The honeybees, *Apis mellifera* Linnaeus (Hymenoptera: Apidae), of woodland savanna of southeastern Africa

S.E. Radloff[1], H.R. Hepburn[2*] & M.H. Villet[2]
[1]*Department of Statistics, Rhodes University, Grahamstown, 6140 South Africa*
[2]*Department of Zoology and Entomology, Rhodes University, Grahamstown, 6140 South Africa*

The morphometric characters and sting pheromones of worker honeybees, *Apis mellifera* Linnaeus, were analysed by multivariate methods to identify discrete populations in the southeastern woodland savanna of Africa. A discrete population in Mozambique is classified as *A. m. litorea* Smith, a second in Zimbabwe as *A. m. scutellata* Lepeletier and a third group in southwestern Zambia as *A. m. adansonii* Latreille. A zone of introgression between the last two subspecies occurs in south-central Zambia and in the Zambezi Valley.

Key words: honeybee, populations, morphometrics, sting pheromones.

INTRODUCTION

The honeybees of Africa have recently been classified into several subspecies and/or ecotypes at the continental macro-level (Ruttner 1988, 1992; Kerr 1992). This biogeographical framework now makes it possible to begin to assess population structure in honeybees at a meso-scale spatial resolution and in ecological-climatological terms. For this purpose, combined analyses of characters of low (morphometric) and high (pheromones) heritability have proven to be useful in defining the phenetic similarity of discrete populations while their heteroscedasticity or variance spectra can indicate areas of introgression between populations (Hepburn *et al.* 1994; Hepburn & Radloff 1996; Radloff *et al.* 1996).

We now report the results of analyses of honeybee populations from the southeastern woodland savanna of Africa, extending from coastal Mozambique through the highveld of Zimbabwe and into the mountains of northwestern Zambia. In terms of the prevailing biogeographical classification of honeybees (Ruttner 1992), this represents a transect through the subspecific areas of *Apis mellifera litorea* Smith, *A. m. scutellata* Lepeletier and *A. m. adansonii* Latreille, respectively. As such, this is one of a series of regional studies to determine population structure in the honeybees of Africa, the possible coincidence/concordance of traits and the ecological factors that affect variation in honeybees (Hepburn & Radloff 1997).

*To whom correspondence should be addressed:
telephone: +27 461 318098.; fax: +27 461 24377;
e-mail: zohh@warthog.ru.ac.za

MATERIAL AND METHODS

Worker bees were sampled from the colonies of small-scale, fixed-site beekeepers at eight different localities extending along a 1500 km transect from Beira (1) in Mozambique, to Mutare (2) in southeastern Zimbabwe, through Harare (3) to Karoi (4) in northern Zimbabwe, Lusaka (5) in central Zambia, through Kitwe (6) and Solwezi (7) to Ikelenge (8) in northwestern Zambia (Fig. 1). While 'captive colonies' were sampled, it must be understood that the bees are simply attracted to empty hives from wild populations. They are not transported and therefore represent a subsample of the wild population. Morphometric measurements were taken on 20 bees per colony and usually six colonies were sampled at each locality. A total of 760 bees was used in the morphometric analysis.

The same eleven characters used in previous studies (Crewe *et al.* 1994; Radloff *et al.* 1996; Hepburn & Radloff 1996) that successfully classified colonies into races of honeybees in Africa were measured. Their Ruttner (1988) numbers are given in brackets (except the wing angle MJI, see Ruttner (1988 Fig. 6.9 page 73)) as follows: length of cover hair on tergite 5 (1), length of proboscis (4), width of wax plate on sternite 3 (11), transverse length of wax plate on sternite 3 (13), pigmentation of scutellum (35), pigmentation of scutellar plate (36),

