall and altitude over all five transects. Significantly larger variations in temperature ($F = 10.6$, $P < 0.0001$), rainfall ($F = 56.4$, $P < 0.0001$) and altitude ($F = 13.3$, $P < 0.0001$) were found along the west central transect and in temperature along the northwestern transect.

DISCUSSION

A morphometrically discrete honeybee population is based on group homogeneity obtained through multivariate analysis (Ruttner et al, 1978; Ruttner, 1988). In the absence of physical, phenological or reproductive barriers, clinal changes between adjacent populations may be reflected in their variance spectra (Futuyma, 1986). The variance may also indicate the 'genetic permeability of statistical boundaries' between neighbouring populations and sometimes also the direction of flow at a point in time. The interpretation of population variance becomes more meaningful in a biogeographical context.

In northwest Africa the structure and variance characteristics of the honeybee populations extending between the Sahara and the Pyrenees can be related to prevailing climatic and biological factors (table I). The

area is a winter rainfall region but with notable discontinuities (Jackson, 1961; Muller, 1982). There is a phase change in the dry season from months 5 to 9 in the south to 7–9 in the north of Morocco; that of Spain is further reduced to months 6–8. There are also discontinuities in rainfall, which is most intense for months 10–4 in the south and north but compressed to months 11–2 in the central area of Morocco; a similar pattern occurs in Spain (Jackson, 1961; Muller, 1982). These factors of climate are reflected in the flowering phenologies of the principal bee plants, which in turn drive the annual colony cycle (Hepburn and Radloff, 1995).

Similarly there are important discontinuities in the temperature profiles of the transect (S Rabat and Puerto de Sagunto) where equableness for honeybee flight is significantly reduced. The swarming season begins early in southern Morocco, gradually shifting over the 1 000 km to the north coast (table I); the same sequence is repeated in southern and eastern Spain (Verdu Gallardo, Garcia Raso, pers comms). The degree of overlapping of swarming seasons between adjacent localities varies from year to year. The general trend of the data shows that centroids of high variance (near edges of clusters defined morphometrically or by mtDNA analysis) are typically associated with climatic and biological areas of transi-

tion (table I), which are regions of ecological instability from the perspective of a contiguous population.

In northeast Africa (fig 1) Ethiopia is a mountainous country of tortuous relief. The central highlands are well-watered and the temperatures are moderated by altitude, which averages more than 2 000 m. While the highlands lack large variations in temperature, rainfall discontinuities and transitions along the transect are pronounced (fig 1, table II). Rainfall diminishes from south to north and is intense during months 6–10 with a correspondingly long dry season, months 11–5 (Jackson, 1961; van Chi-Bonnardel, 1973). Despite widespread bee-keeping activity in this region, it is extremely sparsely documented in the apicultural literature.

There are two major centroids of significantly high variance for this region (table II). The most notable one, to the north, occurs within the *jemenitica* morphocluster and transgresses into the *sudanensis* morphocluster. The boundary between the two clusters is climatically transitional between dry tropical and sahelian zones. The second centroid, at Holeta (very near Addis Ababa), is associated with a thin wedge of sahelian climate between two dry tropical zones.

In west central Africa the population structure of the honeybees can be related to the climatic and biological conditions of the regions studied (fig 1). Cameroon is transitional between the equatorial and the dry tropical zones, a physiographic ensemble extending from sea level, through mountains and massif, gradually descending into depressed alluvial plains in the northern interior (van Chi-Bonnardel, 1983). These physical transitions are associated with different ecological–climatological zones (Walter, 1973, 1976) and significant differences in the honeybee populations of the region reflect the environmental variation (table III).

There are two centroids of significantly high variance in the region; the first is centred on Garoua and the second in the Mamfe-Bamenda area (table III). The two centroids are interpreted, respectively, as zones of hybridization between *adansonii* and the *monticola*-like group to the south and between *adansonii* and *jemenitica* to the north. It is evident from table III that the high variance distribution in the honeybees is coincident with ecological–climatological transitions and their associated discontinuities in temperature and rainfall, indicators of ecological instability. Obviously hybridization between adjacent localities is facilitated by the extent to which their swarming and migration periods overlap (table III).

