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Author(s): G. R. Steele, M. H. Villet, S. E. Radloff and H. R. Hepburn

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Clinal morphometric variation in wild honey bees (Hymenoptera: Apidae) in South Africa

G. R. STEELE[1], M. H. VILLET[1]†, S. E. RADLOFF[2] and H. R. HEPBURN[1] [1]*Department of Zoology & Entomology* [2]*Department of Statistics, Rhodes University, Grahamstown, South Africa 6140*

Abstract. As a result of side effects of the accidental dispersal of the Cape honey bee, it has become of agro-economic importance to delineate the region within South Africa where thelytokous worker honey bees occur so that apicultural movement of bees does not exacerbate the problem. Thelytokous workers are believed to be unique to *Apis mellifera capensis*, so that the problem is to find morphological markers distinguishing this race from its *A. m. scutellata* neighbours. However, no evidence of the expected hybrid zone demarcating races could be found. Factor analysis revealed only one spherical cluster of samples. Trend surfaces of the local mean morphometric factor scores showed a cline that paralleled latitude, with distortions relating to montane and continental effects. Discriminant function analysis implicated certain mountain ranges in amplifying the effects of latitude. Trend surfaces of local intercolony factor variance showed morphometric homogeneity across most of the country. We conclude that there is only a single population of honey bees in South Africa, and that it shows climate-correlated clinal variation.

If the transportation of bees for commercial apiculture is to be successfully regulated to solve the '*capensis* calamity', further research should focus on the geographical distribution of thelytokous workers rather than on the *capensis* phenotype. Such workers have a wider distribution than *capensis*, occurring also at high frequencies around the type locality of *A. m. scutellata*.

Key words. Honey bees, apiculture, applied systematics, climate.

INTRODUCTION

The geographical distribution of the Cape honey bee, *Apis mellifera capensis*, has recently become of great economic importance in South Africa (Allsopp, 1992; Greeff, 1997) because its workers characteristically lay diploid eggs by thelytokous parthenogenesis (Onions, 1912, 1914; Verma & Ruttner, 1983; Hepburn & Crewe, 1991), which enables them to invade colonies and displace *A. m. scutellata* queens. *Apis m. capensis* workers recently became established well within the geographical range of the other South African race, *A. m. scutellata*, where they were discovered in many colonies of *A. m. scutellata* which showed decreased productivity and eventual collapse following thelytokous reproduction by the Cape workers (Allsopp, 1992; Greeff, 1997). It is surmised that drifting of *A.*

m. capensis workers occurred during or following the movement of colonies of both races used for pollination services, and led to reproductive competition that debilitated the host *A. m. scutellata* colonies. Legislative regulation of such transportation would help to stem this problem, and thus it was considered important to map the geographical boundaries of the two races in South Africa.

Various authors (Anderson & van Schalkwyk, 1977; Tribe, 1983; Moritz & Kauhausen, 1984; Ruttner, 1988; Hepburn & Crewe, 1990, 1991; Crewe, Hepburn & Moritz, 1994) have advanced different theories about the geographic distribution of these races, and the whereabouts and geographical extent of hybridisation that exists between them. It was even suggested that *A. m. capensis* was on the verge of extinction (Moritz & Kauhausen, 1984). It was further suggested that the mountain ranges of the southern Cape acted as barriers between the races (Tribe, 1983; Hepburn & Crewe, 1991), helping to define them. However, parallel studies

† Corresponding author; e-mail: m.villet@ru.ac.za

of their mtDNA (Moritz *et al.*, 1994), reproductive biology (Hepburn & Crewe, 1991) and alarm pheromones (Hepburn, Jones & Kirby, 1994) yielded geographic patterns that were mutually discordant and thus at odds with the existence of a hybrid zone between two populations.

