Observations on the Dance Communication and Natural Foraging Ranges of Apis Cerana, Apis Dorsata and Apis Florea in Sri Lanka

R. W. K. Punchihewa, N. Koeniger, P. G. Kevan & R. M. Gadawski

OBSERVATIONS ON THE DANCE COMMUNICATION AND NATURAL FORAGING RANGES OF *APIS CERANA, APIS DORSATA* AND *APIS FLOREA* IN SRI LANKA

R. W. K. PUNCHIHEWA[1], N. KOENIGER[2], P. G. KEVAN[3] AND R. M. GADAWSKI[3]

[1]*Apiculture Development Centre, Department of Agriculture, Bindunuwewa, Bandarawela, Sri Lanka*
[2]*Institut für Bienenkunde, (Volle Technische Gesellschaft) Fachbereich Biologie, Universitat Frankfurt/M, Karl-von-Frisch-Weg 2, 6370 Oberursel, German Federal Republic*
[3]*Department of Environmental Biology, University of Guelph, Guelph, Ontario, Canada N1G 2W1*

Summary

The dance communication of Asiatic honeybees is qualitatively similar to that of *Apis mellifera*. However, in *A. cerana* and *A. florea* foraging at artificial feeders the dance tempo was observed to decline (i.e., the time per dance increased) more rapidly than has been reported for *A. mellifera* as distance to the food source increased. *Apis cerana* and *A. florea* forage over short distances; at 3 of the 6 sites in this trial *A. cerana* did not visit feeders beyond 500 m. In *A. dorsata* the change in dance tempo with increasing distance to forage was much slower and similar, in this respect, to that reported for *A. mellifera*. Both *A. dorsata* and *A. mellifera* are able to forage over long distances, although in this trial 72% of *A. dorsata* foragers did not fly beyond 400 m. *Apis cerana* and *A. florea* may be unable to communicate long distances to food sources, as these distances would be indicated by very slow dances. These potential intrinsic limits, and observed constraints on foraging distance in *A. cerana*, suggests that beekeepers should manage *A. cerana* in small, well separated apiaries. In this way floral resources over small areas would not become so depleted by high densities of bees that honey yields are reduced.

Introduction

The genus *Apis* is represented by 3 species in Sri Lanka, *A. cerana*, *A. dorsata* and *A. florea*. *Apis cerana* and *A. florea* commonly occur in most parts of the lowland plains throughout the year. *Apis dorsata* is common in lowland plains in the early part of the year, but migrates to the central hills at the onset of the dry season. In the mid-country, all 3 species may be found year round, although they are not as abundant as in the lowland plains. In the hill country, only *A. cerana* is found regularly while *A. dorsata* occurs seasonally. The cooler climate of the higher elevations may restrict the distribution of *A. florea* there.

The largest of the 3 species, *A. dorsata*, builds a single vertical comb, usually about 0.5 m^2, on the underside of a rock cliff, the eave of a building or a tree branch. Its communication dance is performed on the vertical comb surface (Lindauer, 1956) and is obvious only when viewed at nest level. The smallest species, *A. florea*, also builds single vertical comb nests exposed from above, with combs about 0.015 m^2 to 0.025 m^2. *Apis florea* dances on top of the open comb (Lindauer, 1956; Koeniger et al., 1982) and is readily observed from above. The nest of *A. cerana* comprises about 5 or 6 vertical, parallel combs in a protected location such as a hollow tree trunk or a rock crevice. Lindauer (1956), Michener (1974) and Seeley (1982) provide further details of the biology of these tropical honeybees and their nests.

Although most climatic factors seem to be favourable for honeybees in Sri Lanka, the honey production of commercially kept *A. cerana* is quite low (2-3 kg/hive according to Lanerolle, 1984). Low production may be caused, in part, by an over-concentration of colonies. Determination of the natural flight range of *A. cerana* is desirable in order to help recommend the appropriate distribution of colonies to optimize honey production.

Although our study included comparisons with *A. dorsata* and *A. florea*, emphasis was given to *A. cerana* as the commercial honey producer. As *A. dorsata* and *A. florea* often share the same habitat with *A. cerana*, their inclusion facilitated our study of flight ranges.