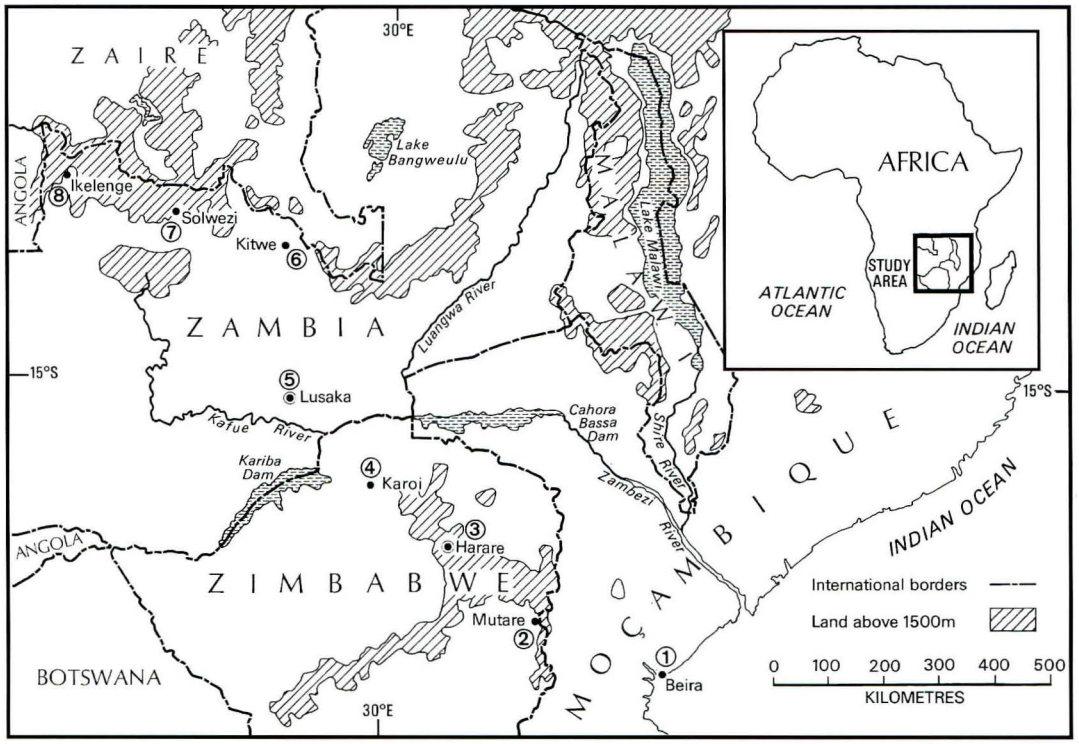

Fig. 1. Localities in Mozambique, Zimbabwe and Zambia sampled in this study.

pigmentation of tergite 2 (32), wing angle B4 (22), wing angle MJI, wing angle N23 (30) and wing angle O26 (31).

For pheromone analysis, five guard bees were collected from each of three to six colonies per locality, a total of 185 bees was used in the analysis. All samples were measured with a Hewlett-Packard 5890 Series II gas chromatograph fitted with a bonded methyl silicone fused silica capillary column (0.3 mm × 25 m) and quantified with an HP 3396 Series II integrator calibrated with authentic standards of sting pheromone compounds. The following pheromone compounds were identified: isopentyl alcohol (1), n-butyl acetate (2), isopentyl acetate (3), benzyl alcohol (4), n-octanol (5), 2-nonanol (6), benzyl acetate (7), octyl acetate (8) and n-decyl acetate (9).

Multivariate statistical analysis of the data included principal component analysis, factor analysis and linear discriminant analysis. Wilks' lambda test was used to compare multivariate population means between groups. The distribution of the statistic was approximated by the *F* distribution (Mardia *et al.* 1979). Levene's *F* statistic for testing the equality of the variances between groups was also used in the analysis. The sequential Bonferroni method of multiple tests of individual significance of correlations was used to ensure that the overall level of significance was not larger than 0.05 (Miller 1981). For the morphometric and pheromone analyses, colony means, standard deviations and covariances of the morphometric characters and pheromone compounds were analysed.

RESULTS

Morphometric analysis

In a principal component analysis of the morphometric characters of 38 colonies, four factors with eigenvalues greater than one were isolated: factor 1, characters associated with size (13), (4) and (1); factor 2, angles of wing venation (30) and MJI; factor 3, pigmentation (35) and angle of wing venation (22); factor 4, size (11) and pigmentation (36). These factors accounted for 67.8 % of the variance in the data. The loadings for each character had an absolute value greater than 0.60. The

