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SKYLIGHT POLARIZATION PATTERNS AS CUES FOR HONEY BEE ORIENTATION; PHYSICAL MEASUREMENTS AND BEHAVIORAL EXPERIMENTS.

A thesis submitted to the Faculty of The Rockefeller University
in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

by

Michael Leo Brines

April 1, 1978

New York

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SUMMARY

This thesis reports the results of behavioral, theoretical, and physical studies of the use of solar and skylight cues by animals for orientation. The principal features of skylight radiation which may be important for orientation are reviewed, together with previous investigations of honey bee polarization sensitivity. The dynamic properties of skylight polarization are shown to be potentially useful for animal navigation. Because the polarization patterns rotate around the celestial poles they could be used to locate the pole point where the earth's axis of rotation intersects the celestial sphere. Observation of the pole point could provide an animal with information about the latitude, cardinal directions, local apparent time, and the solar declination. The behavioral experiments reported here constitute the initial steps in evaluating the possibility that animals can use these temporal aspects for navigation.

The behavioral studies mainly employed bees dancing on a horizontal surface which viewed only small artificial stimuli (maximum of about 5° of visual angle). Under these conditions, bees interpreted a small, white, unpolarized light as the sun. Source elevation did not seem an important variable for orientation. On clear days, small, white, polarized sources were interpreted as the sun. On overcast days, the bees tended to react to the source polarization, but their dances showed large deviations in direction. Thus the reactions of dancing bees to small

spots of light depend on the sky conditions outside the hive some time earlier.

When the visual angle subtended by a white, polarized source not located in the zenith was larger than about 15°, the bees interpreted it on the basis of its polarization. However, small, white, polarized sources in the zenith were always interpreted on the basis of their polarization.

A small, polarized, ultraviolet (UV) stimulus was interpreted as part of the clear blue sky at all elevations tested. When long wavelengths were included in the light beam, the responses to polarization were inhibited and the bees used the source as if it were the sun, except when it was directly in the zenith. These effects were shown to depend upon wavelength, rather than on the intensity of the beam.

In general, a particular E-vector occurs at the same elevation in two different azimuth directions. Thus my small polarized light stimuli could be interpreted as being either of two spots in the sky. This should lead to ambiguity in indicating the direction of a goal. But in my experiments, when bees viewed vertically polarized patterns which correspond to two optically equivalent points on the skyvault, they oriented their dances in the direction which corresponded to an interpretation of the source as being the point to the right of the sun. In other cases, bees always used my stimuli as the point farther from the sun. These "rules" are discussed in detail.

Bees were more precisely oriented to more nearly horizontal E vectors compared to more nearly vertical ones. Also, if clear blue sky

was visible in the sky during the last foraging flight, the bees tended to treat an artificial, unpolarized UV light as if it was a specific point on the skyvault, often in the antisolar vertical. On overcast days, this behavior was not observed and the bees generally used such a source as the sun.

The geometrical aspects of orientation by skylight polarization cues are developed here in analytical detail. By this analysis, in conjunction with the results of the behavioral experiments, I conclude that bees probably do not "calculate" solar position from the skylight polarization patterns. Rather, they may have a specific detector system for polarization patterns which enables them to use skylight cues directly without analysis. Experience may be an important factor in the precision of orientation. Evidence is presented which implies that under the conditions of these experiments the UV receptors do not act independently in the central nervous system in the analysis of polarization; longer wavelengths can have a direct and profound influence on their physiological actions. The emerging picture of honey bee polarization orientation seems to be that there is considerable flexibility in the mechanisms of analysis.

A sensitive, computer-controlled polarimeter was constructed to measure all of the polarization parameters in half the sky within about seven minutes. Using this instrument, I recorded the radiance, degree of polarization, and E-vector orientation at 5° intervals over the sky at the wavelengths 350 (UV), 500 (blue/blue-green), and 650 nm (red) under a variety of atmospheric conditions. This constitutes the first time such extensive data have been recorded within a short period for those

wavelengths relevant for honey bee vision. The results demonstrate that for clear sky longer wavelengths provide better and more extensive information about the sun's position than does the UV. The magnitude of the observed radiance and per cent polarization always diverged greatly from the predictions of primary Rayleigh scattering over much of the sky and at all wavelengths. Except for points in the sky close to the sun and antisun, E-vector orientation was usually close to simple theoretical predictions, which assumed only Rayleigh scattering, and only small differences occurred as a function of wavelength. The proportion of the sky which corresponded closely to theory was always smaller in the UV than at longer wavelengths. With increasing multiple scattering (e.g., in light haze), the deviation of E-vector orientation from theoretical predictions for points in the sky far from the sun was still quite small, but was strikingly dependent on wavelength. UV wavelengths diverged most from the predictions of Rayleigh scattering under these conditions.

Very little polarization from primary Rayleigh scattering was observed under completely overcast conditions at any wavelength, despite previous speculation that useful patterns might exist in the UV underneath cloud cover. If, however, the sun's disc or light patches in the clouds were visible, and some direct sunlight pierced the overcast, low levels of polarization were observed for which the E-vector orientation was close to the simple geometrical expectations of primary Rayleigh scattering. I also observed appropriate polarization patterns against patchy cumulus clouds which were most highly polarized in the UV. The physical basis of this previously unappreciated advantage of UV wavelengths for polarization orientation is discussed, and the still

greater potential importance to insects foraging in or near vegetation is pointed out. I suggest that UV polarization sensitivity is a specific adaptation to use sky information generated by scattering relatively close to an observer which minimizes the disturbances of objects obscuring the sky. However, even E-vector orientation, the parameter which most closely approximates the predictions of simple Rayleigh scattering, does not seem precise enough for successful orientation based strictly on geometrical analysis.

I also attempted to confirm von Frisch's conclusion that bees can orient themselves under completely overcast conditions by viewing the sun's disc through the clouds in the UV. Detailed radiance measurements, however, did not demonstrate any advantage for the UV, and suggest that under many conditions of overcast, the sun's disc should not be visible to bees at all.

Additional topics discussed are: 1) a new training procedure and displacement experiments which demonstrate that a single return flight is all that is necessary for bees to learn the direction to a goal. 2) Sensitivity of honey bees to the geomagnetic field was confirmed for horizontally dancing Italian bees. 3) A general mathematical description of skylight polarization in the form of the Stokes vector is developed. This will prove useful for analyzing the responses of various polarization detecting systems to specific patterns of skylight polarization.

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CHAPTER I.

Introduction.

Honey bees have extraordinarily well developed orientation and communication behavior. This helps them obtain the necessary requirements of their complex societies, which typically contain between 10,000 and 60,000 individuals. They are well adapted for communal life: except for a relatively few males (drones) present only at specific times during the year and a single fertile female (the queen), members of the community (the sterile female worker bees) participate serially in all of the hive maintenance activities. These culminate in the last few weeks of an individual bee's life which is devoted to flying out from the hive and searching for needed materials, whether they are energy rich carbohydrates, proteinaceous pollen for building tissues of developing bees, water for cooling the hive, or honey dilution, and so on.

In a very real sense, each foraging bee does not work alone. If she discovers food which is sufficiently rich and plentiful, soon other hivemates arrive and join her in collecting it. Most of these newly foraging bees learn of the location and distance of the food through direct communication. This in itself is not uncommon, especially for social animals. What is highly unusual, and in fact so far as is known unique among animals besides ourselves, the communication does not depend upon any physical intermediates, such as a scent marked trail to lead naive animals directly to the food source. Rather it is based upon communication by arbitrary, abstract symbolic behavior. The discovery of the details of this communication behavior by von Frisch and his students is

one of the magnificent stories of biological science. But like so many fundamental discoveries, some facets were suspected long before von Frisch began his detailed investigations.

For example, many people have observed that honey bees are not solitary foragers and tend to collect from good food sources in groups. This suggests a facilitation or cooperation among hive members by which the society ultimately derives the greatest amount of food. This idea has been suggested in another way by the common observations of careful naturalists that any food, such as a dish of honey, may sit unnoticed by bees for a long time. If, however, a single bee discovers it and carries some food back to her hive, many more bees arrive rather soon. For many years people, such as Aristotle more than 2000 years ago, thought that the new bees (the recruits) followed the discoverer bee (the forager) on her return to the food. This and some other early theories of honey bee recruitment are partially summarized by von Frisch (1967; pp.3ff.). Gradually the results of specific behavioral experiments contradicted theories like Aristotle's. For example, Maeterlinck (1901) captured foragers as they left the hive so recruits could not directly follow. Yet new bees still arrived in comparable numbers to gather honey from the dish he offered. On the basis of his experiments, Maeterlinck concluded that bees communicated a food location through a "magnetic intuition".

Modern study of the phenomenon of honey bee recruitment began in 1919 when Karl von Frisch, then studying honey bee visual and olfactory sensory physiology, became curious about foraging and recruitment behavior. Central to this careful work are his descriptions, (summarized in von Frisch, 1923) of the curious, often observed "dances" of bees on

vertical honeycomb inside the hive. Though these had been noticed long before, von Frisch understood that they are very special.