In southwestern Africa (fig 1) the multivariate analyses of the bees show a northward progression from *capensis* at the Cape peninsula, through *scutellata* and to *adansonii* in northern Namibia (table IV). Areas of introgression and hybridization can be anticipated from the variance distributions in relation to the climatic zones (table IV). High variances are associated with edge effects between different climatic zones as well as at areas where there are local discontinuities in the rainfall and temperature profiles. The honeybee populations of this region of southwestern Africa appear far less stable than the others studied as evidenced by the distribution widths of high variance values and relatively small morphocluster areas. It is also evident that overlap in swarming also shifts in conjunction with climatic transition.

In southeastern Africa the whole of the Beira–Ikelenge region falls in the same dry tropical climatic zone (fig 1; Walter, 1973; Cole, 1986) but variations occur. The plains of Mozambique are +8 °C above the Zimbabwe highveld and the temperature transition at the Mutare escarpment is abrupt. The temperature profile across the highveld is rather uniform except for an interesting

+6 °C discontinuity at the Zambezi River Valley (Jackson, 1961). This area is a centroid of high variance values and of introgression between *adansonii* and *scutellata* (table V).

The temporal distribution of swarming and migration shows considerable overlap across the transect (table V) but a second swarming season (months 2–4) has developed in recent decades with the introduction of *Eucalyptus* plantations into the Karoi region (Coleman, pers comm). The intercalation of another swarm period, coupled to those of south central Zambia, provides a considerable corridor for gene flow and further instability in a region that is already a centroid of high variance. Reduced contact through swarming and migration in the bees of Zambia can be related to flowering. In the Lusaka–Kitwe area *Brachystegia* and *Julbernardia* support two swarm periods; but *Brachystegia* is virtually absent from the Solwezi–Ikkelenge area, leaving a single swarming season (table V, Silberrad 1976; Chupa, pers comm) and, notably lower levels of variance.

Statistically derived and homogeneous morphoclusters (= subspecies *sensu* Ruttner, 1988) occur in all of the transects of Africa investigated (tables I–V). The linear distance occupied by each subspecific morphocluster, where two boundaries could be measured ($n = 7$), averages 475 ± 282 km and the width of introgression zones between two adjacent populations 125 ± 146 km, a distance within the annual dispersal capacity of these honeybees. Nonetheless different honeybee traits (nuclear and mtDNA, pheromones, flight capacity) disperse between these populations to differing distances and, presumably, at different rates (Hepburn et al, 1994, 1997; Garnery et al, 1995; Moritz et al, 1994, 1997).

All of the transects contain areas of significantly high intracolony and intercolony variance. The former are interpreted as evidence pointing to a high intrinsic genetic

variation in localised drone congregation sites, hence similar percentage of out-cross matings (Moritz and Southwick, 1992). Centroids of high intercolony variance suggest a high genetic ‘permeability’ in the statistical boundaries of populations resulting in introgression zones between neighbouring populations. Centroids of high variance are closely associated with transitions between, and discontinuities of rainfall and temperature within, the different ecological–climatological zones. Finally, high levels of statistical heterogeneity within and between populations go hand-in-hand with ecological instability (table VI).

Résumé — Corrélats biogéographiques de la variance de la population chez l’abeille mellifère (*Apis mellifera* L) d’Afrique. Des ouvrières d’abeilles ont été prélevées le long des transects suivants, faisant chacun plus de 1000 km : Maroc–Espagne, Éthiopie, Cameroun, Afrique du Sud–Namibie et Mozambique–Zimbabwe–Zambie (fig 1). Onze caractères morphométriques ont été analysés par des méthodes statistiques multivariées. On a obtenu des groupes définis morphométriquement (tableaux I–V), qui ont été considérés comme des sous-espèces (Ruttner, 1988). Une attention particulière a été portée à l’estimation de la variance comme moyen d’établir les zones de répartition des sous-espèces et de définir les zones d’introgression entre elles.