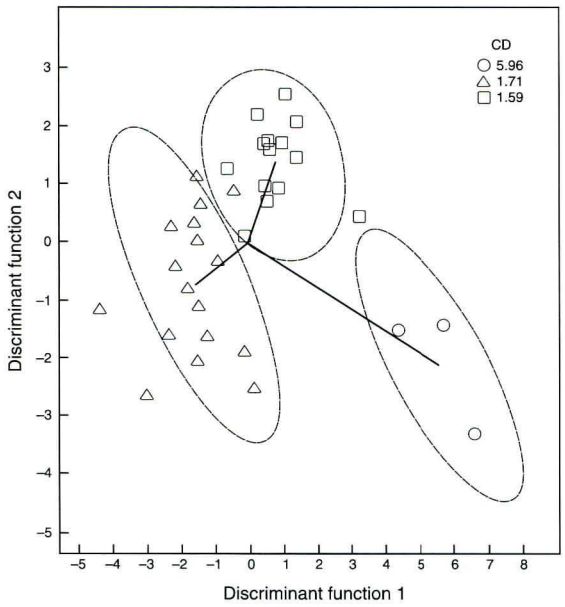

Fig. 2. Discriminant analysis plot using the colony means of the morphometric data. Cluster 1 (○) is composed of colonies from locality 1, cluster 2 (△) is composed of colonies from 2, 3 and 4 and cluster 3 (□) is composed of colonies from 6, 7 and 8. Confidence ellipses at the 90 % level. CD = canonical distances from common centroid of clusters.

graph (Fig. 2) of the factor scores from factors 1 and 2 showed three clusters: colonies from Beira forming a cluster in the lower right-hand quadrant of the plot, colonies from Mutare, Harare and Karoi forming a cluster in the lower left-hand quadrant and colonies from Kitwe, Solwezi and Ikelenge forming a cluster in the upper right-hand quadrant. Colonies from Lusaka were evenly scattered.

A stepwise discriminant analysis using the colony means of the morphometric characters confirmed the separation of the three clusters (Fig. 2). Mahalanobis distances D^2 between the clusters were $D^2 = 73.99$ for 1 and 2, $D^2 = 101.32$ for 1 and 3 and $D^2 = 9.54$ for 2 and 3.

Table 1 shows the four characters entered into the linear discriminant functions ranked according to their discriminatory power. Three of these characters are related to size. Each colony was assumed to have equal prior probability of being in any cluster. The linear discriminant functions obtained using the means of the most discriminatory characters classified 100 % of the colonies from Beira correctly into group 1 with posterior probability $P = 1.0$. 94.4 % of the colonies from Mutare, Harare and Karoi were correctly classsified into group 2 with posterior probability $P = 1.0$ for seven colonies, $0.9 < P < 1.0$ for seven colonies and $0.6 < P < 0.9$ for three colonies. 92.9 % of the colonies from Kitwe, Solwezi and Ikelenge were correctly classified into group 3 with posterior probability $P = 1.0$ for five colonies, $0.9 < P < 1.0$ for six colonies and $0.8 < P < 0.9$ for two colonies. Colonies from Lusaka were classified into groups 2 and 3. A jackknife procedure (Lachenbruch & Mickey 1968) produced the same classification results except for one colony from Karoi that was misclassified into group 3 and one colony from Kitwe misclassified into group 2.

Table 1. Morphological characters entered into the discriminant function ranked according to their discriminatory power.

Character entered	*F*-statistic	*d.f.*	*P*-value
(13)	32.84	2,32	<0.0001
(30)	11.15	2,31	0.0002
(4)	5.80	2,30	0.0074
(11)	4.24	2,29	0.0242

To test for the equality of the group means for the characters used in the discriminant function, Wilks' lambda approximated by the *F* statistic was

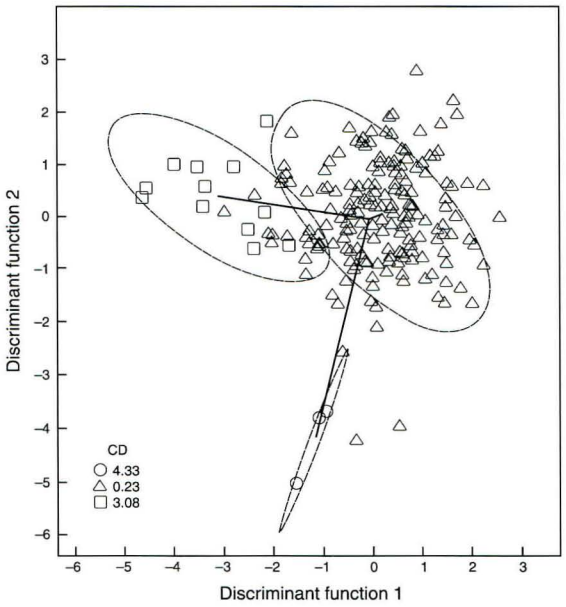

Fig. 3. Discriminant analysis plot using the morphometric data from southeastern Africa, southwestern Africa and northern South Africa. Morpho-cluster 1 (○) is composed of colonies from Mozambique; morpho-cluster 2 (△) is composed of colonies from southern Namibia, northern South Africa and Zimbabwe; morpho-cluster 3 (❑) is composed of colonies from northern Namibia and northwestern Zambia. Confidence ellipses at the 90 % level. CD = canonical distances from common centroid of morpho-clusters.

determined. A significant difference was found between the means of the three groups ($\Lambda = 0.1063$ with 4,2,32 *d.f.*; $F = 14.99$ with 8,58 *d.f.*, $P < 0.0001$). These results indicate that the honeybees of this region in southern Africa resolve morphometrically into three distinct and homogenous populations, a discrete population in Mozambique, a discrete population in Zimbabwe, a discrete population in northwestern Zambia and a heterogeneous population in south-central Zambia. The means and standard deviations of the 11 morphometric characters are shown in Table 2 for the three groups and transition group using all 760 bees from eight localities.