Flight ranges of honeybees can be determined by behavioural experiments involving marked bees which have learned to forage for sugar-water (*c.* 30% sugar) at feeders at known distances from an experimental colony. At the observation hive or nest, the dance language can be monitored for individual foragers as they return from the feeder. The speed of the waggle dance indicates the distance to the food source. This is well described for *A. mellifera*

by Frisch (1967) who was the first person to relate dance time to distance. Lindauer (1956) also studied the dance communication of the Sri Lanka honeybees. His data were essential for the ideas which led to our research.

Materials and Methods

All experiments were conducted in Sri Lanka between December 1980 and July 1981. The general topography of Sri Lanka, the locations of major cities, and our study sites are shown in Fig. 1. Information on numbers of colonies used and types of experiments performed at each site is given in Table 1.

The waggle-dance (Frisch, 1967; Lindauer, 1956) communication pattern was used as the indicator of flight distance. At the beginning of the study the dance pattern was observed (time per dance in s) for predetermined distances. As a bee visited the feeding dish it was marked on the top of the thorax with 'Duco' automobile paint (Smith, 1972). Three to five continuous and complete dance circuits of marked bees were observed and timed. For any one experiment there was a feeding dish at only one given distance, therefore we assumed that the marked bees would indicate only that distance. The possibility that these bees abandoned the dish for other forage cannot be eliminated, but we feel that this would have been unlikely within the short period of the experiments. Later, time per dance for each distance was calculated and the results plotted graphically. In measuring the speed of the waggle dance of the returned
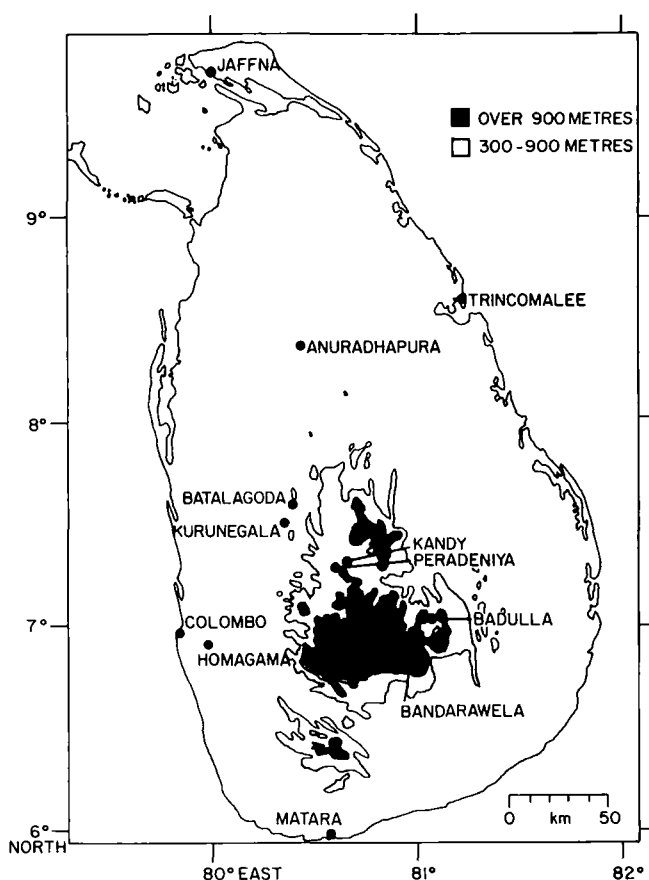

FIG. 1. Sri Lanka: general topography, major cities and experimental sites.

TABLE 1. Locations of experimental sites and numbers of colonies used for obtaining standardization relationship of dance tempo and distance foraged (SC) or data on natural dances (ND) of honeybees.

| District | Place | No. colonies | | | | | |
| | | A. cerana | | A. dorsata | | A. florea | |
		SC	ND	SC	ND	SC	ND
Anuradhapura	Puliyankulama	2	2	—	—	—	—
	Anuradhapura (Old Town)	—	—	—	—	—	1
	Anuradhapura (New Town)	—	—	1	1*	2	—
Badulla	Bandarawela	3	3	—	—	—	—
	Diyatalawa	2	2(1*)	—	—	—	—
Colombo	Homagama	1	1*	—	—	—	—
Kandy	Peradeniya	1	2	1	1*	—	1
Kurunegala	Batalagoda	2	1*	—	—	—	—

*Same colony used for the standard flight curve.

foragers we determined the time per dance rather than the number of dances per 15 s as used by Frisch (1967) and Lindauer (1956). This made measurements more convenient since it was unnecessary to judge what fraction of an incomplete dance circuit was performed.