1. Dances.

When a forager returns to the hive bearing nectar, she often runs excitedly over the surface of the comb actively seeking out other bees. Many of these she interests by regurgitating from her honey stomach some of the nectar she has just collected. Then she often performs very characteristic circling movements (dances) over the honeycomb with attending bees closely following behind her. During the dance, she is frequently stopped by special signals emitted by some of the observer bees, for which she then regurgitates more samples of the food.

1.1 Dance forms.

Figure I-1. The Round Dance. The dancer is followed by three potential recruits (from von Frisch, 1967).

Von Frisch noted two main types of dances. In one, which he called

a "round" dance, the forager completes one small diameter circle, turns around and makes a similar circle in the reverse direction (Figure I-1). Back and forth she alternates while the bees she has excited follow closely behind (von Frisch, 1923; pp. 32 ff.; 1967, pp. 29 ff.). In the other dance form, instead of circling to and fro, the newly returned successful forager makes a semi-circle and moves across its diameter in a straight line, while vigorously shaking her abdomen back and forth,

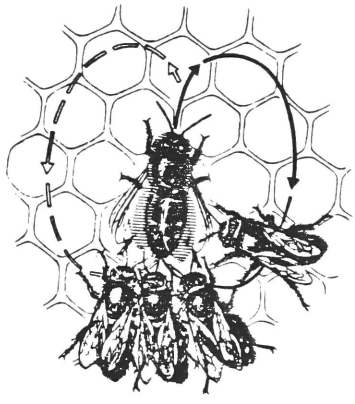

Figure I-2. The Waggle Dance (from von Frisch, 1967).

with a frequency of about 13 Hz (Figure I-2). For this reason, von Frisch called this behavior an "abdomen-waggling" or "waggle" dance for short. During the shaking the bee also often emits a distinctive "buzz" which is highly correlated with the quality of the food source she has just visited (Esch, 1964; Wenner, 1962). After each waggling run, the bee moves in a tight semi- circle and returns to the starting point. Generally, successive circuits of both round and waggle dances alternate regularly between clockwise and counterclockwise turns.

Although honey bee dances had been noticed by other observers long before (summarized by von Frisch, 1967, pp. 4 ff), von Frisch's enormous contribution was that his experiments clearly showed that honey bees used their dances for communication. At this early time (about 1923) he found that bees who attended dances became alerted to search for a food source in all directions around the hive, of a type similar to the samples regurgitated by the forager which matched the odors carried on the forager's body. Von Frisch's observations easily explained why Maeterlinck's experiment failed to prevent recruits from finding the food source-- the forager's presence was not required outside the hive.

Von Frisch originally interpreted that the different dance forms in terms of the type of food collected by the forager. He observed that pollen foragers (easily identified by the filled "pollen baskets" on their rear pair of legs) performed only waggle dances, while at the same time the individually marked bees collecting from his artificial nectar feeders displayed only round dances. Naturally, he assumed that each dance was characteristic of what the bee collected. This was the general picture of honey bee dance behavior until the middle of the 1940's even though a few reports contradicted von Frisch's ideas about dance form. For example, Park in 1923, and Henckel in 1938 (cited by von Frisch, 1967) observed no differences between the dances of nectar and pollen foragers.

Beginning about 1944, von Frisch gradually became convinced that there was a definite relationship between the form of the dance--whether it was round or waggle--and the <u>distance</u> to the food source (for review, see von Frisch, 1967, pp. 129 ff.). Through careful experiments, he

found that for the same food source, round dances gradually changed to waggle dances as the distance from the hive to the food increased. His earlier observations about round and waggle dances were explained: his artificial nectar sources were so close to the hive, that only round dances occurred, while the pollen foragers had to go much farther. Von Frisch also found that the distance at which round dances change into waggle dances as well as the form of the transition depends upon the race of the bees observed. For example, in Apis mellifera ligustica (Italian honey bee) a sickle-shaped transition dance occurs about 35 meters from the hive. This is quite different from the bee commonly used by von Frisch, A. m. carnica (Carniolan bee), which displays a transition in the form of an ∞ starting about 85 meters from the hive (summarized by Lindauer, 1961).

1.2 Distance and Direction Communication.

By using small beehives with transparent walls (observation hives), von Frisch could easily study the dances of individually marked bees on the vertical honey comb. After a while, he noticed that the waggling portion of the dances were not randomly oriented but seemed to depend upon direction the bee had flown to reach the food. With a fixed feeder location, the dance orientation did not remain constant but shifted regularly counterclockwise during the day, like the apparent motion of the sun. It became clear that the orientation of the waggle dance depended upon the angle in the horizontal plane between the sun and the goal--i.e., the relative azimuth, and thus moved opposite to the hands of a clock. This idea was supported in a direct, spectacular manner when von Frisch brought marked, dancing bees out into the full sunlight, and

turned the comb horizontally. He was astonished to see the waggle runs point directly toward the food, even if the dancing bees could not see the feeder.

Ordinarily, honey bee waggle dances occur within a dark hive where most available surfaces are vertical. How can bees orient their dances? Von Frisch found that honey bees have solved this problem by adopting as a reference the direction of gravity. The bees, therefore, symbolically indicate the horizontal angle between the vertical passing through the sun (solar vertical) and the food source as the angle the waggle run makes with respect to vertical.

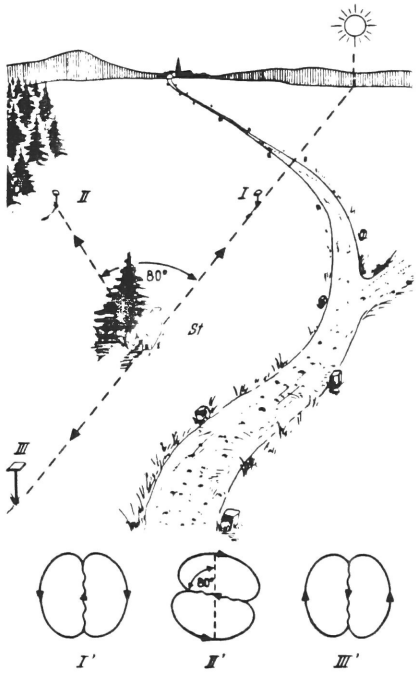

Figure I-3. Indication of goal direction in dances. Three examples of the indication of direction on a vertical comb. St: beehive; I,II,III: feeding stations in three different directions; I',II',III': the observed waggle dances (from von Frisch, 1967).

Specifically, as illustrated by Figure I-3, if a goal is reached by flying directly towards the sun ofter leaving the hive, the dances point

straight up. Similarly, away from the sun is represented by "down", to the right of the vertical means to the right of the sun, and so on.

While these observations are extremely interesting, the complete picture emerged when von Frisch showed that these dances were not just interesting curiosities of no biological significance. Rather, bees which never visited the food source but had observed several dances of established foragers, left the hive and searched for the food in the same direction as the forager's flight. Using arrays of identical feeders, von Frisch concluded that the search of the recruits was not haphazard at all, but actually quite precise. In addition, not only did the recruits seek food in the appropriate direction, but also at the appropriate distance.

Concerning the coding of distance in the dance communication, von Frisch concluded that the duration of the waggling run has the highest correlation with the distance of the feeder from the hive, although in fact a number of other dance parameters also change. Although even today it is uncertain how all of these variables interact, it is very clear that the absolute distance to a goal is not communicated. Rather the distance to a goal seems to be determined by the amount of energy (or some related variable) expended in reaching it. This has been shown by a variety of experimental methods such as weighting down a bee (Schifferer, 1952), observing dances of bees which have flown into wind or uphill (von Frisch, 1967; pp. 109 ff.), or by making bees walk rather than fly to a food source (Bisetsky, 1957). For each experiment, the distances indicated by the bees in their dances were greater than those for the control conditions of normal bees flying to a feeder on windless days.

In summary, the waggle dance is a form of symbolic communication in which both the distance and direction of a goal are transmitted from bees which have discovered it to naive bees, by the use of arbitrary conventions of duration and orientation of the waggle runs. The orientation of individuals outside the hive and the dance patterns are mutually interdependent, and this is a major method by which bees locate sources of necessary materials for the hive. This interrelationship is especially useful and important for behavioral studies because it means that orientation can be directly studied by observing and manipulating communication or vice versa.

1.3 Other information conveyed by the dances.

In addition to distance and direction to a goal, the quality and food type are also communicated during the dances. Regardless of the type, a goal's quality is indicated by the vigor a dancing bee shows in her dancing. For example, if she has discovered a rich, productive food source, she often runs agitatedly through the hive jostling many other bees, and she may dance for long periods before leaving the hive to forage again. Such behavior depends upon the specific circumstances: a poor food source may lead to exuberant dances in starving hives, while even the highest quality food may produce no dances at all in a hive well stocked with honey and pollen. Bees also obtain some information about the quality of a sugar source by directly tasting the samples of collected nectar which are distributed numerous times to the following bees (potential recruits) through regurgitation. Type and location of a source can also be communicated through the olfactory cues which adhere to the hairs on the forager's body or in the regurgitated material, and

are presumably useful to those bees which are familiar with the olfactory environment around the hive.

