Dance dialects and foraging range in three Asian honey bee species

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Summary. We measured the "distance dialects" in the dance languages of three honey bee species in Thailand (*Apis florea, A. cerana,* and *A. dorsata*), and used these dialects to examine the hypothesis that a colony's dialect is adaptively "tuned" to enhance efficiency of communication over the distances that its foragers typically fly. In contrast to previous interspecific comparisons in Sri Lanka (Lindauer 1956; Punchihewa et al. 1985), we found no striking dialect differences among the Asian bees in Thailand. The adaptive tuning hypothesis predicts that the foraging ranges of the three species should also be similar, but comparisons of colonial foraging range using the "forage mapping" technique (Visscher and Seeley 1982) actually revealed marked differences. This raises the possibility that the link between ecology and distance code is more subtle than previously supposed, if a link exists at all.

Introduction

The dance language of honey bees, by which foragers inform nest mates of the location of food, incorporates a striking array of individual and colonial adaptations enabling the rapid discovery and exploitation of rich floral resources in a vast area around the nest (reviewed by von Frisch 1967; Seeley 1985; Seeley and Levien 1987). An enduring mystery concerning the dance language is the existence of geographical and species-specific "dialects" in the code by which bees communicate flight distance (reviewed by von Frisch 1967, pp 293–306). Several features of the dance correlate with flight distance (von Frisch and Jander 1957). For example, circuit duration, the time elapsed from the start of one waggling run to the start of the next, increases monotonically over the entire flight range (von Frisch 1967, pp 69–70). In *A. mellifera,* despite some variation (von Frisch 1967; Esch 1978), the dialect function is similar

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among colonies in a given population, but often differs in slope among different geographical races (Boch 1957). In Sri Lanka, the dialects of the Asian species of *Apis* also differ in slope (Lindauer 1956).

The most widely accepted functional explanation for these differences is that the dialect curve for a given population is optimally tuned to the typical foraging range of colonies in the population (Lindauer 1956; Boch 1957; von Frisch 1967, pp 125–126, 293–296; Gould 1982; Punchihewa et al. 1985; Towne and Gould 1988). The evidence for this hypothesis is mainly indirect, however. This, coupled with the need for information about geographical variation in dances of the Asian *Apis* species, led us to investigate the honey bees of Thailand.

According to the adaptive tuning hypothesis, as we shall refer to it, two factors are considered important in the evolution of the dialect curve. First, steep dialect curves are assumed to be more precise than gentle curves, i.e., a given error in producing or reading the signal should result in a smaller distance error for bees searching for the food (von Frisch 1967, p 101). A second factor, related to foraging range (which is assumed to be determined independently), constrains the steepness of the curve. For example, if foraging range is large, a steep dialect curve might require such long waggling runs (and circuits) to communicate very long flight distances that bees following the dances would have difficulty staying with them (Gould 1982). Whatever the costs, they are assumed to impose a similar upper limit on circuit duration for all honey bees. The optimal slope for a given population is that which is steepest (most precise) subject to this limit; if the foraging range is shorter the curve can be steeper.

Evidence provided for this hypothesis in *A. mellifera* (Boch 1957; von Frisch 1967; Gould 1982) is circumstantial, since the foraging ranges of different races have never actually been compared directly. In comparisons of the Asian *Apis* species in Sri Lanka, Lindauer (1956) found that the steepness of the dialect curve was inversely correlated with body size (and thus, Lindauer as-

sumed, with potential flight range), and with the maximum distance that foragers would fly to an artificial feeding station. However, even if body size constrains flight range in insects, there is no independent evidence that the particular size differences found in *Apis* should result in large differences in flight range. Furthermore, the maximum training distance may underestimate the bees' maximum foraging range unless there is little nectar stored in the nest and a scarcity of competing natural floral resources (von Frisch 1967; pp 66–67; Seeley 1989).