The morphometric data of the transect from Beira to Ikelenge were combined with the data of the same morphometric characters from honeybees collected along a transect in southwestern Africa (Radloff *et al.* 1996) and the data from honeybees collected from other localities in northern South Africa (Crewe *et al.* 1994). A linear discriminant analysis using the morphometric means of 213 colonies confirmed the separation of three morpho-clusters: (1) *A. m. litorea* in Mozambique: (2) *A. m. scutellata* in southern Namibia, northern South Africa and Zimbabwe and (3) *A. m. adansonii* in northern Namibia and northwestern Zambia (Fig. 3). 100 % correct classification of the colonies in morpho-clusters 1 and 3 and 91.7 % correct classification in morpho-cluster 2 were obtained.

A correlation analysis was used to assess the climate-correlated variation in honeybees along the transect. Significant variations in certain body size characters (13 and 4) correlated to increasing altitude and decreasing temperatures (13 and 4) were observed (Table 3). Also, certain angles of venation were significantly correlated to geographic latitude and longitude. No significant correlations were found between pigmentation and the environmental variables (Table 3).

The factor score of each bee was calculated from the first principal component function and the variances of these factor scores were used to test for homogeneity of the variances at each locality. A significant difference was found between the intracolonial variances (Table 4) over all the localities (Levene's test $F = 2.30$ with 7,752 *d.f.*, $P = 0.0251$). Larger variances were found at Karoi and Kitwe. The intercolonial variances (Table 4) were

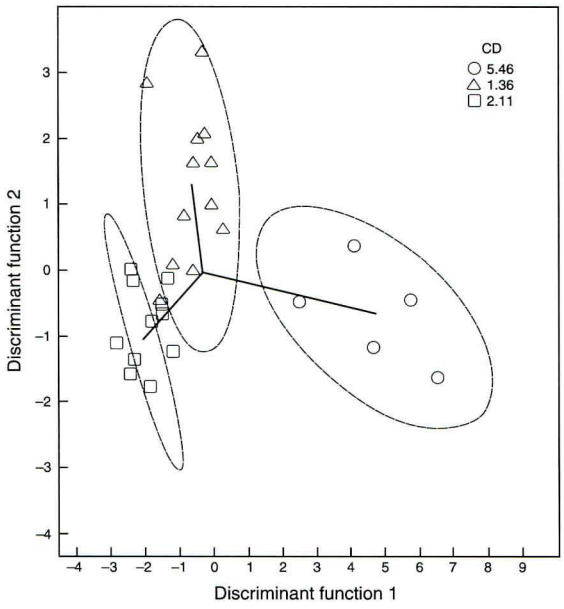

Fig. 4. Discriminant analysis plot using the mean percentages of the sting pheromone data. Cluster 1 (○) is composed of colonies from locality 1, cluster 2 (△) is composed of colonies from 2, 3 and 4 and cluster 3 (□) is composed of colonies from 6, 7 and 8. Confidence ellipses at the 90 % level. CD = canonical distances from common centroid of clusters.

computed by the same method but this time the colony means were used to determine the factor scores of each colony. No significant difference was found in the variances between localities ($F = 1.40$ with 7,30 *d.f.*, $P = 0.2415$). However, the intercolonial variation was again higher between the Karoi and Kitwe regions.

Sting pheromone analysis

In a principal component analysis using the mean percentages of the nine compounds (Table 5) of the sting pheromone complex, three factors with eigenvalues greater than one were isolated and accounted for 74.2 % of the variance of the data: factor 1, (3), (7), (5) and (1); factor 2, (6) and (2); factor 3, (9) and (4). The factor scores plot revealed the same three clusters indicated in the morphometric analysis. A stepwise discriminant analysis of the colony means confirmed the separation of the three clusters (Fig. 4). Table 6 shows the five pheromones entered into the linear discriminant functions ranked according to their discriminatory power.