Although von Frisch's early experiments concentrated on foraging for nectar, as early as 1923 Park discovered that bees frequently dance when they collect water for cooling the hive or for diluting honey. Later studies have clearly shown that bees dance while collecting a wide variety of required hive material (e.g., food, water, propolis) or even in the search for a new hive location by swarms (reviewed by Lindauer, 1961). The important realization is that the abstract, symbolic communication which appears identical is used for diverse goals: the essential variables seem to be its direction, distance, and desirability.

Finally, as pointed out above, it should be realized that successful foragers do not always dance when they return, since so much depends upon the condition of the hive and other variables. In addition, dances are not required for successful recruitment. We know, for example, that frequently odors also can play a large role in foraging behavior (Frisch, 1923, ff.). For example, Ribbands (1954) observed that bees familiar with the food source of characteristic odor, can often be successfully recruited to it by introducing a small amount of the specific odor into the hive.

2. Honey bee visual orientation.

2.1 Landmarks.

Honey bees have relatively good, but quite different visual capacities from ours. In the environment around the hive there are often

features which seem to be conspicuous to bees, as judged by their influence on the bees' flight directions. Ordinarily when a bee is close to a goal-- e.g., a flower on her foraging flight-- distinguishing local features become prominent in their influence on orientation. This does not mean that landmarks are unimportant on far ranging flights--they often are. However, for reasons clarified below, bees usually rely on these local, identifying marks to a lesser degree than they do upon cues from the sky.

2.2 Celestial cues.

2.2.1 The Sun as a Compass. The sun is a prime orientation cue for honey bees. This fact can be readily appreciated by contemplating the integral role of solar position in the dance communication. That the sun should be such an important reference point can be easily understood: proper functioning of the dance communication depends upon an unambiguous reference point. Landmarks, which under certain circumstances are important visual cues for bees, cannot serve this purpose over long distances because usually they cannot be kept in view. Also, their close proximity usually means that parallax is a severe problem: their relative orientation to an animal is a function of the animal's position. But there is even a more stringent requirement: to avoid confusion in communication, the same, unambiguous reference point must be used by all bees. Obviously, which specific landmark to use as the reference would be problematical. None of these comments apply to use of the sun as a reference point, since it is an unique, obvious cue in the sky for for which the relative direction remains constant regardless of an animal's motion.

That insects can use the sun for orientation was known much earlier than von Frisch's studies. For example, Cornetz (1911) observed that if ants were picked up as they were returning to the nest and were moved to another place, they continue to walk in the same compass direction as before, although that direction was now inappropriate. Obviously the ant preserved its orientation somehow. Cornetz thought, however, that ants do this independently of solar orientation by preserving a "pure direction" in their nervous system. He offered as proof the observation that ants continue appropriately on their paths even when they were shaded and could not see the sun.

These and other results interested Santschi (1911) who repeated these observations with his classic experiments which showed clearly that the sun can be an important orientation cue. A famous demonstration was that ants turned around and traveled in the opposite direction when they viewed a mirror image of the sun placed opposite to the true solar direction (which Santschi had obscured). He could fool the animals at will. In his discussion, Santschi compared an ant's eye to a ship's compass: Just as the bow of a ship can be pointed in a specific compass direction by keeping a fixed angle to the compass, ants can always keep a section of the eye pointed towards the sun and by this means travel in a specific direction.

The ability of organisms to use the sun as a compass and align their body axis and locomotion at a particular, fixed angle to it is a special case of the more general "light compass reaction". Fraenkel and Gunn (1960) define this as "locomotion at a temporarily fixed angle to light rays, which usually come from one side". (This is the same as the

"menotaxis" of Kuhn, 1919). Such reactions do not require the sun, of course, and in fact similar reactions to other lights were noticed earlier than the Cornetz/Santschi experiments. For example, Lubbock (1884) noticed that ants (Lasius niger) oriented their running by the light of a candlelabrum they could see from the experimental table. In more extensive experiments, Turner in 1907 (described by Bouvier, 1922) studied the orientation of ants running on a horizontal platform connected to the nest only by several bridges, with a light visible from any part of the arena. If he threw larvae in the center, ants retrieved them. After a number of trials the ants learned how to quickly return to the nest without detours. He proved that they used the light as an orientation cue by transferring the lamp to the opposite side of the platform. Then the ants ran back to their nest by an opposite, more circuitous route.

Although light compass reactions are a very common type of insect visual behavior (as realized by von Buddenbrock, 1917), such behavior is not limited to invertebrates alone. Rather, this behavior is widespread in the animal kingdom, including vertebrates (e.g., birds (Kramer, 1950)). But, as far as we know, honey bees use the common light compass reaction in a unique way: as an integral part of their dance communication. Therefore, not only can they use the sun in their individual orientation, but they also tell other bees how to use it to travel to a specific place, such as a food source.

Besides the obvious fact that the sun is often not visible, there is a possible major drawback to using it for orientation: the sun appears to be constantly moving, although slowly. Therefore, the ability to use the

sun as a compass over short time periods is quite different from being able to use it over longer ones: for individuals to assume a fixed orientation over an extended period of time, continuous adjustments must be made in the angle between the body axis and the sun. In nature, for example, a bee often spends more than an hour foraging in the field before returning to the hive. If she uses the sun's position to guide her back to the hive--which she seems to do to a large extent, especially if she has traveled far from the hive (Wolf, 1927; von Frisch 1967)--she must correct for the movement of the sun since she left the hive. She has a similar problem when she dances in the hive for extended periods indicating the direction to a goal to potential recruits or when she leaves the hive herself to return to the goal. Therefore it is important to know whether animals can accommodate for the movement of the sun.

Brun (1914) was one of the first to attack this question experimentally when he confined individuals returning to the nest for several hours in the dark. When released these ants ran with their <u>former</u> orientation with respect to the sun: in Brun's case they erred by more than 37° in their movement towards the nest. Wolf (1927) reported that honey bees acted much the same: They did not seem to account for the apparent solar movement and if prevented a view of the sun, they gradually became more and more incorrect in their compass orientation (as they returned to the hive), since they kept a fixed angle between themselves and the sun. Obviously, if this is true it means that orientation by solar cues is mainly useful only when animals orient a relatively short time after they last saw the sun. But this thought is disturbing because under natural conditions animals would face a very severe problem: how can animals

which must frequently see the sun to update their orientation use the morning sun which stands in a very different position from where they last saw it in the evening before? And also among the myriad of questions, even if animals can continuously update their orientation by frequent views of the sun, what reference point do they use to calibrate it against? All of these questions, which arise because of the apparent motions of the sun, are central to the understanding of the mechanisms of celestial animal orientation. Do honey bees use the sun as a true compass or mainly as a reference to enable them to send recruits to previously discovered goals?

The observation that the waggle dance orientation of honey bees constantly shifts throughout the day following the sun's movement does not in itself provide decisive evidence. Every time a forager flies from the hive she might update the angle between the sun and the goal. Neither did the fact that honey bees fly readily to feeders in the morning even though they have had only previous experience with them only in the afternoon: bees could reach the goal by using familiar landmarks. Then the dances could be derived from direct observation of the sun during her most recent (morning) flight from the hive.

To decide whether bees are able to accommodate for the sun's motion von Frisch performed a simple but elegant displacement experiment in 1949 (von Frisch, 1950; reviewed 1967, pp. 334 ff.) which eliminated the possibility that landmarks were necessary to determine solar position. Basically, he allowed individually marked bees to collect sugar water for several days from a feeder in a fixed compass direction. When a number of foragers became experienced with it, the hive was closed after dark

and moved the next morning to an unfamiliar location having obviously different landmarks. Feeders, identical to the ones previously used, were placed in four compass directions, with one corresponding to the original training direction. When the hive was opened in the morning the sun stood in a very different compass direction from where it was last seen by the foraging bees the afternoon before. Any bee visiting a station was killed so that she could not return to the hive and recruit new bees. In one experiment, the bees' last view of the sun the previous day was to the northwest, while during the experiment the sun was southeast. Twenty seven bees were captured at the feeders: five in the South, one in the North, one in the East, and twenty to the West, the original training direction. These results show that honey bees, at least in the absence of familiar landmarks, can rely to a high degree on celestial cues (see von Frisch, 1967; pp. 339 ff). The results of other experiments imply that honey bees use celestial cues to a large extent even when foraging in familiar landscape (von Frisch, 1967, pp. 339 ff).