Base on studies using spatial resolutions of the order of 10^3 kilometres for an area of 30 million km^2, some eleven races and/or ecotypes of honey bees are currently accepted to occur in Africa (Ruttner, 1988, 1992; Kerr, 1992). However, finer sampling resolutions reveal morphometric variation within races previously defined at the larger scale (Mogga, 1988; Cornuet & Fresnaye, 1989; Daly, Hoelmer & Gambino, 1991; El-Sarrag, Saeed & Hussein, 1992), including *A. m. scutellata* in southern Africa (Smith, 1969; Ruttner, 1988; Daly, 1991; Radloff *et al.*, 1996; Radloff, Hepburn & Villet, 1997).

These lines of research indicate the need for finer spatial sampling of the South African honey bees. Further data have been collected since the last study of the morphometrics of the southern African races and their hybrids (Crewe *et al.*, 1994). The overall mean distance in some areas has thus been decreased from about 200 km to about 50 km in an attempt to get a clearer picture of the putative hybrid zone between the races. We have also examined the role of mountains in producing geographic variation in the honey bees of southern Africa.

MATERIALS AND METHODS

Data from eighty-five different locations throughout South Africa (Table 1, Fig. 1) were used in this study: thirty-two locations (two of which were resampled) used by Crewe *et al.* (1994) and fifty-three new locations. A total of 393 colonies were sampled, ranging from one to eleven colonies per location (eleven locations were represented by four colonies; twenty-four locations by five colonies; and twenty-five locations by six colonies). Twenty bees from each colony were measured. All samples were collected in December or January.

Twelve of the thirteen morphometric characters used by Crewe *et al.* (1994) to differentiate between the two southern races were measured (Table 2). The transverse width of the forewing was excluded from the character set due to missing data for some colonies.

Factor analysis and linear discriminant analysis were applied to the colony means for each character. The first factor loadings from the factor analysis were used to determine a factor score at each colony. Means and variances of these factor scores were calculated for each of the locations, and trend surface maps of these data were generated by krigeing using an inverse-square method of interpolation that would model gene flow. This method assumes that there is a gradient between the sample points, an assumption which is justified in this case because one expects genes to spread from any point where they are found, so that neighbouring localities are not independent unless local selection is very strong. The inverse-square method assumes spherical diffusion of genes from each source, the simplest model in the absence of evidence of the actual pattern of gene dispersal. This also takes into account the fact that, the further apart points are, the less accurately contours between them can be interpolated. One must be alert for artifacts on the edges of the trend surface, but where sample points surround the contours the latter are reliably placed.

RESULTS

Factor analysis

No significant correlation between any of the twelve morphometric variables was obtained, supporting the inclusion of all of them in multivariate analyses. When the first two components of the factor analysis were plotted against one another as a scatter diagram, the points formed one large spherical cluster with no elongation or any suggestion of subclusters. The trend surface of the mean first factor scores shows a trend of increasing score from the southwest to the northeast, with a notably sharper increase in the most southwestern parts of the subcontinent (Fig. 2). The factor loadings for the first component of the factor analysis showed that this was indicative of the bees in the southwest being smaller and more darkly pigmented than the bees in the northeast.

The trend surface of the factor score variances (Fig. 3) showed low levels of within-site variation across most of the country, with a northeast-southwest trend towards higher values along the western edge of the subcontinent. There is a zone of very high variance on the west coast between Elandsbaai and Clanwilliam, and a low peak on the southeast coast near East London.

Table 1. Locality, latitude and longitude of the eighty-five locations sampled in this study, with the number of colonies at each site predicted to belong to groups, 1, 2, or 3 by the discriminant analysis, and the phenon to which the bees of the locality were assigned (1, *A. m. capensis*, 2, Eastern Cape *A. m. scutellata*; 3, northern *A. m. scutellata*), based on their location relative to the mountain ranges of South Africa (Fig. 1).