The linear discriminant functions obtained using the colony means of the most discriminatory compounds classified 100 % of the colonies from Beira correctly into group 1, 16 out of 18 colonies from Mutare, Harare and Karoi correctly into group 2 and 11 colonies out of 12 from Kitwe, Solwezi and Ikelenge correctly into group 3. A significant difference was found between the population mean percentages between the three groups ($\Lambda = 0.0800$ with 5,2,32 *d.f.*; $F = 14.20$ with 10,56 *d.f.*, $P < 0.0001$). These results again indicate the presence of three distinct homogeneous populations in this southern African region. The means and standard deviations of the nine pheromone compounds are shown in Table 5 for the three groups and transition group using all 185 bees from eight localities.

Sting pheromone data obtained from honeybees along a transect in southwestern Africa (Radloff *et al.* 1996) were combined with the pheromone data of this study. The linear discriminant functions determined using the mean compound percentages of the 58 colonies correctly classified all the colonies from Beira, 85.7 % of the colonies from southern Namibia and Zimbabwe and 84.6 % of the colonies from northern Namibia and northwestern Zambia.

To test for heteroscedasticity in the variances of the sting pheromone percentages between localities, the first principal component coefficients of

Table 2. Means and standard deviations of discriminant morphometric characters (measurements in mm, angles in degrees).

Character	Group 1 (n = 60)		Group 2 (n = 360)		Transition Group (n = 58)		Group 3 (n = 280)	
(1)	0.21	(0.03)	0.24	(0.03)	0.22	(0.03)	0.23	(0.03)
(4)	5.40	(0.33)	5.96	(0.15)	5.99	(0.10)	5.86	(0.24)
(11)	2.51	(0.07)	2.54	(0.07)	2.55	(0.07)	2.51	(0.06)
(13)	1.99	(0.07)	2.13	(0.07)	2.13	(0.05)	2.11	(0.05)
(35)	5.57	(1.36)	5.26	(1.70)	5.31	(1.84)	5.29	(2.09)
(36)	1.02	(1.42)	1.77	(1.37)	0.83	(1.26)	1.25	(1.64)
(32)	8.65	(0.48)	8.35	(0.92)	8.36	(0.52)	8.32	(1.00)
(22)	105.24	(6.20)	104.62	(6.20)	102.78	(5.24)	102.00	(5.87)
MJI	18.83	(2.24)	19.04	(2.63)	20.36	(2.28)	20.98	(2.63)
(30)	78.77	(4.14)	78.83	(4.19)	83.54	(3.86)	82.59	(4.08)
(31)	35.02	(3.61)	35.33	(3.92)	36.94	(4.06)	36.50	(3.93)

Table 3. Correlation coefficients with corresponding P-values between mean annual temperatures, latitude, longitude and altitude and the colony means of the morphometric characters.

Character	T_{max}		T_{min}		Latitude		Longitude		Altitude	
(1)	−0.41	0.0110	−0.48	0.0022	0.06	0.6998	−0.04	0.8235	0.40	0.0117
(4)	−0.51	0.0010	−0.78*	<0.0001	−0.10	0.5686	−0.22	0.1848	0.70*	<0.0001
(11)	−0.44	0.0055	−0.26	0.1143	0.38	0.0193	0.40	0.0141	0.05	0.7765
(13)	−0.64*	<0.0001	−0.83	<0.0002	−0.04	0.8166	−0.11	0.4976	0.75*	<0.0001
(35)	−0.09	0.5894	0.09	0.6109	0.07	0.6618	0.09	0.5997	−0.09	0.5791
(36)	−0.28	0.0921	−0.21	0.2107	0.26	0.1186	0.33	0.0448	0.05	0.7579
(32)	0.10	0.5568	0.24	0.1385	0.14	0.4153	0.13	0.4542	−0.22	0.1816
(22)	−0.38	0.0184	0.01	0.9718	0.53*	0.0006	0.62*	<0.0001	−0.28	0.0942
MJI	0.21	0.2159	0.01	0.9701	−0.52*	0.0009	−0.43	0.0075	0.22	0.1843
(30)	0.34	0.0370	0.02	0.8942	−0.60*	0.0001	−0.57*	0.0002	0.23	0.1594
(31)	0.11	0.5019	−0.03	0.8381	−0.25	0.1281	−0.18	0.2746	0.11	0.5300

*Significant correlation ($P < 0.05$) as determined by Bonferroni's adjustment in the level of significance for simultaneous testing.

Table 4. Intracolonial and intercolonial variances of factor scores of the morphometric and pheromone data at each locality.