A recent study of the Sri Lankan populations of the Asian honey bees (Punchihewa et al. 1985) compared foraging ranges using the more realistic method of constructing "forage maps," i.e., observing dances to natural foraging sites and then using the colony's own dialect curve to infer the distances the dancers must have flown (Visscher and Seeley 1985). Punchihewa et al. interpreted their results in favor of the hypothesis that dialects are tuned to flight range in the Asian species. However, as discussed later, their data actually are not consistent with this hypothesis.

We examined the adaptive tuning hypothesis by comparing dialect and flight range in the three *Apis* species in Thailand. To measure flight ranges we constructed forage maps in an undisturbed natural habitat during the flowering season. The adaptive tuning hypothesis predicts either a negative correlation between flight range and the steepness of the dialect curve for different species or similar flight ranges for species whose dialects are similar.

Methods

Species, observation colonies, and study sites

Apis cerana, *A. dorsata*, and *A. florea* are distributed widely throughout southern Asia (Ruttner 1988). Although basically similar in their social organization, in the resources they exploit (Koeniger and Vorvohl 1979), and in their use of dance communication as part of a social foraging strategy, they differ markedly in body size, colony size, and nesting behavior (Seeley et al. 1982; Dyer and Seeley 1987, 1991).

Differences in dancing behavior (Lindauer 1956; Dyer 1985a, b, 1987) required different methods of observation. The Asian hive bee, *A. cerana*, like *A. mellifera*, dances in an enclosed nest cavity on vertical sheets of comb, encoding the angle of flight relative to the sun in the angle of waggling runs relative to gravity. We studied complete *A. cerana* colonies in an observation hive with the entrance arranged to divert returning foragers to the comb surface visible through a Plexiglas window. The giant bee, *A. dorsata*, nests in the open on a large (1-m diameter) sheet of comb attached to a tree branch or other overhanging structure. Dances, which are oriented to gravity, are performed in plain view on the outside of the curtain of bees protecting the comb. The small (15-cm diameter) nest of the "dwarf" bee, *A. florea*, consists of a single sheet of comb suspended from a thin twig. Bees dance on a rounded platform atop the nest, orienting to celestial cues in the horizontal plane rather than to gravity in the vertical plane. We collected *A. florea* nests without disturbing the bees (Seeley et al. 1982; Dyer 1985a) and placed them in a box that was about 1 m on a side. The box was enclosed (for shading) except for four openings in the top through which foragers could come and go and dancers

on the nest could see the sky. We observed the dancers through the same openings.

All measurements of the distance dialects of *A. cerana* and *A. florea* were performed between December 1984 and February 1985 at Suwan Farm (National Corn and Sorghum Research Center, Pak Chong, Nakhon Ratchasima Province), using a single colony of each species. *Apis dorsata*'s distance dialect was measured in January 1985 using a colony nesting on an office building in the northern city of Chiang Mai.

We measured foraging ranges in Khao Yai National Park (14°30′N, 101°20′E), which comprises 2200 km³ of mostly evergreen tropical rainforest. We used different colonies from those used to measure the dialects. An *A. dorsata* colony nesting on a large tree was observed through a telescope from a hillside 50 m away. One colony of *A. cerana* and one of *A. florea* were captured near Suwan Farm and then placed in a clearing about 50 m from the *A. dorsata* colony. Wild colonies of *A. cerana* and *A. florea* also lived in the area. All observation colonies were about average in size and in good health, and foraged actively for both pollen and nectar during our studies (Dyer and Seeley 1991). We allowed colonies brought from Suwan Farm to adjust to the new site for at least 10 days before beginning forage mapping studies.

We compiled forage maps from March to May 1985, during the transition from the dry season to the rainy season. Various evidence, including data from other tropical sites receiving similar patterns of rainfall (Janzen 1967; Frankie et al. 1974), suggests this is the season of maximal flowering of the insect-pollinated plants likely to be exploited by the bees.