Von Frisch concluded from this and similar experiments that honey bees use the sun as a compass in a highly sophisticated way by accounting for its motion. Even when confined for extended periods of time, they are not disturbed and somehow keep track of its position. Although as noted above, Wolf's (1927) studies implied contrary conclusions, the differences probably depend on his methods. Mainly, he watched the departing direction of bees released after being confined for a time. However, because bees are so small and fly very fast, it is difficult to determine in which direction they actually depart. Meder (1958) repeated Wolf's experiments with much improved methods with which he could measure

with relatively high accuracy the flight bearings of bees which had been confined in the dark for various lengths of time. According to von Frisch (1967), Meder examined practically all possibilities and concluded that honey bees do compensate precisely for the sun's movement.

Two further questions are of interest since their answers may have broad implications in understanding animal orientation behavior in general: (1) The results of many orientation experiments show that the solar azimuth seems more important than elevation. Although the sun's movement is 15°/h in arc, the rate of change of azimuth and elevation depend upon the position of the observer on the surface of the earth and the local time. Usually, the rate of change of azimuth varies widely throughout the day. How do bees accommodate for its motion? Is it exact or only approximate? (2) Another important question is whether bees learn how to accommodate for the sun's motion or whether these abilities are innate. Good experiments by Lindauer (reviewed, 1961) clearly show that honey bees learn to orient by experience. Only after several hundred flights outside the hive do young, naive bees start to use the relative solar azimuth to approach the feeder. But at this time, they treat such angles as being constant, as if the sun were fixed in position. Only after about 500 flights do they become experienced enough to be able to make the appropriate adjustments for solar motion.

2.2.2 Other skylight compass cues. After von Frisch discovered that horizontally dancing bees attempt to point directly towards the food source, he modified an observation hive so that it could be easily placed in a horizontal position to study the orientation. If he arranged for dancing bees to see the sky on a clear day, their dances pointed directly

towards the food source. But von Frisch was extremely puzzled by the fact that the dances continued to be well oriented even if the sun was shielded from the bees' view. In addition, Santschi type mirror experiments, where the position of the sun was experimentally "moved", fooled the bees, but only to a point: their dance directions were not completely in the predicted directions based upon the assumption that the bees only used the sun as a compass. Some other cue was apparently being used by the bees for orientation. As pointed out above, similar observations had been made about ant orientation by Cornetz (1911) and Santschi (1911) when they observed that walking ants continued to proceed along a direct path even when they were shaded and could not see the sun. Santschi hypothesized that perhaps they remained oriented because they could see stars even in broad daylight. (However, he also thought it was possible that ants could deduce solar position by the brightness differences in the sky, since brightness of the sky increases in the direction of the sun.)

After eliminating many possibilities, von Frisch realized that there was one situation when horizontal dances of honey bees could be made oriented or disoriented at the experimenter's will, merely by allowing them a view of the sun or occluding it respectively: when the bees could see no blue sky. Thus, when bees had a view of both the sun and the blue sky, eliminating the sun from view had no effect on orientation, and they remained well oriented. But under cloudy conditions with no blue sky visible, the same experiment produced disoriented dances.

2.2.3 Why Blue Sky? The observation that blue sky is important for honey bee orientation was initially puzzling. But von Frisch soon discovered that the important aspect for the bees was its polarization. This was an astounding discovery with rich implications for much of the biology of animal orientation behavior, and has fostered much continuing work.

The blue sky has always fascinated us. Its color exemplifies the magnificence of natural phenomena, being a prime subject of our artistic and philosophical endeavors. The physical process which imparts the sky its color (mainly scattering from air molecules) also produces partial linear polarization. This aspect of skylight was not appreciated until observed by Arago in 1809.[1] The phenomenon of polarization was itself discovered many years before (1669) by Bartholinus during his investigations into crystal optics. The rather lengthy delay between the discovery of the physics of polarization and the realization that blue skylight is partially polarized can be explained mainly by the fact that humans are virtually blind to polarization. Therefore to a large degree we cannot appreciate its widespread occurrence in our environment, especially in clear blue skylight. This is why von Frisch's discovery was so astounding. Only by the development and use of appropriate instruments could we begin to appreciate the extent and nature of this polarization[2].

1. Although these patterns were discovered and used earlier by the Vikings for navigational cues (Binns, 1971; 1972; Ramskou, 1966; 1969), this practical use was not widely known.

2. Most people can, with some effort, perceive that a light is polarized by observing the transient visual phenomenon called "Haidinger's brushes" (see also "Boehm's brushes", Boehm, 1940). This interesting effect was discovered in 1844 by Haidinger when he observed, while looking at a source of

2.2.4 Polarization. Polarization, as a physical state, occasionally seems confusing and foreign to some people. It actually is quite simple and its basic aspects in the context of this thesis are described below. The polarization characteristics of light are best understood by considering it as a wave phenomenon. Its transverse electromagnetic waves consist of magnetic and electric components mutually perpendicular to each other and to the direction of propagation. Any beam of light involved in visual processes consists of the superposition of many independent emissions of a source. Each wave train lasts about 10^{-8} seconds and has a frequency of about 10^{14} Hz. These emissions can be (individually) completely characterized. A measurable beam, however, generally consists of the unrelated emissions of a very large number of independent radiators which have no preference among their constituents and thus are "unpolarized". Numerous physical processes impose a relationship either by constraining the electric wave to vibrate predominately in one plane and/or spiral around the direction of propagation. Such a beam is "polarized". Natural polarization frequently occurs by scattering, reflection, and absorption. See Angel (1974), Clarke and Grainger (1971) or Shurcliff (1962) for relatively complete descriptions of the physics of polarization.

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polarized light, a faint yellow brush-like structure surrounded by a hyperbolic-shaped blue region. Due to physiological factors, this image fades after a few seconds. This can be demonstrated easily by rotating a polarizer before the eye: then the brushes are perceived to rotate without fading. This effect is usually seen better in one eye than the other and is observed especially well in blue light. It probably arises from an interaction of light with the yellow and isotropic macular pigments. A few people cannot see the brushes, even under the best viewing conditions: Presumably they lack these pigments. (For details, see Seleiger and McElroy, 1965, pp. 300 ff.).

The electric component (E-vector) of light is involved in the typical interactions of matter (e.g., reflection, scattering, absorption) because it directly interacts with atomic electrons. Consider the E-vector by looking back from the fixed point in space towards a source of light. Over a time much greater than the period of the wave, the end point of the E-vector sweeps out a characteristic cross sectional pattern ("snapshot"). This is analogous to viewing a pattern on an oscilloscope: The screen is a fixed plane and the observed pattern results from the behavior of the electron beam over time. If the E-vector is equally likely to be in any position at any time, the snapshot is uniform and the light is unpolarized (Figure I-4a). (For the oscilloscope, over a sufficiently long time the beam would travel everywhere over the screen making it appear uniformly bright.) If the E-vector spirals around the propagation direction, it is "elliptically" polarized because its end point appears to sweep out an ellipse, as illustrated by Figure I-4b. Points labelled "a" through "c" show the position of the E-vector at successive times. The sense of rotation gives a "handedness", in this case counterclockwise. Such an ellipse has two axes: (1) Along its maximum length (major axis) and (2) perpendicular to the major axis (minor axis). The orientation of the major axis to the vertical is defined here to be angle X, with positive measured clockwise, negative counterclockwise. Finally, if the major and minor axes are equal, angle X cannot be specified and the light is "circularly" polarized (Figure I-4c). If the minor axis is zero, the E-vector vibrates in a fixed plane and the beam is "linearly" polarized (Figure I-4d). (For a more complete discussion see Shurcliff, 1962 or Hansen and Travis, 1974.)

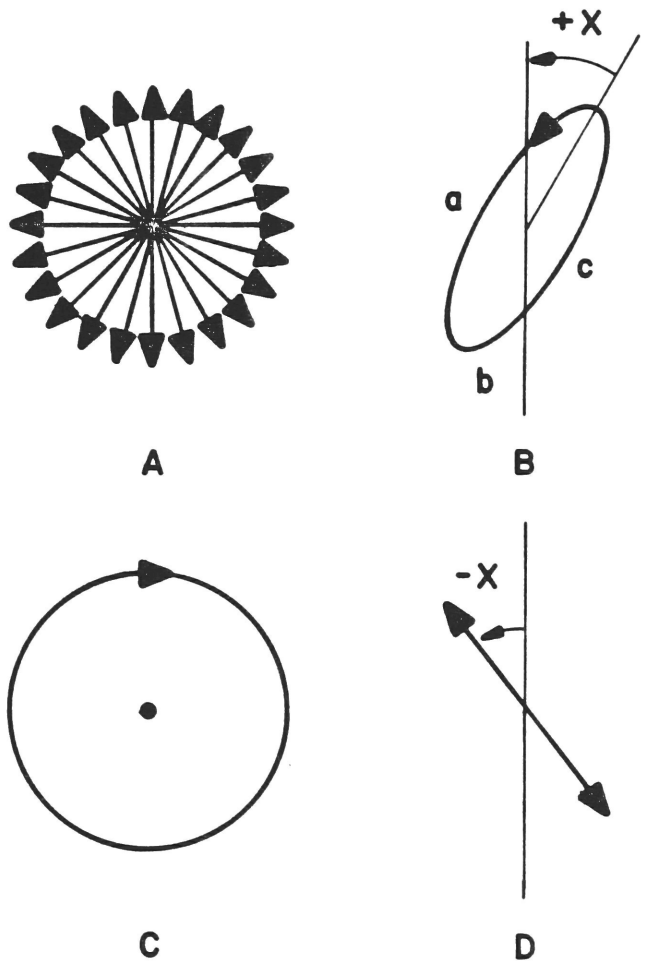

Figure I-4. Schematic form of polarized Light. Ray is coming out of the page. Orientation of major axis to vertical is angle X. Positive is measured clockwise; negative counterclockwise.