Locality	Morphology		Stings	
	Intracolonial	Intercolonial	Intracolonial	Intercolonial
Beira	4.92	1.02	23.32	16.49
Mutare	5.27	2.72	17.94	12.62
Harare	5.64	2.22	20.82	6.91
Karoi	6.17	4.73	16.91	7.96
Lusaka	4.77	3.45	27.50	22.31
Kitwe	5.85	3.36	20.54	7.72
Solwezi	5.02	3.33	11.29	6.03
Ikelenge	4.90	2.79	19.25	7.21

Table 5. Mean percentages and standard deviations of the sting pheromones.

Pheromones	Group 1 (n = 23)		Group 2 (n = 90)		Transition Group (n = 12)		Group 3 (n = 60)	
isopentyl alcohol (1)	1.90	(2.88)	4.99	(3.47)	5.93	(8.42)	5.89	(3.69)
n-butyl acetate (2)	17.45	(7.19)	7.86	(6.14)	5.15	(7.66)	8.73	(10.74)
isopentyl acetate (3)	3.89	(4.16)	7.94	(4.97)	12.38	(10.38)	11.02	(4.74)
benzyl alcohol (4)	2.27	(4.06)	5.60	(2.89)	5.35	(6.56)	4.95	(2.64)
n-octanol (5)	17.63	(10.42)	5.07	(4.47)	2.85	(2.86)	4.31	(3.84)
2-nonanol (6)	14.59	(12.60)	30.44	(16.26)	19.86	(12.05)	26.25	(12.79)
benzyl acetate (7)	8.60	(9.91)	17.07	(7.08)	20.46	(11.52)	22.46	(8.43)
octyl acetate (8)	23.69	(11.33)	15.09	(9.51)	14.11	(14.69)	12.21	(7.71)
n-decyl acetate (9)	9.97	(10.18)	5.94	(6.64)	13.92	(19.61)	4.16	(1.85)

Table 6. Sting pheromone compounds entered into the discriminant function ranked according to their discriminatory power.

Pheromone entered	F-statistic	$d.f.$	P-value
n-octanol (5)	38.08	2,32	<0.0001
benzyl alcohol (4)	8.29	2,31	0.0013
benzyl acetate (7)	6.35	2,30	0.0050
isopentyl acetate (3)	4.91	2,29	0.0146
n-butyl acetate (2)	3.71	2,28	0.0372

the pheromone compounds were calculated and used to determine the factor scores of each bee. Although no significant difference between the intracolonial variances (Table 4) of these factor scores (Levene's test, F = 1.73 with 7,176 $d.f.$, P = 0.1041) was found, higher variance was evident in the transition region at Lusaka. No significant difference was found in the intercolonial variances between localities (F = 1.63 with 7,30 $d.f.$, P = 0.1665). However, higher intercolonial variation was again found at Lusaka (Table 4).

DISCUSSION

The suite of multivariate analyses employed in this study establish three morphometrically and pheromonally distinct populations (Figs 2, 4). The bees of Mozambique correspond to *A. m. litorea* which extends northwards along the coastal plain to the Kenya-Somalia region (Ruttner 1988, 1992). A second group begins above the escarpment at the Chimanimani Mountains and extends across Zimbabwe very probably as far as the Zambezi Valley. This group is part of a contiguous subspecies, *A. m. scutellata,* (Fig. 3) that extends for the length of the east African highlands from South Africa to Ethiopia (Ruttner 1988, 1992; Crewe *et al.* 1994). The third group in northwestern Zambia corresponds to *A. m. adansonii* which is spread throughout West Africa and southwards to northern Namibia and Zambia (Ruttner 1992; Radloff *et al.* 1996).

The multivariate analyses also demonstrate that the bees of south-central Zambia, centred on Lusaka and the Zambezi River Valley, are morphometrically and pheromonally extremely heterogeneous (Figs 2, 4) and were consistently misclassified. This is characteristic of zones of introgression between different discrete honeybee populations (Hepburn & Radloff 1996; Radloff *et al.* 1996) and, in this case, indicates a hybrid zone between *A. m. adansonii* to the northwest of Zambia and *A. m. scutellata* to the southeast in Zimbabwe (when subspecies are defined morphometrically). Because morphological traits are generally of low heritability (Falconer 1989; Moritz & Southwick 1992), further support for a hybrid zone is derived from the high heritability of sting pheromones (Collins *et al.* 1987). The pheromonal variances of Lusaka are greater than all other localities and reflect the heteroscedasticity associated with other hybrid zones in southern Africa (Hepburn *et al.* 1994; Radloff *et al.* 1996).