Locality	Location South	East	DFA prediction 1	2	3	Actual classification	Locality	Location South	East	DFA prediction 1	2	3	Actual classification
Aberdeen	32°29″	24°03″	2	1		1	Murraysburg	31°58″	23°47″		1		2
Addo	33°29″	25°46″		5		2	Napier	34°28″	19°54″	5			1
Alexander Bay	28°40″	16°30″			6	3	Nelspoort	32°07″	23°01″		1	1	3
Aliwal North	30°45″	26°45″		6		2	Nieuwoudsville	31°24″	19°06″	1	1	3	3
Ariamsvlei	28°08″	19°05″			4	3	Nigel	26°30″	28°28″			6	3
Badplaas	25°58″	30°34″			6	3	Paarl	33°45″	18°56″	5			1
Beaufort West	32°18″	22°36″	6	2	2	1	Port Elizabeth	33°58″	25°40″	6			1
Bitterfontein	31°03°	18°16″			3	3	Piketberg	32°54″	18°46″	4	1		1
Boesmanskop	32°00″	24°19″		3		2	Posmasburg	28°18″	23°05″			4	3
Bonnievale	33°55″	20°05″	5			1	Queenstown	31°52″	27°00″		7	4	2
Booiskraal	31°50″	22°30″		2		2	Richmond	31°23″	23°56″		1	1	2
Botterkloof	31°49″	19°17″		1	2	3	Riviersonderend	34°10″	19°55″	3			1
Britstown	30°37″	23°30″			4	3	Sandvlei	33°36″	19°52″	5			1
Burgersdorp	30°59″	26°20″		4		2	Skipskop	34°33″	20°24″	3	2		1
Calvinia	31°25″	19°45″		1	4	3	Smithfield	30°09″	26°30″		4		2
Ceres	33°21″	19°18″	3			1	Somerset West	34°08″	18°50″	5			1
Citrusdal	32°36″	19°00″	4	1		1	Sonop	31°57″	19°44″			3	3
Clanwilliam	32°11″	18°54″	1	4		3	Springfontein	30°19″	25°36″			6	3
Cradock	32°08″	25°36″	1	5		2	Sterkstroom	31°34″	26°33″		6		2
Darling	33°23″	18°23″	5			1	Steynsburg	31°20″	25°50″		1	2	3
Dordrecht	31°20″	27°03″		6		2	Stutterheim	32°33″	27°28″		6		2
Durban	29°55″	31°00″			5	3	Sutherland	32°24″	20°40″	1		5	3
East London	32°58″	27°55″		3	3	2	Swellendam	34°02″	20°26″	5			1
Elandsvlei	32°20″	19°33″		1	3	3	Tarkastad	32°01″	26°16″		6		2
Elandsbaai	32°17″	18°25″	1		4	3	Thabazimbi	24°41″	27°21″			5	3