Stop-watches were used to time counted numbers of waggle-dance circuits of foragers returning from feeders at known distances, or of bees returning from natural foraging trips.

A colony of A. cerana was transferred from its own hive to an observation hive, as described by Frisch (1967) for A. mellifera except that the observation hive was suitably modified to accommodate the smaller bee. Experiments were conducted in 6 locations (see Fig. 1), Puliyankulama (Anuradhapura District), Bandarawela and Diyatalawa (Badulla District), Homagama (Colombo District), Peradeniya (Kandy District) and Batalagoda (Kurunegala District). The site at Puliyankulama was a large tract of rice fields, the site at Peradeniya was an open, predominantly grassland area in the university campus, and the Bandarawela site was surrounded by tea plantations. We deliberately selected sites with few blossoms or natural nectar sources to induce A. cerana to fly long distances when foraging from artificial feeders, thereby providing a more extensive data-set for the standard curve. At a total of 39 feeding stations, a mean of 34 bees (SD = 19) at each was observed.

A wild colony of A. dorsata was brought to the experimental site at Harischandra, Mawatha, New Town, Anuradhapura from Nochchiyagama (20 km) on 17 February 1981, using the technique of Koeniger and Koeniger (1980). At the experimental site the bees quickly became accustomed to the experimenters and, unless deliberately provoked, were quite docile. It was possible to begin experimental work within one day of moving the colony. In Peradeniya natural dances were observed in a colony established on the edge of the roof of a building at the university. For this experiment a mean number of 58 bees (SD = 5·6) was observed for each feeding distance.

Two wild colonies of A. florea were brought to our experimental site at Anuradhapura (New Town, Harischandra, Mawatha) from Nuwara Wewa area on 28 December 1980 and 5 January 1981. The transfer of these colonies was comparatively easy because of their small size, but had to be done at night to prevent loss of bees from their flying off and absconding from the open-comb nest. A mean number of 56 bees (SD = 24·3) was observed for each of 10 distances.

Observations on natural foraging dances

The dances of natural foragers that had returned from their foraging flights were observed as they entered the colony, and timed as described above. As soon as the dance time of one forager was recorded, the dance of the next to enter the colony was timed. In this way a random sample was taken. The three A. cerana colonies used previously for the standardization procedure were used together with 8 additional colonies to measure the natural

foraging dances. Times per dance of foragers returning from natural sources were calculated and foraging distance inferred from the standard curve. Bees marked for standardization experiments were omitted from natural dance observations. Observations were begun after a lapse of one day from the withdrawal of the artificial feeding dish, to induce them to seek out natural sources of food. The colonies used for observations on *A. dorsata* were the same as those described above. Natural flight ranges were observed and timed for *A. florea* in the same way as for *A. dorsata* and *A. cerana*. The observations at Anuradhapura and Peradeniya were made on natural colonies in their natural habitat.

Statistical analysis

Mean, standard deviation and standard error were calculated for the dance time of each species at each foraging distance. A simple linear-regression analysis was then used to describe the functional relationship between dance time and foraging distance for each species. Analysis of covariance was used to test whether the regression equations were identical, and the Student-Newman-Keuls multiple-range test (q statistic) was employed to determine differences between slopes and between elevations. The maximum probability of a Type I error was set at 0·05 for all procedures.

Results
Standardization of dance time–distance curves

Table 2 and Fig. 2 present the standard curve for *A. cerana* tabulated with the composite data gathered from 5 experimental sites (see Table 1). We have made a comparison with the data of Lindauer (1956) with which our results do not agree exactly. Due to lack of methodical information given by Lindauer (1956) it is difficult to surmise the reasons. Nevertheless, both curves indicate that short flight-ranges (steep slope: fast decline in dance tempo with increasing distance to food) are preferred by *A. cerana* (*cf. A. mellifera* and *A. dorsata*, Fig. 4).