Distance dialects. To measure distance dialects we followed the methods used by Lindauer (1956) in Sri Lanka. We trained individually labeled bees to a feeding station offering a scented sucrose solution (2.25 mol/l); we then moved the station in steps away from the nest while observing the dances at given intervals. After 45 min or more at a new site (to allow bees to adjust to the new flight distance), we measured the duration (in seconds) of a series of 1–15 consecutive circuits performed by a dancer; we then divided to obtain the average circuit duration for that dance. We measured 13–64 dances to each flight distance. For *A. dorsata* and *A. cerana*, but not *A. florea*, we continued moving the feeding station outward until bees stopped visiting the feeder (maximum training distance).

Whatever the actual distance signal in the dance (see von Frisch and Jander 1957; Wenner 1962; von Frisch 1967), measurements of circuit duration should fairly represent similarities and differences among dialects. Supporting this assumption, bees from *A. mellifera* races having different curves of circuit duration versus flight distance apply their race-specific codes to obtain distance information in racially mixed colonies, even if the dancer's code specifies a different distance (Steche 1954; cited by von Frisch 1967, pp 298–301; Boch 1957). Thus differences measured by human observers reflect real differences in the codes used by the bees.

To compare our data with those of previous studies in Sri Lanka, we measured the numerical value of each data point plotted on the dialect curves of Lindauer (1956) and Punchihewa et al. (1985). We have assumed, as did Lindauer (1956) and von Frisch (1967, pp 300–306), that the dialect curve measured for a single colony represents the local dialect for the population. Within each of the Asian species, the curves measured in Sri Lanka by Lindauer do not differ in slope from those measured by Punchihewa et al. ($P > 0.25$, *F*-test). Also, in both *A. mellifera* (von Frisch 1967, p 124) and *A. cerana* (Punchihewa et al. 1985), a given local dialect curve is observed consistently among numerous colonies.

Foraging range. To use the forage mapping technique of Visscher and Seeley (1982), we randomly sampled from dances indicating natural sources of nectar or pollen in Khao Yai Park, measured the average circuit duration of a sampled dance, and used the species-specific dialect curve to infer the distance the dancer must have flown. This method of inferring foraging distance seems the

most appropriate for testing whether the dialect is related to flight range since the flight range in question is that over which bees use dances for recruitment.

We observed each colony continuously during daylight ($\approx$ 0545–1830 hours) over 1–2 periods of 3–4 consecutive days (*A. florea*, 18–20 March; *A. cerana*, 27–30 March and 20–23 April; and *A. dorsata*, 6–9 April and 2–5 May). All dances on the *A. florea* colony took place in our view. Some of *A. cerana*'s dances may have been performed in parts of the hive not visible through the window, and some of *A. dorsata*'s foraging and dancing took place when ambient light was too low to use the telescope. We assume our samples were not biased because of these gaps.

Dancers to be measured were selected by reference to a grid of numbered squares superimposed over the dance floor; our assistant called out numbers from a random number table until a grid square was found with a dance in progress (Visscher and Seeley 1982). For *A. dorsata* we used a grid drawn on an index card; the observer looked through the telescope with one eye, held the grid in front of the other eye, and aligned the stereoscopically merged images. For each selected dance, we timed the duration of 1–30 circuits with a stopwatch and also measured its orientation.

To infer the distances indicated by the sampled dances, we assumed that the non-linear distance dialect curve of each species could be broken into two linear segments of different slope. We decided by inspection the interval within which the "break point" should fall and then calculated least-squares regression lines for the data at shorter and longer distances. The break point is the intersection of the lines. The slope covering longer distances was used for extrapolating the dialect curve to interpret dances to sites beyond the maximum training distance. This method of extrapolation is justified further in the Results. The reference for all statistical analyses is Sokal and Rohlf (1981).

Results

Dialect curves

The dialect curves we measured in Thailand have the non-linear shape found in many *Apis* populations when circuit duration is plotted against flight distance (Fig. 1). By extension from *A. mellifera*, curves based on waggling run duration (which is probably the actual distance signal) might be less bowed (von Frisch 1967, p 124) or even linear (Wenner 1962).