Les populations d’abeilles des cinq transects montrent une alternance séquentielle de régions ayant une homogénéité statistique (sous-espèces) et de zones de forte variance et d’hétérogénéité (tableaux I–V). Ces dernières sont interprétées comme étant des zones d’introgression entre populations subséquentielles adjacentes. Des régions localisées de forte variance intracolonyale existent et sont considérées comme une preuve de l’ample variation génétique sur les sites

de rassemblement de mâles et d'un nombre élevé de croisements entre les sous-espèces. Il existe aussi des centres de forte variance intercoloniale le long de chacun des transects (tableaux I–V) ; ils sont interprétés comme des zones d'introggression. Ils sont étroitement associés à des transitions entre différentes zones écoclimatologiques (fig 1) et à des discontinuités précipitations/températures à l'intérieur de ces zones. Ainsi sont associés de façon caractéristique un fort degré d'hétérogénéité au sein des populations, et entre elles, et des régions d'instabilité écologiques.

Une analyse de corrélation a montré l'existence d'une relation forte variance–instabilité écologique (tableau VI). Elle a mis en évidence des corrélations significatives entre l'ensemble des caractères morphologiques et l'ensemble des variables du milieu (température, précipitation et altitude). Parmi ces dernières, la température est le facteur le plus significatif.

***Apis mellifera* / génétique des populations / morphométrie / variance / phénologie / Afrique**

Zusammenfassung — Biogeographische Korrelation von Populationsvarianzen bei Honigbienen (*Apis mellifera* L) von Afrika. Proben von Honigbienen wurden entlang von fünf Schnittlinien mit Längen von über 1 000 km in folgenden Gebieten gesammelt: Marokko–Spanien, Äthiopien, Kamerun, Süd Afrika–Namibia und Mozambique–Simbabwe–Sambia (Abb 1). Elf morphologische Merkmale wurden mit multivariablen statistischen Methoden analysiert. Es wurden morphometrische definierte Cluster gefunden (Tab I–V) und Rassen (Ruttner, 1988) zugeordnet. Besondere Aufmerksamkeit galt der Bestimmung der Varianz als Mittel, um die Reichweite der Rassen festzulegen und um Zonen ihrer Hybridisierungen zu definieren.

Die Honigbienenpopulationen dieser fünf Schnittlinien zeigten einen aufeinanderfolgenden Wechsel von Regionen statistischer Einheitlichkeit (Rassen) mit Gebieten mit hoher Varianz und Verschiedenheit (Tab I–V). Letztere werden als Überlappungszonen zwischen den benachbarten rassetypischen Populationen interpretiert. Begrenzte Regionen mit hoher Varianz innerhalb eines Volkes wurden als Beweis für eine große genetische Variation auf den Drohnensammelplätzen und für hohe Anteile von Auskreuzungspaarungen angesehen.

Entlang aller Schnittlinien gab es Schwerpunkte mit hoher Varianz zwischen den Völkern (Tab I–V), die als Zonen der Hybridisierung angesehen werden. Diese hochvariierenden Schwerpunkte sind mit Übergängen zwischen den verschiedenen ökologisch-klimatologischen Zonen und unregelmäßigen Temperaturen während der Regenfälle (Abb 1) klar verbunden. Demnach ist ein hoher Grad der Verschiedenartigkeit innerhalb und zwischen den Populationen typischerweise mit Regionen von ökologischer Instabilität assoziiert.

Eine hohe varianz-ökologische Beziehung der Instabilität wurde in einer kanonischen Korrelationsanalyse gezeigt (Tab VI), die signifikante Korrelationen zwischen der Wertmenge der morphologischen Merkmale und der Wertmenge der Variablen der Umwelt (Temperatur, Regenfall und Höhe) ergab. Von diesen Variablen war die Temperatur der bedeutendste Faktor ($R^2 = 0.62$, $P < 0.001$).

Honigbienen / Population / Morphometrie / Varianz / Phänologie / Afrika

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