Fort Beaufort	32°48″	26°38″		4		2	Tontelbos	30°56	20°23″			3	3
Garies	30°30″	18°00″			4	3	Touwsrivier	33°20″	20°00″	4	1		1
Harrismith	28°18″	29°03″			6	3	Tweerivier	33°10″	19°48″	4			1
Heidelberg	34°06″	20°59″	6			1	Underberg	29°50″	29°22″			1	3
Hermanus	34°25″	19°16″	4			1	Upington	28°25″	21°15″			5	3
Hoedspruit	24°21″	30°57″			6	3	Venterstad	30°47″	25°48″		2		2
Hofmeyer	31°39″	25°50″		3		2	Victoria West	31°25″	23°04″			3	3
Ixopo	30°08″	30°00″			5	3	Villiersdorp	33°59″	19°17″	4	1		1
Jamestown	31°07″	26°48″		3		2	Vonkfontein	31°56″	21°50″			2	3
Kendrew	32°31″	24°30″	5	1		1	Vryheid	27°52″	30°38″			6	3
Klerksdorp	26°58″	26°39″			6	3	Warrenton	28°09″	24°47″			6	3
Kraaifontein	33°50″	18°43″	6			1	Warmbaths	24°53″	28°17″			6	3
Laaiplek	32°47″	18°09″	2	1		1	Wiegenaarspoort	32°38″	23°12″		2		2
Langebaan	33°06″	18°03″	3			1	Winburg	28°37″	27°00″			6	3
Lutzville	31°46″	18°21″			5	3	Wittedrif	34°01″	23°22″	6			1
Malmesbury	33°28″	18°44″	5			1	Worcester	33°39″	19°27″	4	1		1
Middlewater	32°30″	22°00″		1	1	2	Zastron	30°18″	27°07″			6	3
Molteno	31°22″	26°22″		4		2							
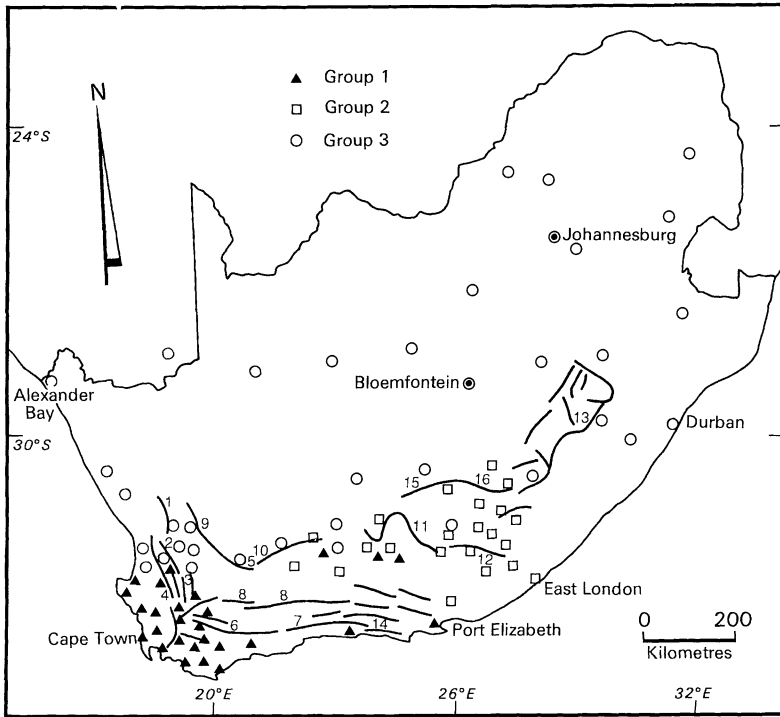
Fig. 1. Map of southern Africa showing the major mountain ranges, the study sites and the modal classification of each site produced by the discriminant function analysis. (▲) *A. m. capensis*; (□) eastern Cape *A. m. scutellata*; (○) northern *A. m. scutellata*; 1, Bokkeveld Mountains; 2, Cedarberg Mountains; 3, Kouebokkeveld Mountains; 4, Olifantsrivierberg; 5, Hex River Mountains; 6, Langeberg; 7, Outeniekwa Mountains; 8, Klein Swartberg and Groot Swartberg; 9, Roggeveldberg; 10, Nuweveldberg; 11, Sneeuberg; 12, Winterberg; 13, Drakensberg; 14, Tsitsikammaberg; 15, Kikvorsberg; 16, Bamboesberg.