TABLE 2. A summary of the parameters used to describe the simple linear regression equation for each bee species.
P = probability associated with F; r^2 = coefficient of determination.

Species	n	Slope	Y intercept	F for $H_0:b=0$	P	r^2
A. cerana	1326	0·0061	1·3989	20967·28	<0·0001	0·941
A. cerana[a]	—	0·0075	1·2192	—	—	—
A. florea	561	0·0065	1·4700	1762·52	<0·0001	0·759
A. florea[a]	—	0·0079	1·7260	—	—	—
A. dorsata	230	0·0021	1·6932	194·97	<0·0001	0·461
A. dorsata[a]	—	0·0031	1·3266	—	—	—
A. mellifera[b]	274[c]	0·0022[c]	1·3761[c]	—	—	—
A. mellifera[b]	243[d]	0·0029[d]	1·4650[d]	—	—	—

[a]From transformed data of Lindauer (1956)
[b]From transformed data of Schweiger (1958)
[c]For rapid dancers (young bees)
[d]For slow dancers (older bees)

The data of this study (Fig. 3 and Table 2), as well as those of Lindauer (1956), show a resemblance of *A. florea* to *A. cerana* in its preference for short flight ranges (steep slope). The data on *A. dorsata* from our study, as well as from that of Lindauer (1956), are indicative of an ability to forage over long distances (shallow slope: slow decline in dance tempo with increasing distance to food, Fig. 4). In this characteristic it resembles *A. mellifera* which has the ability to forage over long distances (Frisch, 1967).
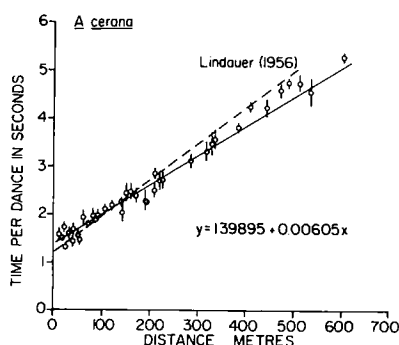
FIG. 2. Relationship between foraging distance and dance time for *A. cerana* in Sri Lanka. Solid line is for present study, broken line for data from Lindauer (1956).
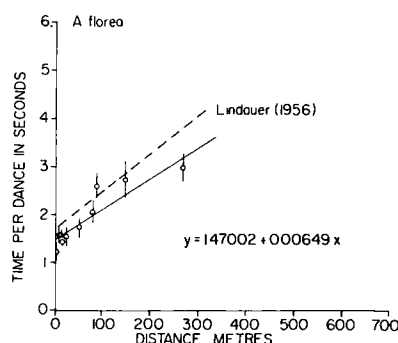

FIG. 3. Relationship between foraging distance and dance time for *A. florea* in Sri Lanka. Solid line is present study, broken line is data from Lindauer (1956).
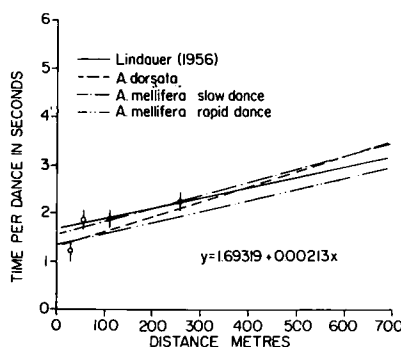

FIG. 4. Relationship between foraging distance and dance time for *Apis dorsata* in Sri Lanka, compared with data of Lindauer (1956) for the same species and with slow and rapid dances of *A. mellifera* from Schweiger (1958).

In Table 2 we show the standings of these curves to each other as well as to the curve for *A. mellifera* (see also Fig. 4) based on the data of Schweiger (1958) for young and old bees (we could not distinguish between the ages of the bees). The slope and Y-intercept of the simple linear regression equation for dance time and distance for each bee species are compared, and the significance of each regression and the corresponding probability that the calculated slope could have come from sampling a population with a slope $= 0$ are also given in Table 2, as is the coefficient of determination for each regression.