To simplify the extrapolation of the curve to long flight distances, we broke each curve into two linear segments of different slope (Fig. 2). This procedure seems justified by the observation that *A. m. carnica*'s dialect rises in a virtually linear fashion over flight distances from about 1 to 9.5 km, after a steeper, and approximately linear, rise over shorter flight distances (Fig. 1C inset). Furthermore, when observing trained *A. cerana* dancers, we saw some dances to a distant natural source that seemed best explained by a linear extrapolation of the dialect curve. These dances, performed by bees bearing no pollen, had a circuit duration of 7.81 ± 0.75 s (mean ± S.D.; $n = 11$). The only natural source for > 3000 m in the direction indicated (NE) was a row of flowering trees (not identified) 1970 m from the hive, running perpendicular to this direction through an extensive plowed field. We saw *A. cerana* foragers collecting nectar, but not pollen, from the flowers. If the circuit duration of 7.81 s is plotted at 1970 m, it

falls almost exactly on the linear regression fitted to the dance data from 500 to 1200 m (after the breakpoint).

In estimating distances within the maximum training distance, the error should be relatively small even if it is not strictly true that the curve consists of two linear portions.

Intraspecific dialect comparisons

The dialect curves we measured in Thailand differed from those Lindauer (1956) measured for the same three species in Sri Lanka (see Fig. 1). Comparisons of our data with Lindauer's means (treated as single observations because he published no sample sizes or variances) revealed significant differences at most flight distances for all three species. Furthermore, least-squares linear regressions fitted to the data from each population are significantly different for each species. Pending further studies with more colonies, we interpret our data as preliminary evidence for regional dialect differences within each of the Asian species, analogous to the differences observed among geographically separated populations of *A. mellifera*.

Interspecific dialect comparisons

Whereas Lindauer (1956) and Punchihewa et al. (1985) observed marked interspecific dialect differences among the honey bees in Sri Lanka, we observed hardly any differences among the same species in Thailand (Fig. 2). The slopes of regressions fitted to Lindauer's data all differ significantly from one another, though *A. florea* and *A. cerana* are less different ($P < 0.025$) than either is from *A. dorsata* ($P < 0.001$). Punchihewa et al. found *A. cerana* and *A. florea* not to differ, but *A. dorsata* differed significantly from these two species. In Thailand, by contrast, we found no significant interspecific differences in the mean circuit durations at each flight distance or in the slopes of the regressions fitted to each set of data.

Flight range

If distance dialect is tuned to flight range, then the close similarity we observed in the distance dialects in Thailand leads to the prediction that the flight ranges of the three species should be similar. As shown in Fig. 3, however, there are substantial differences in the boundaries enclosing 50% (median) and 95% of the distances indicated, and in the maximum distances indicated (see Table 1).