Table 2. List of the twelve morphometric characters (after Ruttner, 1988) used in this study, and the means of each for the three groups of bees identified by discriminant function analysis (1, *A. m. capensis*; 2, Eastern Cape *A. m. scutellata*; 3, northern *A. m. scutellata*).

|	Phenon		
Character	1	2	3
Length of cover hair on tergite 5 (mm)	0.139075	0.184375	0.177123
Scutelum pigmentation	1.55000	3.59091	4.51525
Scutelum plate pigmentation	1.16165	1.30341	1.97395
Angle ABE (°)	101.24181	101.30307	102.22302
Angle IJM (°)	21.70556	20.69954	21.36722
Angle JNP (°)	76.31196	76.09171	74.73772
Angle ROG (°)	37.41917	37.64511	37.38593
Extended probosis length (mm)	5.49662	5.05784	5.72698
Longitudinal width of wax plate on sternite 3 (mm)	2.58353	2.69727	2.60327
Transverse length of wax plate on sternite 3 (mm)	2.12083	2.11591	2.17296
Width of stripe posterior to the tomentum on tergite 3 (mm)	0.20880	0.25670	0.26537
Pigmentation of tergite 2	5.31353	7.32102	8.24154
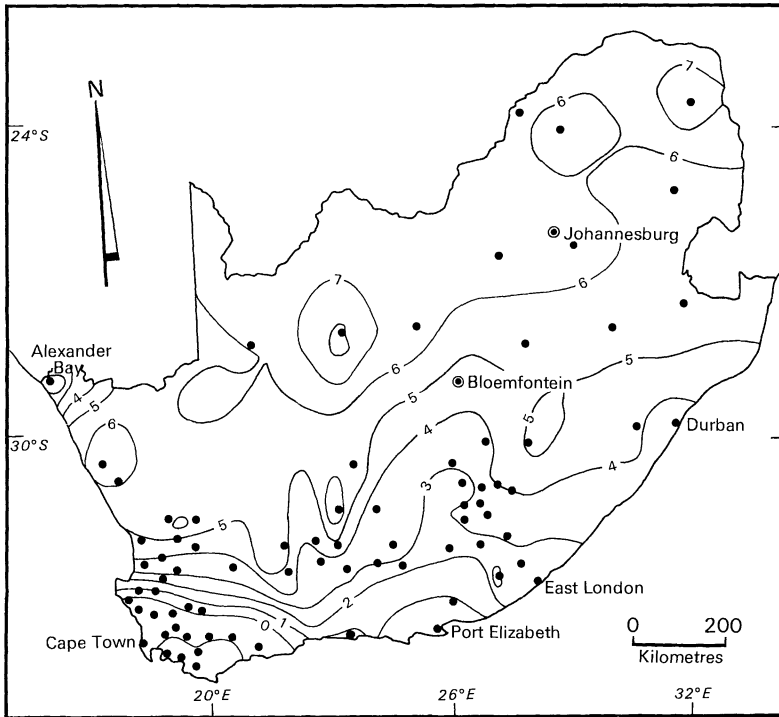
Fig. 2. Trend surface map showing the means of the factor scores of colonies at each locality.

Discriminant analysis

Stepwise discriminant function analysis was run using a classification based on the mountain ranges which could possibly separate different populations. First a five-group classification system was used with the following groups (numbers in brackets refer to Fig. 1):

Group 1 Southern bees found between the coast and the Bokkeveld (1), Olifantsrivierberg (4), Langeberg (6), Outeniekwa (7) and Tsitsikammaberg (14) mountain ranges.

Group 2 Southwestern bees found between the Olifantsrivierberg (4) on the west and the Cedarberg (2) and Kouebokkeveld (3) mountain ranges on the east and north of group one and south of the Hex River (5) and Klein and Groot Swartberg (8) mountain ranges.

Group 3 Southcentral bees found between the Bokkeveld (1), Cedarberg (2) and Kouebokkeveld (3) on the west and the Roggeveldberg on the east, north of Groups

1 and 2 and south of the Nuweveldberg (10), Sneeuberg (11) and Winterberg (12) ranges.

Group 4 Southeastern bees found on the east of the subcontinent between the Sneeuberg (11) and Winterberg (12) in the south and the Kikvorsberg (15) and Bamboesberg (16) in the north.

Group 5 Bees found north of the Bokkeveld (1) Roggeveldberg (9), Nuweveldberg (10), Sneeuberg (11), Kikvorsberg (15) and Bamboesberg (16) mountain ranges.