The regression lines for the 3 bee species do not have the same slope (F $= 92\cdot4$, P$<0\cdot0005$), or elevation (F $= 1\cdot84 \times 10^5$, P$<0\cdot005$). The slope for *A. dorsata* is different from the slope for *A. cerana* ($q = 13\cdot52$, P$<0\cdot001$) and *A. florea* ($q = 9\cdot12$, P$<0\cdot001$); however, *A. cerana* and *A. florea* have slopes which are not significantly different ($q = 1\cdot64$, P$>0\cdot20$). The elevation of the line for *A. cerana* is significantly different from the elevation of the line for *A. florea* ($q = 25\cdot00$, P$<0\cdot001$) and *A. dorsata* ($q = 17\cdot55$, P$<0\cdot001$); however, the elevations of the lines for *A. florea* and *A. dorsata* are not significantly different ($q = 0\cdot05$, P$>0\cdot50$).

Dance time and natural foraging distance

The time per dance of returning foragers from natural sources was calculated as described above. These times were then categorized into different time intervals of $0\cdot5$ s and the results used to construct histograms showing the frequency for each dance time. These histograms were then fitted with the standard foraging-distance regression curves (Fig. 5 to Fig. 7). This
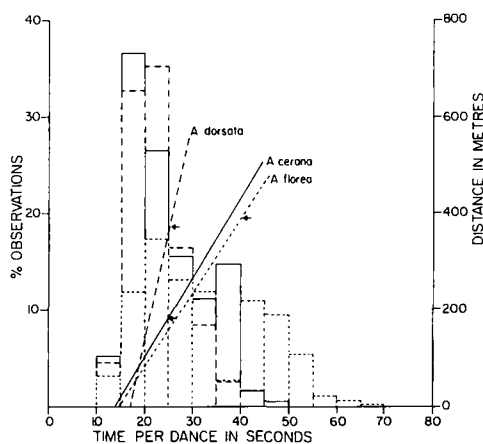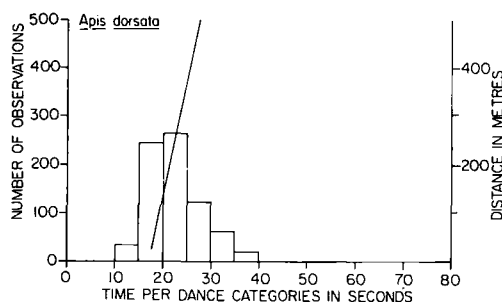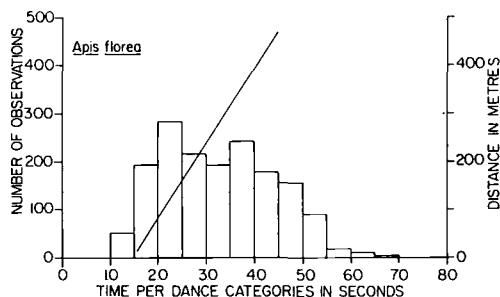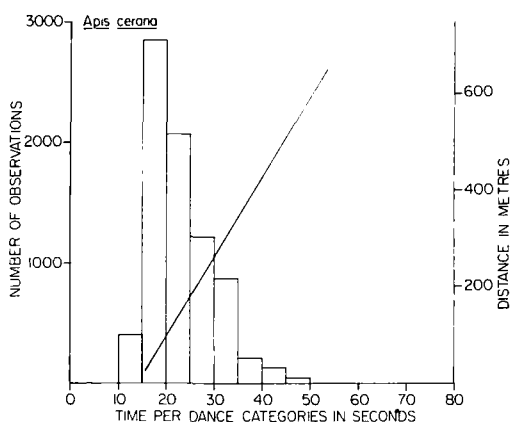
FIG. 5 (*upper left*). Natural foraging ranges for *A. cerana* in Sri Lanka shown by the frequency of dance-time categories (bar graph) and the corresponding distances represented (oblique line). Data from Fig. 2.