All pair-wise interspecific comparisons of the distributions of distances indicated revealed highly significant differences ($P \ll 0.001$; Mann-Whitney U-test); flight distance appeared to be greatest in *A. dorsata*, followed by *A. florea* and then by *A. cerana*. A somewhat different pattern of differences emerges when maximum flight range is compared. As a measure of maximum flight
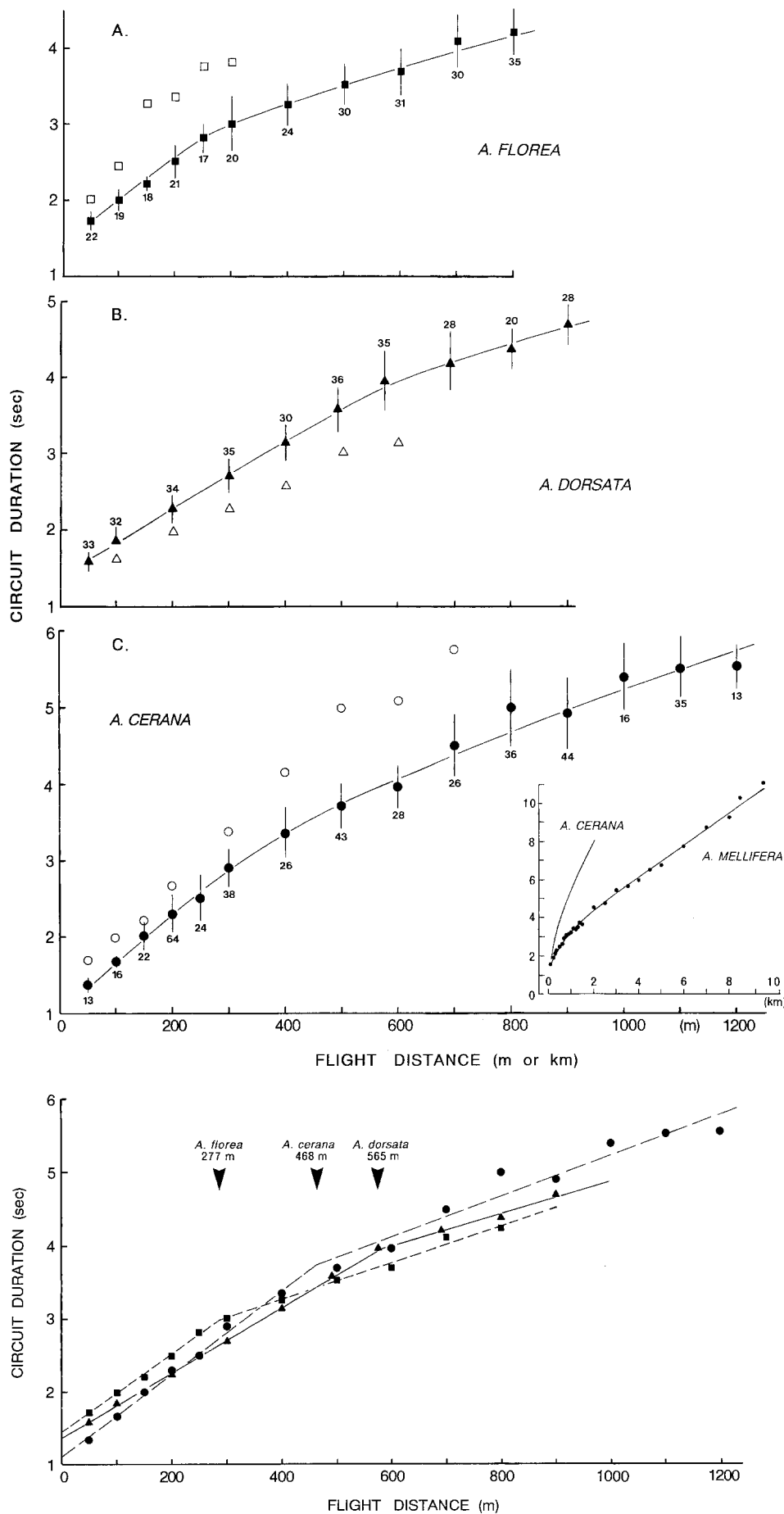
230

Fig. 1A–C. *Solid symbols:* new measurements of the distance dialects of the three Asian honey bee species in Thailand (error *bars* indicate ±1 SD); *numerals* indicate the number of dances measured at each distance). Curves are fitted by eye. *Open symbols*: data of Lindauer (1956) from same species in Sri Lanka, plotted for comparison at distances for which we also obtained data. The figure *inset* in C shows data for *Apis mellifera carnica* replotted from von Frisch (1967, pp 69–70). Also shown in the *inset* is the curve for *A. cerana* in Thailand, extended to include the circuit duration (7.81 s) corresponding to the putative foraging site at 1970 m (see text). Statistical comparisons: in *A. florea*, Lindauer's measurements differed from ours at the 0.05 level (*t*-test) at every flight distance except 300 m ($P \approx 0.051$). In *A. cerana*, Lindauer's measurements differed from ours at every flight distance except 150 m, 200 m, and 300 m. In *A. dorsata*, Lindauer's value differed from ours at flight distances ≥ 300 m. Comparing a single least-squares linear regression fitted to the data from each population, the slopes differ significantly between Thailand and Sri Lanka for all three species, but the difference is less pronounced for *A. dorsata* ($0.025 < P < 0.05$, *F*-test) than for *A. florea* ($P \ll 0.001$) and *A. cerana* ($P \ll 0.001$)