This a priori classification resulted in many colonies being misclassified by race. In particular, Groups 1, 2 and 3 were almost indistinguishable, and so they were pooled and the analysis repeated with the three resulting groups:

Group 1 Southern bees found south of 33S, between the coast and the Bokkeveld (1), Cedarberg (2), Kouebokkeveld (3), Hex river (5), Langeberg (6), Outeniekwa (7) and Tsitsikammaberg (14) mountain ranges.
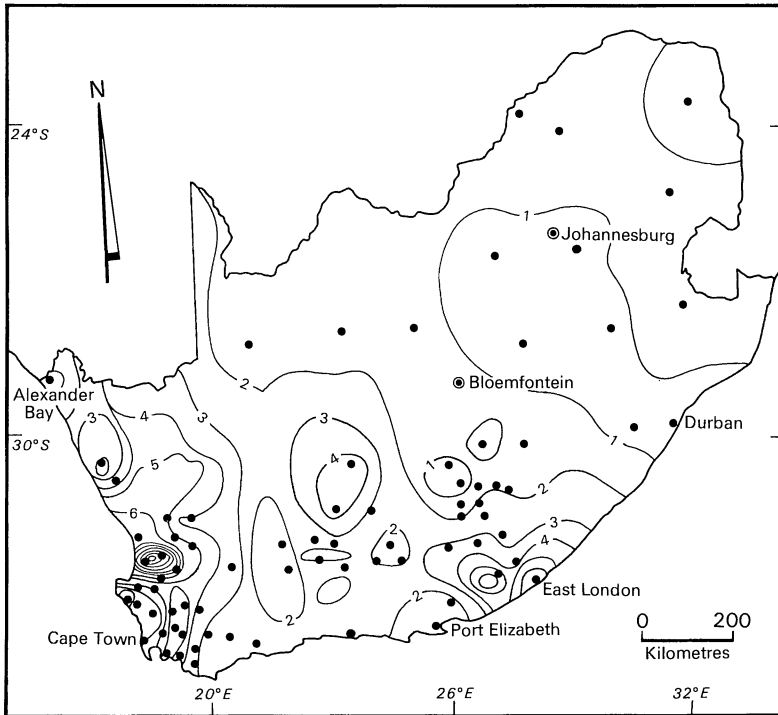
Fig. 3. Trend surface map showing the variances of the factor scores of colonies at each locality.

Group 2 Northern bees found north of 33°S on the west coast and the Roggeveldberg (9), Nuweveldberg (10), Sneeuberg (11), Kikvorsberg (15) and Bamboesberg (16) mountain ranges.

Group 3 Eastern bees found between the Kikvorsberg (15) and Bamboesberg (16) mountain ranges in the north and the Sneeuberg (11) and Winterberg (12) mountain ranges in the south.

The colonies were classified into these groups with 89.5% (Group 1: 27 locations, 133 colonies), 93.8% (Group 2: 36 locations, 162 colonies) and 88.6% (Group 3: 22 locations, 94 colonies) accuracy, which represents a substantial decrease in misclassifications. In some cases there were still one or two misclassified colonies at a location (Table 1). When the first two canonical axes of the analysis were plotted as a scatter diagram, each group formed a reasonably separate cluster with an area between the clusters where misclassified colonies occurred.

The means of the twelve characters (Table 2) show definite trends among the three groups. Group 1 contains the smallest and darkest of the three; the northerly Group 2 bees are the largest and most yellow; and the eastern Cape bees of Group 3 are generally intermediate in size and pigmentation, but with the shortest proboscis.

DISCUSSION

Biogeographic differentiation

The prime aim of this study was to define the geography of an interface between the two nominal races of South African honey bees, and multivariate analysis of morphometrics is the method-of-choice for discriminating between subspecies of honey bees generally (Daly, 1985, 1991, 1992; Ruttner, 1988; Radloff *et al.*, 1996, 1997). From their size and pigmentation, the honey bees south and west of the 1.0 contour in Fig. 2 would clearly be identified as *A. m. capensis* (Smith, 1969; Tribe, 1983; Ruttner, 1988), while those north of the 3.0 contour are similar to the more variable *A. m. scutellata* (Smith, 1969; Ruttner, 1988). The bees

between these contours are intermediate in size and pigmentation between these groups, and have generally been referred to as hybrids (Moritz & Kauhausen, 1984; Hepburn & Crewe, 1990; Crewe *et al.*, 1994; Hepburn *et al.*, 1994; Moritz *et al.*, 1994). It is taxonomically significant that the type material of *A. m. scutellata* was collected about 100 km west of East London in the Eastern Cape (Ruttner, 1988; Daly, 1991), in what is currently this hybrid zone.