The structure of the honeybee populations along the transect is further reflected in their variance spectra. While clinal changes in the traits measured might have been expected in the absence of barriers to gene flow, there were few significant correlations between change in latitude and both bee size and pigmentation (Table 3). Although no significant difference in intracolonial variance was

observed there are clinal asymmetries in the morphometric characters at Karoi and in the pheromones at Lusaka (Table 4). Intracolonial variation is attributed to the multiple matings of queens with several-to-many drones of differing allelic frequencies (Moritz & Southwick 1992). The high intercolonial variances in the pheromones associated with the Lusaka area are interpreted as direct evidence for introgression between *A. m. adansonii* and *A. m. scutellata* in this region.

While statistical inference is a powerful adjunct to the delineation of subspecific groups, explanations for the results obtained must be sought in a biogeographic context. Gene flow within and between honeybee populations requires movements of the kind associated with swarming, absconding and, especially in Africa, migrations, the chances of success of which are heavily dependent on environmental conditions. The entire area between Beira and Ikelenge falls within a single ecological-climatological zone of tropical savanna woodland with a long dry-season (Walter 1973; Cole 1986). Nonetheless variations occur along this transect that positively influence the current distributions of the three subspecific groups indicated in Figs 2 and 4.

Throughout the year the plains of Mozambique are consistently about 8 °C warmer than on the highveld above the escarpment of the Chimanimani Mountains at Mutare. Here the transition in temperature profiles is quite abrupt (Jackson 1961) and this is the border between *A. m. litorea* and *A. m. scutellata.* The average costs of both basal metabolism as well as flight at the higher temperatures of Mozambique are significantly in excess of those on the highveld and should require physiological or behavioural adaptations for this region (Worswick 1987; Balderrama *et al.* 1992). There is little variation in the annual temperature profiles across the highveld except for a thermal discontinuity at the Zambezi River Valley, which is about 6 °C warmer than all of the areas along the 1200 km expanse from Mutare to Ikelenge (Jackson 1961). This discontinuity is geographically proximate to the zone of introgression between *A. m. scutellata* and *A. m. adansonii.*

Although swarming, absconding and migrations by the honeybees of Africa occur throughout the year, there are nevertheless peak periods of seasonal movements. In general, the main swarming/migration periods occur in months 8–11 across Mozambique and Zimbabwe, the end of which varies with the onset of the rainy season (Papadopoulo 1969; McIntosh 1990; C.J. Coleman, pers. comm.). Since the development of massive gum (*Eucalyptus* spp.) plantations, a second swarming season has begun to develop on the Zimbabwean highveld in months 2–4 (C.J. Coleman, pers. comm.).

Swarming in Zambia is particularly closely tied to the flowering of the bee forage trees *Brachystegia* in months 8–9 and then *Julbernardia* in months 3–4 in the Lusaka-Kitwe areas. However, *Brachystegia* presence is greatly reduced to the northwest and there is a single swarming/migration season at the higher altitudes of Solwezi and Ikelenge during months 8–9 (Silberrad 1976; T.P. Chupa, pers. comm.). This intercalation of a second swarming season on the Zimbabwean highveld coupled with two synchronous swarming seasons in south-central Zambia thus provides a phenological corridor that should increase the probability of gene flow in the zone of introgression between *A. m. scutellata* and *A. m. adansonii* as it now exists.

A further biological indication of an introgression zone is related to honeybee aggressiveness. It is the long-standing opinion of experienced apiculturists that the honeybees of Zambia are considerably more aggressive than those to the south in Zimbabwe. Indeed, both C.J. Coleman (pers. comm.) in Zimbabwe and T.P. Chupa (pers. comm.) in Zambia agree on this point and both also aver that there is a marked transition in aggressiveness associated with the Zambezi River Valley. In this context it is particularly noteworthy that isopentyl acetate, a potent releaser of stinging behaviour (Kerr *et al.* 1974), reaches its highest percentage as a pheromonal constituent in the *A. m. adansonii* of Zambia and in the introgression zone with *A. m. scutellata* (Table 5, group 3 and transition group respectively).

In summary, the delineation of three subspecies of honeybees along a transect from coastal Mozambique to the mountains of northwestern Zambia and the identification of a zone of introgression is established through multivariate analyses. These interpretations are strongly supported by correlative data of the sting-gland pheromones and field experience of honeybee aggressiveness. The geographic distributions of these groups of honeybees are also associated with asymmetries of climate along the transect. Finally, the swarming and migratory seasons of the bee groups facilitate their introgression in the Zambezi River Valley.