FIG. 6 (*upper right*). Natural foraging ranges for *A. florea* in Sri Lanka shown by the frequency dance-time categories (bar graph) and the corresponding distances represented (oblique line). Data from Fig. 3.

FIG. 7 (*lower left*). Natural foraging ranges for *A. dorsata* in Sri Lanka shown by the frequency of dance-time categories (bar graph) and the corresponding distances represented (oblique line). Data from Fig. 4.

FIG. 8 (*lower right*). Comparisons of natural foraging ranges of the three *Apis* species in Sri Lanka. (————), *A. cerana*; (- - -), *A. florea*; (—— ——), *A. dorsata*. Frequency of a dance-time category is presented as percent of observations (data from Fig. 5, Fig. 6 and Fig. 7) and corresponding distance represented (oblique lines from Fig. 2, Fig. 3 and Fig. 4). Arrows show cumulative percentage (to 70%) of the populations of foragers for each species.

allowed interpolation of the distance that the bees in each category foraged from each dance-time category.

For interspecific comparisons we have combined in Fig. 8 all the findings presented in Fig. 5, Fig. 6 and Fig. 7. To facilitate this combination we have transformed the dance-time category for each species into a percentage category of the total number of observations. This transformation also allowed us to compare the behaviour of a comparable group of foragers in each species. In this comparison we have taken about 70% (68·3% to 72·5%) of the population studied for each species of bee to compare their foraging radii. For *A. cerana* (Fig. 5) we have used categories 1–3 (i.e., the percentage of bees with flight ranges indicated by waggle-dance circuit times of 1·0–2·5 s inclusive), which represents 68·3% of the foraging bees. For *A. florea*, categories 1–6 (i.e., the percentage of bees with flight ranges corresponding to dance circuit times of 1·0–4·0 s inclusive) represent 72·3% of the foraging bees. For *A. dorsata* (Fig. 7), categories 1–3 (i.e., the percentage of bees with flight ranges corresponding to waggle-dance circuit times of 1·0–2·5 s inclusive), represent 72·5% of the foraging bees.

Discussion

All three species of *Apis* have preferred short foraging distances of not more than 400 m (Fig. 8). The comparative flight curves (Fig. 4) show that *A. dorsata* and *A. mellifera* are similar. Though the shallow standard flight-distance curve of *A. dorsata* indicates the ability to forage as widely as *A. mellifera*, it seemed to prefer to forage close to the nest (Fig. 7); 72% of the foragers did not fly beyond 400 m. This may explain, in part, our inability to train these bees to a feeding dish beyond 250 m (Fig. 4). Presumably, there was plenty of forage in the vicinity of most experimental sites to which the bees went in preference to the more distant feeding dish.

There is also a similarity between *A. cerana* and *A. florea*. Both foraged within a small radius (Fig. 5 and Fig. 6). The standard flight-distance curves suggest that they are unable to communicate longer distances to food sources. These bees perform a relatively longer dance for the distance they travel than do *A. dorsata* and *A. mellifera*; the slope of the line is steeper (Fig. 8). Only at 3 of the 6 experimental sites were we able to entice *A. cerana* foragers to visit feeding dishes beyond 500 m. These sites (Puliyankulama, Peradeniya and Bandarawela) were especially chosen as they were devoid of the mixed floral types and dense vegetation typically found in tropical countries (see above).

The dispersion in data points in Fig. 2, Fig. 3 and Fig. 4 may be due to the age differences of the marked bees trained to the feeding dish (*cf.* Schweiger, 1958) or to other factors such as individual colony differences, weather, topography, etc. which are known to affect the dance language (Frisch, 1967), but which we did not or could not control.