Polarization is not an all-or-nothing phenomenon and exists in many degrees. The ratio of the intensity of polarized light to unpolarized light in a beam (in per cent) is a useful measure, called "degree of

polarization". The polarization produced by use of a "polaroid" filter, for example, is virtually 100% polarized, while typical maximum values for skylight polarization range from 30% to 90%, depending on the wavelength and prevailing atmospheric conditions. Finally, it is important to realize that the polarization present in the natural visual environment results from the interaction of direct sunlight (which is unpolarized) with atmospheric and terrestrial surface features and therefore depends to a large degree upon the characteristics of solar radiation. This polarization is practically always linear: strong elliptical forms are rare (Dave, 1970) and are not known to be important cues in animal orientation. Therefore, this thesis considers mainly linear polarization.

3. Animals and polarized light.

Initially, von Frisch's discovery that honey bees can perceive and use the polarization of skylight seemed unlikely in view of the fact that earlier workers had studied the behavioral reactions of various insects to polarized light with completely negative results. A notable example is the experiments reported by Crozier and Mangelsdorf (1924). They performed three different tests in which they observed the behavioral reactions of (1) the negatively phototactic blowfly larvae and the isopod Cylisticus and (2) the positively phototactic milkweed beetle Tetraopes, to vertically and horizontally polarized light. (3) Also, they measured the amount of polarized light needed to induce a Tenebrio larva to leave a glass surface (i.e., the intensity of light necessary to overcome the strong "stereotropism" causing the larva to press itself against the

glass). In no case could they find any effects dependent upon the polarization (i.e., the E-vector orientation) of the light.

Although the Russian scientist Verkhovskaya (1940) has the distinction of first reporting that some organisms (Drosophila and Daphnia) are sensitive to linear polarization, these findings went unnoticed in the West. Von Frisch's later discoveries were much more significant and exciting, however, because he found that honey bees were not only sensitive to polarization but could use the natural polarization patterns of the sky in their orientation.

Experimental work with polarized light before the late 1940's was technically difficult since there were available only small optical devices which could be used to polarize light. This was a problem because while experiments possible using naturally polarized skylight were important,they were limited in scope. To discover specific aspects of the behavior, well controlled experiments were necessary, such as producing particular forms of polarization and observing the responses of bees. Therefore, only when the first large sheets of "polaroid" polarizing filters became available (which he obtained during his 1949 lecture trip to the United States) could von Frisch (1950) directly investigate the bees' sensory capabilities. In the simplest experiments, he placed a polarizer between horizontally dancing bees and the clear blue sky they saw. If the polarizing filter was rotated, thus changing the E-vector orientation observed by the bees, the dance orientation also changed. Here was a very clear demonstration of how honey bees use polarization cues for their orientation.

The discovery that at least one animal could perceive and use skylight polarization was, of course, extremely interesting. Soon, other investigators searched for similar abilities in a wide variety of organisms. Today the list of species known to be sensitive to polarization is increasing continuously and is most recently summarized by Waterman (1973). Perception of polarized light is not limited to invertebrates, but even includes homing pigeons (Kreithen and Keeton, 1974; and Delius et al., 1976). However, it is not clear whether birds actually can use skylight polarization in their orientation. The use of polarization for orientation is documented for some other vertebrates, such as a salamander[3] (Taylor and Adler, 1973) and fish (Waterman and Forward, 1974).

3.1 Honey bee orientation to polarized light.

Mainly because of von Frisch's work, honey bee use of skylight polarization remains the best studied example of such orientation behavior. Von Frisch's experiments made extensive use of a "skypipe"-- a tube which limited the bees field of view to only small sections of the sky about 10°-15° of visual angle (von Frisch, 1967; pp. 380 ff.). By observing dances on the comb of a horizontal hive, von Frisch found that the bees oriented themselves their dances directly towards the food source only when they could view blue sky through the pipe. If this window was covered or pointed at uniform clouds, the dances were disoriented. Von Frisch tried a version of Santchi's classic mirror experiment: if bees use skylight cues, they might be able to be fooled by replacing one part

3. These amphibians perceive polarized light by an extraocular photoreceptor system (Adler and Taylor, 1973).

of the sky by another. To do this, he allowed bees foraging from a western feeder to view a portion of the northern sky. They pointed their dances precisely westward. With a mirror, von Frisch then reflected the pattern visible in the southern blue sky down the tube so that the bees, although looking geographically north, actually saw the southern sky. Although he did in fact observe a reverse in the bees' orientation, they showed much inferior orientation than controls viewing the natural north sky.[4]

3.1.1 Degree of polarization necessary for orientation. That light from the clear blue sky was necessary to orient the horizontal dances of bees was shown dramatically by the fact that as clouds passed in front of the

4. With characteristic thoroughness in experimental design, von Frisch selected these two compass directions for the bees to view because the orientation of the E-vector in these parts of the sky was approximately horizontal and vertical respectively at the time of the experiments. These, he believed, would not be changed drastically by reflection from a mirror. But since the southern pattern he used was not quite horizontal, upon reflection it actually became somewhat unnatural. He hypothesized that the observed increase in deviation depended on this factor. There was probably another contributing factor: The E-vector orientation in general undergoes more than just "reflection"from a mirror since the metallic surface is optically active so that directions parallel and perpendicular to the plane of incidence are analogous to the optic axes of a waveplate. This means that a beam of light with a specific E-vector orientation aligned with one of these directions is reflected, preserving its linear polarization. Thus, in the general case, (E-vector not parallel or perpendicular to the plane of incidence) the light is separated into components which undergo large relative phase changes and become elliptically polarized. In von Frisch's case any E-vector not satisfying these special conditions of incidence (as his only approximately did) would be converted to elliptically polarized light. This would equivalently reduce the degree of polarization seen by the bees, which might decrease the precision of their orientation. This factor illustrates the difficulty of using mirrors for many polarization experiments.

skypipe the bees changed from being oriented to disoriented. Von Frisch found that the waggle dance orientation did not exist in an all-or-nothing fashion, since as cloudiness increased or the part of the blue sky viewed by the bees approached the sun's position, large decreases in the precision of the dance orientation occurred. Since these areas of the sky are characterized by a greatly diminished degree of polarization, it is obviously of great importance to know the magnitude of the perceptual threshold for polarization orientation in honey bees.

To measure the degree of polarization needed by the bees to orient their dances, von Frisch built a device to measure per cent polarization which could be swung into the end of the skypipe.[5] Using this, he correlated the precision of the bees' dances with actual measurements, and he found that about 10% polarization was necessary for good orientation. If the amount of polarization in the light viewed by the bees fell to less than 7%, the dances were completely disoriented. If the degree of polarization was greater than 15%, the dances were well oriented (summarized in Tables 39 & 40, von Frisch, 1967; p. 404).

One very interesting discovery was that above this minimum threshold, increases in the degree of polarization (e.g., by use of a polaroid

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5. Although von Frisch tried to measure the degree of polarization as a function of wavelength (rather than just for white light) his UV filters transmitted substantial amounts of long wavelengths. Typically, it is the long wavelengths which are substantially more highly polarized in skylight radiation than short ones (see Chapter III). In addition, his photodetector was probably much more sensitive to longer than to shorter (UV) wavelengths. These factors would lead him to overestimate the minimum degree of polarization necessary for perception by the bees. Thus, honey bees may be able to do even better than his figures indicate.

which produced virtually 100% polarized light) did not further increase the precision of the dance orientation. Zolotov and Frantsevich (1973) confirmed von Frisch's conclusions by performing similar, but more extensive experiments. Their results show clearly that the degree of polarization plays a subordinate function (if any) in the bees's normal use of skylight cues.

3.1.2 Area of blue sky needed for orientation. By progressively limiting the amount of sky visible to horizontally dancing bees, von Frisch (1948; 1949; 1967) found that a patch of blue sky about 10°-15° of visual angle was of sufficient area for bees to be well oriented. In addition, under some circumstances associated with poor orientation (e.g., when the sky was hazy and possessed a low degree of polarization), allowing the bees to view larger areas of the skyvault often substantially improved their dance precision (von Frisch, 1967; p. 404). Thus, it was clear that under at least some circumstances significant spatial integration of receptors occurred which improved the orientation.