ACKNOWLEDGEMENTS

We thank M.P. Robertson, Z. Davidson, G.E. Jones, R.P. van Hille and G. Johnson (Rhodes University) for technical assistance. We especially thank C.J. Coleman (Mazowe, Zimbabwe) and T.P. Chupa (Beekeeping Division, Forest Department, Mwekera, Kitwe, Zambia) for their observations and data.

REFERENCES

BALDERRAMA, N.M., ALMEIDA, DE B. L.O. & NUNEZ, J.A. 1992. Metabolic rate during foraging in the honeybee. *Journal of Comparative Physiology* **B162**: 440–447.

COLE, M.M. 1986. *The Savanna, Biogeography and Geobotany.* Academic Press, London.

COLLINS, A.M., BROWN, M.A., RINDERER, T.E., HARBO, J.R. & TUCKER, K.W. 1987. Heritabilities of honey-bee alarm pheromone production. *Journal of Heredity* **78**: 29–31.

CREWE, R.M., HEPBURN, H.R. & MORITZ, R.F.A. 1994. Morphometric analysis of two southern African races of honeybee. *Apidologie* **25**: 61–70.

FALCONER, D.S. 1989. *Introduction to Quantitative Genetics.* 3rd Edition. Longman, Harlow.

HEPBURN, H.R. & RADLOFF, S.E. 1996. Morphometric and pheromonal analyses of *Apis mellifera* L. along a transect from the Sahara to the Pyrenees. *Apidologie* **27**: 35–45.

HEPBURN, H.R. & RADLOFF, S.E. 1997. Biogeographical correlates of population variance in the honeybees (*Apis mellifera*) of Africa. *Apidologie* (in press).

HEPBURN, H.R., JONES, G.E. & KIRBY, R. 1994. Introgression between *Apis mellifera capensis* Eschscholtz and *Apis mellifera scutellata* Lepeletier: the sting pheromones. *Apidologie* **25**: 557–565.

JACKSON, S.P. 1961. *Climatological Atlas of Africa.* CCTA/CSA, Lagos.

KERR, W.E. 1992. Abejas Africanas su introduccion y expansion en el continente americano. Subespecies y ecotipos Africanos. *Industria Apicola* **13**: 12–21.

KERR, W.E., BLUM, M.S., PISANI, J.F. & STORT, A.C. 1974. Correlation between amounts of 2-heptanone and iso-amyl acetate in honeybees and their aggressive behaviour. *Journal of Apicultural Research* **13**: 173–176.

LACHENBRUCH, P. & MICKEY, R.M. 1968. Estimation of error rates in discriminant analysis. *Technometrics* **10**: 1–11.

MARDIA, K.V., KENT, J.T. & BIBBY, J.M. 1979. *Multivariate Analysis.* Academic Press, London.

MCINTOSH, D.M. 1990. Keeping honeybees and flora on rural wooded Zimbabwe highveld. *South African Bee Journal* **62**: 6–11.

MILLER, R. 1981. *Simultaneous Inference.* 2nd Edition. Springer, New York.

MORITZ, R.F.A. & SOUTHWICK, E.E. 1992. *Bees as Superorganisms.* Springer-Verlag, Berlin.

PAPADOPOULO, P. 1969. Introducing a foreign queen to *adansonii* colonies. *XXII International Beekeeping Congress.* 529–535. Apimondia, Bucharest.

RADLOFF, S.E., HEPBURN, H.R., ROBERTSON, M.P., VAN HILLE, R., DAVIDSON, Z. & VILLET, M.H. 1996. Discriminant analysis of the honeybee populations of southwestern Africa. *African Entomology* **4**: 1–6.

RUTTNER, F. 1988. *Biogeography and Taxonomy of Honeybees.* Springer-Verlag, Berlin.

RUTTNER, F. 1992. *Naturgeschichte der Honigbienen.* Ehrenwirth, München.

SILBERRAD, R.E.M. 1976. *Bee-Keeping in Zambia.* Apimondia, Bucharest.

WALTER, H. 1973. *Die Vegetation der Erde in Öko-physiologischer Betrachlung. I: Die Tropischen und Subtropischen Zonen.* Fisher, Jena.

WORSWICK, P.V. 1987. Comparative study of colony thermoregulation in the African honeybee, *Apis mellifera adansonii* Latreille and the Cape honeybee, *Apis mellifera capensis* Eschscholtz. *Comparative Biochemistry and Physiology* **86A**: 95–102.

Accepted 16 September 1996