Fig. 2. Dialect curves of the Asian honey bees (*Apis*) in Thailand showing the regression lines used to infer flight distance from the mean circuit durations of dancers indicating natural food sources in Khao Yai Park. *Symbols* as in Fig. 1. The *arrows* indicate the "break points" of the dialect curves (see text)
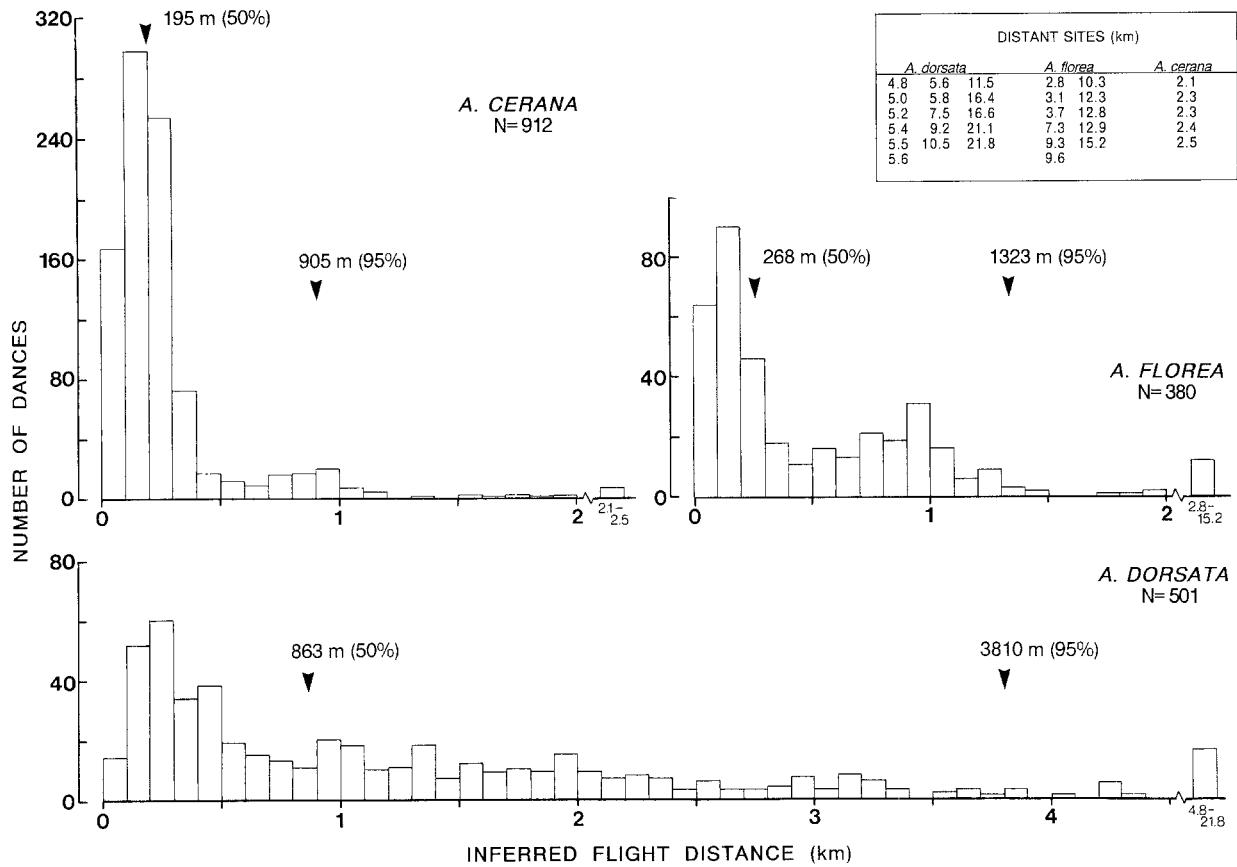
Fig. 3. Distribution of flight distances inferred for all dances to natural food sources observed in Khao Yai National Park. *N* gives the number of dances observed for each species. The *table* lists for each species the distances inferred for the dances contributing to the right-most bar of the distribution. For *Apis florea* and *A. dorsata*, the list reveals a gap between the tail of the main distribution and a few much more distant sites