The 1.0 contour of Fig. 2 marks the edge of the Mediterranean climatic region, suggesting an eco-climatic boundary to the *capensis* phenotype. However, thelytokous workers are known to extend from this region to just beyond the 3.0 contour in the western and eastern Cape (Hepburn & Crewe, 1991), so that the marker trait (thelytoky) of the *capensis* taxon extends just over the putative boundary of the *scutellata* phenotype, including the type locality of the latter.

The factor analysis indicated continuous morphological variation, distributed clinally (Fig. 2). Although the bees in the eastern Cape 'hybrid' area can be distinguished efficiently by discriminant analysis, one should not be misled into thinking that this group is morphometrically discrete. The most distinctive feature of the group, short tongue length (Table 2), is notoriously hard to measure reliably (Waddington & Herbst, 1987), so that the taxonomic value of this character is poor, and its remaining traits intergrade with those of its neighbours. The success of the second discriminant analysis in defining three groups of bees was in fact due to the coincidence of the defining mountain ranges (Fig. 1) with the contours produced by the factor analysis (Fig. 2), and not to the existence of spatially or morphologically discrete phenotypes. This, and the even spacing of the contours in well-sampled areas raises the question of whether there are any distinct races in the region. Three lines of evidence need to be examined in this regard.

The first line concerns the absence of sharp geographical discontinuities in traits between the (putatively genetically distinct) taxa. Factor analysis showed that the bees of South Africa display continuous morphometric variation, manifested as a fairly smooth north–south cline (Fig. 2). The contours lie roughly parallel to latitude, with some distortion to the southwest of the Lesotho highlands and around the boundary of the Mediterranean climatic region in the southwestern Cape (Fig. 2). This continuity echoes Daly's (1991) report of an 'intergrade of clusters' in the morphology of southern African honey bees. The nominal races intergrade smoothly into one another.

The second line of evidence involves the expectation that zones of hybridisation are indicated by higher phenotypic variance within the hybrid samples (Crewe *et al.*, 1994). Rather than the expected belt of higher variance lying between two races, the local variance in colony factor scores was generally rather uniform, with the exception of two very localised centres, again implying a single population (Fig. 3). A parallel study of sting pheromones revealed a similar pattern of variances (Hepburn *et al.*, 1994). However, the unsampled area between the 1.0 and 2.0 contours of Fig. 2 might contain a narrow belt of higher variance running along the margin of the Mediterranean climatic zone. If this is the true margin of *A. m. capensis*, it lies more than 400 km south and west of the border of the thelytoky trait (Hepburn & Crewe, 1991). This means that thelytoky is also found in the *A. m. scutellata* phenotype, i.e. that race and reproductive biology are not concordant.

Finally, the lack of concordant and discrete geographic variation in other traits such as alarm pheromones (Hepburn *et al.*, 1994), thelytoky, ovariole number, spermatheca size, body size, malate dehydrogenase allozymes (Hepburn & Crewe, 1991), and morphometry (Crewe *et al.*, 1994), including the lack of significant correlation between the morphological traits used in this study, supports the conclusion that only one population is present, since distinct populations or races would show concord and correlation in their character suites. Finally, the putative hybrids and their neighbours share the same monomorphic mtDNA restriction fragment polymorphism (Moritz *et al.*, 1994).