Zolotov and Frantsevich (1973) repeated and extended von Frisch's studies of the minimum visual angle by presenting areas of the blue sky ranging from a minimum of 6° to a maximum of 30°. They used a tent with forty removable sections, each equal to about 2.5% of the total area of the sky. In the tests (which they carried out at the same time each day only under clear blue sky) the bees viewed spots close to or in the band of maximum polarization which for the UV corresponded to a maximum of about 30-40%. The results of these experiments showed that about 6°-13° of visual angle of the sky were necessary for well oriented dances and therefore, correspond very well with von Frisch's observations. The most

accurate dances they observed required about 15° under these conditions of 30-40% maximum polarization. Although their measurements of visual angle of sky needed for orientation cannot be precisely reduced to the minimum number of receptors needed (due to the large changes of the divergence between adjacent receptors on a bee's eye as a function of position on the compound eye), an approximation can be easily made. Zolotov and Frantsevich estimated that the number of receptors required for the threshold orientation was about 25-50 ommatidia and for the best orientation, the number corresponded to about 150-200 ommatidia.

Recently, Edrich and von Helversen (1976) have found that even very small polarized sources (less than 1° of visual angle) of various spectral compositions can be used accurately as orientation cues by dancing bees. Their sources of polarization, which were artificial, were presented from the zenith to bees dancing on a horizontal surface so that approximately the same ommatidia were always stimulated by the light, regardless of how the bee circled about in her dance. By using Kirschfeld's (1972) technique of antidromic illumination[6], they could determine which ommatidia viewed this polarization source. Edrich and von Helversen estimated that for good orientation, between three and seven ommatidia had to be simultaneously stimulated by a source of polarized light. They found this small group of receptors is located adjacent to but not actually in an area on the most dorsal part of the eye which has been found to be anatomically unique. Because of the fine structure of its receptor cells, these characteristics have led some authors to

6. This technique consists of illuminating a compound eye from inside and noting the optic axis of each ommatidia by observing the light patterns over the surface of the eye.

hypothesize that this area may be important in orientation to skylight polarization (Schinz, 1975).

3.1.3 Importance of wavelength. In his pioneering studies, von Frisch was interested in how polarization orientation of bees depended upon the wavelength. Typical experiments consisted of showing dancing bees spots of natural skylight at about 40°-50° in elevation, through various spectral filters (which he placed either over the end of the skypipe or directly over the dancing bees), and correlated the changes in the precision of their waggle dances with the particular experimental manipulations. Using a large range of filter combinations he determined: 1) UV wavelengths are sufficient for polarization orientation and (2) blue light, even without UV, is also sufficient. But (3) bees did not orient to polarized lights of longer wavelength. In addition, the results of control experiments showed that intensity changes over a wide range were shown to be be unimportant. Thus, short wavelength sensitivity seemed authentic (e.g., von Frisch, 1967; p. 400). Von Frisch argued that these data imply that only the UV photoreceptors are used in polarization orientation.

Knowledge of the spectral sensitivity of bees was greatly extended by the work of von Helversen and Edrich (1974), who determined the action spectrum of honey bee orientation to polarized light. Their results showed that sensitivity to polarized light peaked at about 347 nm and diminished to practically zero by 430 nm. Recent electrophysiological work, including single visual cell recordings (e.g., Menzel and Blakers, 1976) seems to support fully these behavioral findings with electrophysiological evidence.

3.1.4 Relationship of direction of polarization and dance orientation. Von Frisch clearly showed that bees use the polarization of skylight in their orientation when he placed a large polarizing filter over horizontally dancing bees. Turning this filter often produced changes in the waggle dance orientation (von Frisch, 1950; 1967; pp. 387 ff.). The specific characteristics of these changes are interesting and may give insights into the mechanisms of polarization orientation. An understanding of his general experimental methods is a help in comprehending the significance of these experiments.

Bees trained to an artificial feeder were individually marked and when they returned to a horizontal hive they were allowed to view a patch of blue sky about 30°-40° centered on an elevation of about 45°. A large polarizing filter was placed over the dance surface to be parallel to the horizon. To visualize the E-vector orientation directly, von Frisch used a simple polarization detector[7] to view that part of the sky which the bees saw and arranged for the polarizer to produce the same pattern. With this procedure, von Frisch knew what polarization pattern the bees viewed and also could search the sky for similar, natural patterns. Then the relative bearings of these patterns could be directly compared to the observed waggle dance orientation.

As a specific example of how this worked in practice: bees were trained to forage to a feeder due West and were tested upon their return

7. The instrument was his "star-analyzer" which consisted of 8 equilateral triangles of polaroid radially assembled into an octagon. In this configuration, the E-vector orientation of the incident light was indicated by dark and light wedges, and the contrast was directly related to the degree of polarization.

from the hive by a view of the clear western sky--the polarization patterns they saw were identical to those they had faced on their way to the goal. Von Frisch observed the dances to be precisely oriented toward the West (towards the sky patterns and the feeder). Then he placed a polaroid over the hive oriented so that the E-vector of the light the bees saw corresponded to the approximate E-vector orientation he measured in the western sky.[8] He observed that the horizontal dances were as precise as without a filter. If, however, he rotated the polarizing filter 30° clockwise, the waggle dance orientation changed in the same sense and about the same amount. In one specific case, the bees changed their dance orientation 35° south of east for a 30° rotation of the polaroid. Von Frisch determined with his star analyzer that this E-vector orientation corresponded to a point in the natural sky about 34° north of west. Changes in dance orientation were thus easily explained: the dancing bees interpreted the artificial pattern as if it was a point on the sky 35° north of west. (Since the pattern was actually in the west, they danced about 35° south of west.) Thus, E-vector orientation was the important parameter, and by changing it von Frisch could effectively "rotate" the sky in azimuth (see von Frisch, 1950; 1967; pp. 387 ff.).

Von Frisch summarized his behavioral data from these experiments into four categories: 1) Bees viewed part of the sky through a polarizer oriented so it did not change the E-vector orientation of natural skylight (i.e., the transmission axis of the filter was parallel to the skylight E-vector orientation). Although the polarization direction remains unchanged, the degree of polarization increases to essentially

8. Use of the polaroid increased the per cent polarization so that the patterns were not identical.

100%. For tests with the sky in all compass directions, the results clearly showed that bees were as well oriented as controls without a filter (mean error of 6°).

2) The orientation of the E-vector was changed to correspond to another pattern visible in the natural sky at that time. With these stimuli bees changed the direction of their dances by an amount exactly equal to the difference in bearing between the two points on the skyvault (mean error of 8°).

3) The artificial pattern was not directly observable anywhere on the skyvault at the time of the experiment. Under these conditions, the waggle dances were completely disoriented. This experimental situation occurred under two different circumstances: A) when the amount of polarization in the sky seen by the bees on their previous foraging flights was below the sensory threshold of about 15% (a function of the condition of the atmosphere), and B) when the pattern could not satisfy the geometry of Rayleigh scattering for any part of the sky at that time. For the first case, von Frisch observed a number of marginally oriented dances and a primary characteristic was that the bees ran in circles, apparently searching for cues to orient their dances. It is important to note that these marginally or disoriented dances occurred for bees viewing virtually 100% polarization when the natural polarization was very low. Presumably, these could be easily observed by the bees and thus the test did not just fall below their perceptual threshold.

4) The bees saw an E-vector orientation which existed at <u>two</u> different places in the natural sky. Under these experimental circumstances

von Frisch reported that bees always orient some dances in each direction, and that single bees alternated between these two directions.

After the behavioral experiments of this thesis were completed, Rossel, Wehner, and Lindauer (1978) published data on E-vector orientation in bees. This is important material since it offers parallel, independent behavioral experiments on of honey bee orientation to small spots of polarized light. These workers begin by pointing out that given a small area of the sky with a specific E-vector orientation, if no other polarization parameters are used, honey bees (and other animals) should be unable to distinguish between the two possible positions where this E-vector occur at that elevation in the natural sky. To test this, they allowed horizontally dancing honey bees to view 10° spots of the sky which were either naturally or artificially polarized so that the E-vector orientation and elevation corresponded to part of the natural sky. If the bees used only the E-vector orientation, they should perform ambiguous dances. Although their observations bear this possibility out to some degree, Rossel et al., unlike von Frisch, found that the bees danced two directions neither of which was correct considering the actual E-vector distribution of the natural sky. One dance direction was only approximately correct, while the other was exactly 180° opposite to this. From these observations, Rossel et al. concluded that honey bees possess a generalized representation of skylight polarization patterns which are based upon the rate of change of the E-vector orientation with respect to relative azimuth for a specific, constant elevation (almucantar). If honey bees do actually use the derivative of the E-vector orientation as a function of relative azimuth for determining the position of the sun,

there are several other behavioral predictions which can be made, such as the fact that there should be an optimum elevation for such an orientation strategy. In fact, Rossel et al. claim that their data fit more closely the pattern of the E-vector orientation around the zenith than to other parts of the sky. Although in general their findings compare rather well with some of the behavioral work reported here (Chapter V), in other respects they are quite different. These differences are discussed in detail in Chapter VI.