Table 1. Flight ranges observed in bees trained to artificial feeding stations and inferred from dances to natural feeding sites in four species of *Apis*. Data are from the present study in Thailand, and from studies in Sri Lanka (Lindauer 1956), in Europe (reviewed by von Frisch 1967), and in North America (Visscher and Seeley 1982). Mean maximum circuit duration (in $s \pm SD$) and flight distance (in $km \pm SD$; sample size in parentheses) were obtained from upper 2% of distribution of dances to natural sites in Thailand

	Trained bees		Natural feeding sites				Mean max. circuit duration (s)
	Maximum distance flown (m)	Maximum distance danced (m)	Parameters of distance distribution				
			50% (m)	95% (m)	Max. (km)	Mean max. (km)	
Apis florea							
Thailand[a]	>800	>800	268	1323	15.2	11.2 ± 2.5 (n=8)	30.3 ± 6.3
Sri Lanka	350	300					
Apis cerana							
Thailand	1300	1200	195	905	2.5	1.9 ± 0.4 (n=18)	7.6 ± 1.1
Sri Lanka	750	700					
Apis dorsata							
Thailand	1000	900	863	3810	21.8	12.0 ± 6.1 (n=11)	28.9 ± 13.3
Thailand[b]			811	2501	13.2	7.4 ± 5.4	
Sri Lanka[a]	>600	>600					
Apis mellifera							
Europe	12500	10000					
North America			1650	6000	10.9	7.9 ± 0.9 (n=37)	≈ 9.5

[a] No attempt was made to train to maximum distance
[b] Distances recalculated using single regression on dialect data, instead of two regressions. See text for details

range, we averaged the circuit durations and the inferred distances in the upper 2% of each species distribution (Table 1). Means for *A. dorsata* and *A. florea* do not differ ($P > 0.5$, *t*-test), both rivaling *A. mellifera*'s foraging range (Visscher and Seeley 1982), but both were significantly greater than *A. cerana*'s ($P \ll 0.001$).

In extrapolating the dialect curves to infer long distances, the greatest potential for error arose for *A. dorsata*, since about 50% of its inferred foraging sites were beyond the maximum distance indicated by trained dancers (as opposed to 2% for *A. cerana* and 27% for *A. florea*). To see if we could skew *A. dorsata*'s distribution toward those of the other species, we estimated its flight distances with a single linear regression fit to our data in Fig. 1 B. This lowered the distances inferred for longer circuit durations. The median and 95th percentile of the distribution were changed to 811 m and 2501 m, respectively, but these conservative values are still much higher than those of the two other species (Table 1). *Apis dorsata*'s recalculated mean maximum flight range is still greater than *A. cerana*'s ($P \ll 0.001$), but is now less than *A. florea*'s ($P < 0.02$).

The dances by *A. florea* and *A. dorsata* to the most distant sites (see table inset in Fig. 3) differed from those of *A. cerana* in being isolated from the tail of the main distribution and even from one another. Also, none of the dancers indicating these sites carried pollen, whereas the *A. cerana* dancers indicating the six most distant sites all carried pollen. Since we could not determine whether the *A. florea* and *A. dorsata* dancers carried nectar, the possibility arises that they were indicating not feeding sites but new nesting sites; *A. dorsata* performs dances of very long circuit duration just prior to colony migration (Dyer and Seeley, in preparation). At least in the case of *A. florea*, however, such long circuit durations are seen for foraging sites. On a colony at Suwan Farm, we saw a pollen-bearing *A. florea* dancer perform 13 circuits averaging 23.5 s in duration, which indicates a distance to the pollen source of about 8.5 km, comparable to the longest observed in Khao Yai Park. The longest dances observed for *A. cerana* at Suwan Farm indicated 2.0 km, which is also comparable with our observations in Khao Yai Park.