The conclusion that there is only one spatially heterogeneous, clinally structured population of honey bees in South Africa should not be particularly startling in view of the ubiquity of honey bees, the continuity of their distribution in the subcontinent (Fig. 1), their migratory habits (Kerr, 1992; McNally & Schneider, 1992; Hepburn *et al.*, 1993), and the rapidity with which their morphology adapts to local conditions (Daly *et al.*, 1991). The racial classification of *A. mellifera* in South Africa apparently has its basis in a taxonomic artifact arising historically from sampling at widely-spaced locations. It is relevant that as knowledge of geographic variation in morphology increases, trinomials are increasingly falling out of use (Minelli, 1993), even in hymenopteran systematics (Bolton, 1994).

If the '*capensis* calamity' (Allsopp, 1992) is to be addressed by the regulation of transportation of

bees for commercial apiculture, further work should focus on detailing and explaining the geographical distribution of thelytokous workers themselves (Greeff, 1997), since such workers have a wider distribution (Hepburn & Crewe, 1991) than the *capensis* phenotype.

Mechanisms underlying differentiation

The mountain ranges that successfully defined groups of bees in the discriminant analysis run parallel to latitudes, while those that were not successful run perpendicular to latitudes or the boundary of the Mediterranean climatic region (Fig. 1). Since both body size and pigmentation are often correlated with latitude in honey bees (Ruttner, 1988), it is suggested that the successful use of some mountain ranges in predicting honey bee morphology comes largely from their correlation with latitude, and that latitude is a major factor indirectly structuring the cline found in this study. It is also significant that higher altitudes and higher latitudes have a similar effect on honey bee morphology (Ruttner, 1988; Meixner *et al.*, 1989; Verma, Mattu & Daly, 1994), so that mountain ranges and latitudes running in parallel would amplify one another's effects. This might also explain the distortion of the factor contours to the southwest of Lesotho.

However, this does not explain the compression of the factor contours in the Clanwilliam area of the western Cape (Fig. 2). This area is traversed by the Olifants River, with mesic Mediterranean fynbos to the south and xeric karoo to the north. It represents one of the steepest large-scale climatic gradients in the country (P. Lloyd, pers. com.). Adaptation to local climates has previously been suggested to differentiate the South African races, and climatic variation in California (Daly *et al.*, 1991) and northwestern India (Verma *et al.*, 1994) is correlated with morphological variation in their local honey bees. The Clanwilliam area is also the site of highest phenotypic variance in South Africa (Fig. 3). This might be explained directly or indirectly by unusually high climatic variances, and by local movements between climatic zones, since honey bees easily migrate over such distances (Kerr, 1992; Hepburn *et al.*, 1993). The Clanwilliam area is also a focus of migratory beekeeping and pollination services (M. Allsopp, pers. comm.) that add to local variance. However, there is evidence of the evolution of local feral ecotypes in California over a period of only 138 years, despite the large and mobile apicultural industry there (Daly *et al.*, 1991), suggesting that feral populations can be large enough to absorb this genetic source of variance.

Latitude and altitude are both moderators of climate. Climate, especially temperature, has a direct impact on honey bee ontogeny and pigmentation (Soose, 1954; Tsuruta, Matsuka & Sasak, 1989; Spivak *et al.*, 1990; Daly *et al.*, 1991). In particular, pigmentation patterns have heritabilities on only 0.21 to 0.39 (Szabo & Lefkovitch, 1992). Altitude-related morphological variation has been found in the morphometry of East African and Indian honey bees (Mattu & Verma, 1983, 1984a, b; Meixner *et al.*, 1989), but not in feral Californian bees (Daly *et al.*, 1991). Seasonal morphological variation that might be related to climate has also been found in European and Indian honey bees (Mattu & Verma, 1984c; Nazzi, 1992). Climate may therefore be a key correlate in understanding the biogeography of South African honey bees, although genetic differentiation correlated to climate, particularly through floral phenology (Hepburn & Jacot-Guillarmod, 1991), cannot be ruled out. It would be easy (and important) to decompose the phenotypic variation between genetic and environmental effects by reciprocally rearing bees from one end of the cline at the other end of the cline (Bulmer, 1985).

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