To clarify these relationships it is helpful to discuss in detail the geometrical and physical aspects of skylight polarization patterns.

CHAPTER II.

Sky Geometry.

Theoretically, any part of the environment which can be individually identified can function as an orientation cue. In the sky, for example, the radiation characteristics of each part--radiance, polarization, and color--could constitute important optical reference points. In the simplest case, these "skymarks" play a role in an animal's visual orientation similar to landmarks, except that sky cues have no associated parallax. Although in this sense orientation to skylight cues is simpler than other kinds, use of sky patterns probably requires a more sophisticated behavior, since they constantly change in form and quality as the sun moves and atmospheric conditions change.

Because of their radiation characteristics (especially polarization), small areas of the sky can also supply much more than relatively fixed, individual reference points. Since the characteristics of skylight depend largely on the atmospheric scattering of direct rays of the sun, any particular part of the sky is, in theory, geometrically related to the sun's position. In nature, this close relationship determines to a large extent the form of the radiation coming from each skypoint. Thus, even if the sun is hidden (e.g., by clouds), its position may be determined by observing the sky. The possibility that parts of the sky can substitute for the sun is especially important in view of the results of a large number of behavioral experiments which show that the sun is an important source of directional information in the orientation of many animals.

Sky patterns can provide useful cues in another, more sophisticated way: besides their well known geometrical relationship to the sun's position, skylight polarization patterns also possess dynamic aspects which provide useful navigational cues. By observing the sky, animals could theoretically determine their position on the surface of the earth. This possibility is discussed in detail in section 2 at the end of this chapter.

Sky patterns are not only geometrically diverse, but also depend upon the prevailing atmospheric conditions at the instant considered. Therefore to appreciate the possible importance of particular cues for animal orientation, an investigator must understand the basic, physical aspects of the patterns of skylight polarization: both theoretical and actual.

The question of what cues are important for animal orientation and how they are used has been largely unexplored since until now most work has concentrated on the biology of specific animals. Except for von Frisch's classic behavioral experiments and a recent study by Rossel, Wehner, and Lindauer (1978), most investigations have have focussed on either elucidating the biophysical mechanisms by which receptor systems are sensitive to polarization or on determining whether specific animals detect and use polarized light in their orientation. The goal of this thesis is to bridge some of these gaps, especially by characterizing what cues exist in the sky and how they might be used as orientation cues.

Biological work reported in this thesis is concentrated entirely on the orientation of the Italian honey bee, Apis mellifera ligustica.

These animals make excellent experimental subjects for the study of orientation behavior, because their physiology is among the best known in insects, a large and important industry is devoted to their cultivation, and we already know a great deal about their behavior. Furthermore, honey bees communicate through the dance language, and this behavior enables an investigator who cannot directly study the flight of individual bees outside the hive to analyze their orientation by observing their dances.

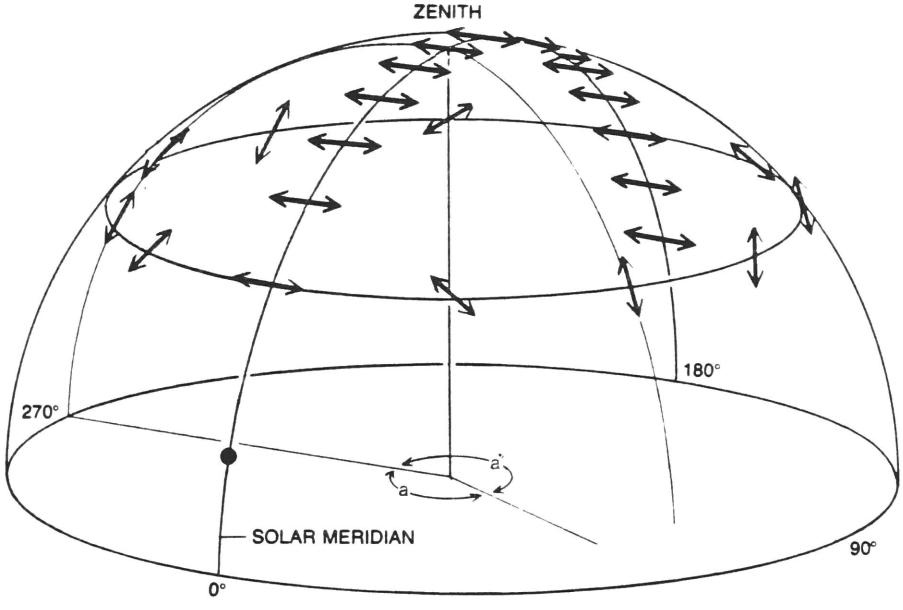
Besides important information about orientation behavior, study of honey bees shows how sophisticated a nervous system must be to process and use orientation information. The orientation behavior of bees, which includes both learned and innate components, is produced by a central nervous system containing fewer that one million neurons. Honey bees therefore provide excellent examples of the diverse capabilities of small nervous systems.

1. Skylight orientation cues

The light from each part of the skyvault possesses a certain spectral distribution, E-vector orientation (plane of polarization), degree of polarization (per cent polarization), and radiance (intensity). The values of these parameters depend both on the position of the sun and the atmospheric conditions at the instant of observation. The first factor is the geometry predicted by simple theory and is discussed in this chapter; the second is the actual values observed in the natural sky and is developed in Chapter III.

1.1 Principal Features of Skylight Polarization

Since its discovery more than 150 years ago, skylight polarization has been synonymous with its E-vector orientation. For the simplest possible case of primary scattering of sunlight, the E-vector orientation depends in a simple way on the relative position of the sun and the observed point, as



GENERAL PRINCIPLES OF THE POLARIZATION of the light of the sky are outlined. The arrows indicate the directions of polarization as they would be seen by an observer in the center of the hemisphere. Along the solar meridian (the arc through the sun and the zenith) the direction of polarization is parallel to the horizon. Along most circles of a given elevation the direction of polarization varies through all possible angles. Here the angles are plotted for the circle lying roughly halfway between the horizon and the zenith. In general each direction of polarization is found twice at each circle of elevation. (The angles *a* and *a'* denote the angular difference between the positions of identical polarization.) For this reason there is ambiguity in polarized-light navigational cues unless the insect can view more than one part of the sky.

Figure II-1. Pattern of E-vector orientation over the surface of the skyvault (from Wehner, 1976).

illustrated by Figure II-1. Here the position of the sun and the observed point are shown on the surface of the sky (the celestial hemisphere) with the observer located at O. The E-vector orientation (sym-

bolized by a double headed arrow) is always perpendicular to the plane containing the sun, observer, and observed point. Since an infinite number of these specific planes can be constructed over the sky, many points possess an identical E-vector orientation.[1] But at any elevation there are generally only two points with the same E-vector orientation. By geometrical symmetry, the plane of the solar vertical divides the skyvault into two halves for which the E-vector orientation at each point is a mirror image of the corresponding point on the opposite side. Ordinarily, this constitutes the only axis of symmetry in the sky, except for the special case when the sun is on the horizon (sunrise/sunset). Then the corresponding mirror image E-vectors are directly across from each other in the sky.

Another prominent feature of skylight polarization is that light from each point is not equally polarized: direct sunlight is unpolarized, and the degree of polarization increases gradually to a maximum along a circle about 90° from the sun. Similarly, the spectral distribution of skylight depends largely on the angular distance from the sun, changing predictably so that parts of the sky 90° from the sun are generally the most saturated in short wavelengths. Also, sky brightness (radiance) decreases from a maximum at the sun to a minimum 90° to it. The radiance then increases slowly again until the antisolar point is reached.[2]

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1. As defined in Chapter I, positive X (E-vector orientation) corresponds to clockwise angles measured from vertical, and negative to counter-clockwise. Thus, $-90^{\circ} \leq X \leq +90^{\circ}$ where $X = 0^{\circ}$ refers to vertical polarization.

2. For all of these characteristics, the angular distance from the sun is the principal variable of skylight radiation. However, parts of the sky with small elevation angles diverge greatly from this situation, due to the greatly increased thickness of the atmospheric paths toward the horizon.

Study of the physics of skylight radiation has had an interesting history. Like many scientific disciplines, its early phases concentrated mainly on measuring the obvious features just outlined, especially the magnitude and distribution of polarization over the skyvault as a function of season and some atmospheric conditions. Interest peaked in the late nineteenth century because of two major developments: (1) objective photoelectric methods largely replaced the laborious visual measurements and (2) the first tenable theory of sky color and polarization was proposed by Lord Rayleigh (Strutt, 1871).