Discussion

Our studies, taken together with previous work in Sri Lanka (Lindauer 1956; Punchihewa et al. 1985), suggest that there may be regional dialect differences in the dances of each of the Asian species of *Apis*, similar to the differences that have been observed among races of *A. mellifera* (Boch 1957). We also found that there is not a consistent pattern of interspecific differences in Sri Lanka and Thailand. In Sri Lanka the dialect curves of the three species are clearly divergent. In Thailand they rise virtually in parallel. Such a difference between the two regions would not be expected if there were a functional relationship between dialect and other traits, such as body size, in which the Asian bees differ consistently across their overlapping ranges in Asia.

These patterns need to be investigated further with more intensive studies, involving several colonies in each region being compared.

On the question of whether distance dialects are adaptively tuned to flight range, our forage map data favor a negative answer, at least for comparisons among species in Thailand. In contrast to a key prediction of the adaptive tuning hypothesis, we observed similarities in dialect but marked differences in flight range, with *A. dorsata*'s flight range being the greatest, *A. florea*'s slightly smaller, and *A. cerana*'s by far the smallest. This pattern undermines the assumption (Lindauer 1956) that flight range increases with increasing body size (since *A. cerana* is larger in size than *A. florea*). It is consistent, however, with our finding (Dyer and Seeley 1987, 1991) that various scaling relationships are reversed in *A. cerana* and *A. florea*.

Punchihewa et al. (1985) suggest that their forage map studies in Sri Lanka support the adaptive tuning hypothesis. However, their data are actually consistent with our results in revealing *A. florea* and *A. dorsata* to have similar maximum foraging ranges, which exceed that of *A. cerana*, and in not finding the association between flight range and dialect predicted by the adaptive tuning hypothesis. In Sri Lanka, *A. cerana*'s dialect was similar to *A. florea*'s but its flight range was more restricted, and *A. dorsata* and *A. florea* had markedly different dialect curves but essentially identical foraging ranges.

Leaving aside the inferred flight ranges, our data weigh against the basic assumption of the adaptive tuning hypothesis that dialects in different species are shaped by a common constraint on the maximum allowable circuit duration (or waggling run duration), and hence on slope (Gould 1982). In *A. cerana*, the maximum circuit duration we observed was 9.5 s. In *A. mellifera carnica*, the greatest flight distances (8–10 km) are also encoded by a circuit duration of about 10 s (von Frisch 1967, p 70; Visscher and Seeley 1982). In both *A. dorsata* and *A. florea*, however, many dances had average circuit durations > 20 s. As shown by the *A. florea* dancer observed indicating a source of pollen with circuits of 23.5 s in duration, such long dances can certainly indicate feeding sites. This makes it difficult to argue that *A. m. carnica*'s dialect curve is limited in slope and precision by a universal requirement that circuit duration not exceed about 10 s. If there is such a constraint on distance communication, it must not apply across species.

In fact, the association between maximum circuit duration and nesting behavior (*A. dorsata* and *A. florea*, with relatively long maximum durations, nest and dance in the open while the two other species nest in cavities), raises the intriguing possibility that there is a constraint that varies with nesting behavior. For example, the constraint could be sensory. Visual signals appear to play some role in dance communication in open-nesting species, but not in cavity-nesting species, which use only acoustic and tactile signals (Towne 1985). Perhaps, in turn, visual communication allows the use of greater maximum circuit durations. If so, tests of the adaptive tuning hypothesis might have to be restricted to compar-

isons among honey bees which have similar nesting behavior.

Whatever the plausibility of these speculations, our observations in Thailand suggest that there is not an inevitable or universal relationship between dialect and flight range, between dialect and climate, or between dialect and body size. The most important limitation of our study is that both our measurements of dialects and our measurements of foraging ranges were made with single colonies of each species. Moreover, we were unable to observe the bees year round and in a range of different habitats. For these reasons we regard our conclusions as preliminary. Nevertheless, the patterns we describe are sufficiently robust to suggest that geographic and interspecific variations in the dance language remain a mystery, and deserve to be considered afresh.

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