During the early part of the year, after the monsoonal rains, the lowland plains (e.g., Anuradhapura District) offer abundant food for all 3 species of bees. Hence they would be able to fulfil their food requirements within a short distance. Probably the large *A. dorsata* and medium-size *A. cerana*, with large colony populations, are able to exploit all the large flowers in an area. Within the same area, smaller *A. florea* may exploit the flowers that the larger bees do not reach, or which are undesirable because of size or anatomical differences in flowers, or bees, or both. This combination of phenomena may enable the 3 species to coexist. However, with the approach of the dearth period, the smaller *A. florea* and *A. cerana* appear to become more successful competitors for nectar than *A. dorsata*. Then the option left for the larger *A. dorsata* is to make a long-distance migration to an altogether different environment. The experiments of Koeniger and Vorwohl (1979) on the competition among Apini further strengthen this point; they found that *A. dorsata* was a poorer competitor than other, smaller social bees feeding at dishes. Once *A. dorsata* removes itself from local foraging niches, *A. cerana* and *A. florea* may coexist through a system of resource partitioning. From the results of pollen analyses of natural honeys, we suspect that the different bees forage at different types of flowers. Some data supporting this are given by Koeniger and Vorwohl (1979), but certainly this is an area for important future research.

The trends we have described agree in general with those of Lindauer (1956, 1957). He suggests that the short foraging ranges of these bees are in response to rain, the abundance of tropical flowers, lack of climatic seasonality, and a weaker hoarding instinct than in *A. mellifera*. We are doubtful of the importance of rain because it is not rainy year round in Sri

Lanka and even during the rains there is ample warning for bees to return to the nest from a distance of over 1 to 2 km before being washed out. The abundance of tropical flowers certainly will restrict observed foraging ranges and is probably important for *A. florea* and *A. cerana*, but not for *A. dorsata*. The lack of climatic seasonality may account for the bees' reduced requirements for hoarding, and so effect a lesser need for extensive foraging ranges. These ideas are, in part, paralleled by suggestions of the reasons for differences in dialect among races of *A. mellifera* (Gould, 1982).

The demonstrated short foraging range of *A. cerana* indicates that large bee-yards are not appropriate for this species. Large numbers of bees in small areas will deplete floral resources rapidly and result in severe interspecific competition and low honey yields and high rates of absconding, as observed. Thus we suggest that beekeepers using *A. cerana* should spread their hives out with only a few at each location.

Acknowledgements

References

BUTLER, C. G. (1953) The present status of beekeeping in Ceylon and possibilities for its future development. *Br. agric. Bull.* 6 : 125-128

———(1975) The honey bee colony life history. *pp.* 39-74 *from* The hive and the honey bee. *eds* Dadant and Sons. *Hamilton, IL, USA : Dadant & Sons*

FRISCH, K. VON (1976) The dance language and orientation of bees. *Cambridge, MA, USA : Belknap Press of Harvard University Press*

GOULD, J. L. (1982) Why do honey bees have dialects? *Behavl Ecol. Sociobiol.* 10 : 53-56

KOENIGER, N.; KOENIGER, G.; PUNCHIHEWA, R. K. W.; FABRITIUS, M. O.; FABRITIUS, M. I. (1982) Observations and experiments on dance communication in *Apis florea* in Sri Lanka. *J. apic. Res.* 21 : 45-52

KOENIGER, N.; VORWOHL, G. (1979) Competition for food among four sympatric species of Apini in Sri Lanka (*Apis dorsata, A. cerana, A. florea, Trigona iridipennis*). *J. apic. Res.* 18(2) : 95-109

LANEROLLE, G. A. (1984) Beekeeping in Sri Lanka. *pp.* 217-221 *from* Proceedings of the expert consultation on beekeeping with *Apis mellifera* in tropical and subtropical Asia. *Rome : FAO*

LINDAUER, M. (1956) Über die Verständigung bei indischen Bienen. *Z. vergl. Physiol.* 28 : 521-557

———(1957) Communication among the honeybees and stingless bees in India. *Bee Wld* 38 : 3-14,34-39

MICHENER, C. D. (1974) The social behavior of the bees. *Cambridge, MA, USA : Belknap Press of Harvard University Press*

SCHWEIGER, E. M. (1958) Über individuelle Unterschiede in der Entfernungs und Richtungsangabe bei den Tänzen der Bienen, *Z. vergl. Physiol.* 41 : 272-299

SEELEY, T. D.; SEELEY, R. H.; AKRATANAKUL, P. (1982) Colony defense strategies of the honeybees in Thailand. *Ecol. Monogr.* 52 : 43-63

SMITH, M. V. (1972) Marking bees and queens. *Bee Wld* 53 : 9-13