The basic assumption of Rayleigh's theory is that direct sunlight, during its transmission through the atmosphere, is scattered only once from isotropic particles which are very small with respect to the wavelength.[3] If these conditions are met (which usually happens to a relatively large extent in the real atmosphere) sunlight scatters by a dipole reradiation which produces a typical spatial pattern for which the scattered intensity is proportional to the inverse fourth power of the wavelength. Although Rayleigh himself was unsure at first what the light scattered from, we now know that air molecules are responsible. Thus this type of scattering is often called "molecular scattering".

Even in its fundamental form the Rayleigh theory explained several obvious features of the daytime sky: its color, the position of a band of maximum of polarization about 90° from the sun, the general distribution of radiance, characteristic orientation of the E-vector, and the existence of neutral points (places on the skyvault where the light was

3. Practically, the dimensions of the scattering centers must be less than about 0.1 the wavelength of the light.

unpolarized). The theory failed, however, to adequately explain several details: (1) The degree of polarization actually observed was never as large as theoretical predictions and (2) three neutral points (rather than the two predicted by Rayleigh theory) could generally be observed, and they were not at the expected locations.

Subsequent study has shown that radiation from the real sky departs from the predictions of Rayleigh theory because: (1) direct sunlight is often multiply scattered in its propagation through the atmosphere. (2) Contrary to the Rayleigh assumption, air molecules possess a small anisotropy: they are not actually electrically neutral. (3) Larger particles (aerosols) are universally present in the atmosphere, especially close to the ground. In this case, scattering does not depend on wavelength in the way Rayleigh theory predicts: rather the intensity and polarization must be explained using "Mie theory", of which Rayleigh scattering is a special case. (See McCartney, 1976; pp. 216 ff.) (4) Light is frequently reflected from the ground or vegetation producing diffuse reflection or even different forms of polarization in the sky. Finally, (5) many atmospheric constituents <u>absorb</u> light and this factor must frequently be considered. As a specific example of the magnitude of these effects, Gehrels (1962) noted that areas of the clear blue sky were typically 75% polarized, rather than the theoretical 100% predicted by Rayleigh theory. Of this difference, he attributed 6% to multiple scattering, 6% to molecular anisotropy, 5% to ground reflection, and 8% to aerosols.[4]

4. These percentages, of course, are appropriate only for one specific case. The interactions and dependences of each of these factors on actual atmospheric conditions is extremely complex and are not yet fully understood. These are discussed in Chapter III.

1.2 Geometry of the sky

To understand in detail how the features of skylight radiation might be used by animals as orientation cues, it is necessary to consider the geometry of the sky. In the basic Rayleigh case this is quite simple: variables such as E-vector orientation and degree of polarization are related to each other and directions on the earth's surface by spherical geometry. To appreciate this, consider an animal looking at part of the sky. Since the eye cannot reliably determine distance to a light source, only a direction can be specified. This means that under ideal conditions all skylight seems to come from an equal (arbitrary) distance and the observer appears to be at the center of a hemisphere.[5] Each source of light such as the sun, the stars, or diffuse sky light can be considered as fixed on the inner, curved surface of the skyvault. The apparent location of a source, called its "position", is defined by the intersection of an observer's line of sight with the surface of the hemisphere. Since natural measures of a sphere are angles and arcs, these are used to specify position.

To consider these relationships analytically, it is necessary to use spherical geometry. Although the geometry of a sphere generally appears quite formidable (e.g., its analytical relationships are trigonometric in nature) modern calculating machines, especially the ubiquitous, hand-held calculator, fortunately have eliminated the tedium of calculation and

5. For us at least, the apparent shape of the skyvault depends upon wavelength of the viewing light and never appears truly hemispherical. For example, the sky viewed in red light looks more nearly hemispherical than when observed in blue light (see Minnaert, 1954; pp. 153 ff.). Obviously any deviation from sphericity will affect the following arguments.

make important relationships more readily accessible. In my opinion, understanding the basic geometry of possible skylight cues can provide considerable insight into how the cues might be used in specific cases of animal orientation. At the very least it is necessary to derive these relationships to know what information theoretically exists in the sky under specific experimental conditions.

Unfortunately, the sky geometry which applies to the study of orientation behavior is not easily available in the literature.[6] In the case of skylight polarization cues, as far as I can tell the appropriate relationships are not available anywhere. With this in mind, the following section, in conjunction with appendix A, develops the geometrical relationships of skylight cues to a level which should be sufficient to enable an investigator, using a calculator, to analyze a large number of celestial relationships corresponding to specific experimental conditions and design appropriate experiments by considering both sky geometry and animal orientation behavior.

1.2.1 Geometrical properties of a sphere One important geometrical property of a sphere is that a plane always intersects it in a circle. For an observer at the center of a sphere (such as the celestial sphere), any plane which passes through him intersects the sphere by forming the largest possible circle (a "great" circle), with a radius equal to the sphere's radius.

If three directions are selected, they pierce the sphere at three

6. This is compounded by the fact that standard navigation texts still rely largely on the use of tables for the solution of problems.

points P1, P2, and P3 (Figure II-2). The three great circles connecting these points intersect to form a "spherical triangle" because sides a, b, and c are arcs of great circles.

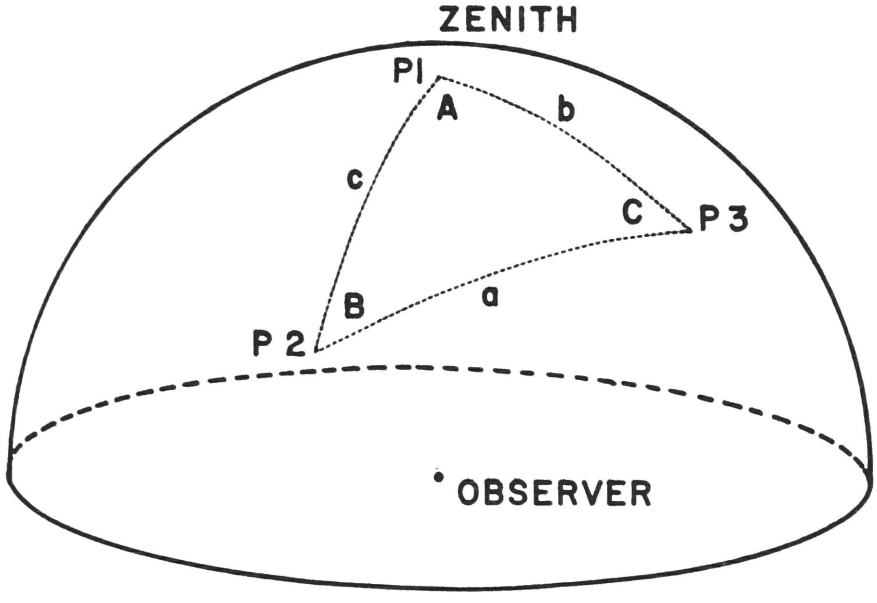

Figure II-2. Spherical triangle formed by great circle arc lengths a, b, c.

As illustrated in Figure II-2, the angles opposite to these sides are A, B, and C. The geometrical relationships among these six parts are quite similar to those of a plane triangle. The sides and angles are related to each other by three basic equations:[7]

(1) law of sines:

$$\frac{\sin(A)}{\sin(a)} = \frac{\sin(B)}{\sin(b)} = \frac{\sin(C)}{\sin(c)}$$

(2) law of cosines:

e.g., $\cos(a) = \cos(b)\cos(c) + \sin(b)\sin(c)\cos(A)$

(3) law of transposed cosines:

e.g., $\sin(a)\cos(B) = \text{cosine}(b)\sin(c) - \sin(b)\cos(c)\cos(A)$

Since each point on the surface of the sphere is the same distance (the radius) from the center only two variables are required to completely specify the position of any point. For the skyvault, a natural reference system is conveniently derived from the direction of gravity (which for purposes here is always towards the earth's center) and its perpendicular. Experimentally, these are easily established by the intersection of an extension of the direction of a plumb bob with the overhead surface of the skyvault (the "zenith" position) and its perpendicular plane (the "horizon"). Thus one variable is the angular distance from the zenith ("zenith distance") measured in a vertical (great) circle.[8] The complement of zenith distance (i.e., measured vertically up from the horizon) is called "elevation".

The second natural coordinate is the angle in the horizon plane: the "azimuth". Azimuth is usually referenced to a cardinal direction defined by the intersection of the great circle which passes through the pole and the zenith (the meridian). By convention it is measured from 0° to 360°

7. Similar relationships exist for other combinations of sides and angles and can be determined by cyclically replacing sides and angles with corresponding components. Formulae helpful in the solution of specific problems, especially those developed by Gauss and Napier, can be found in many mathematical handbooks.

8. Since the great circle arc of a unit sphere is equal to the angle it subtends at its center, zenith distance can also be called "zenith angle".

clockwise from North. Previous study of animal orientation has shown that for many animals only the relative azimuth (i.e., the horizontal angle between the vertical circles passing through the points in question) seems important for orientation. The zenith distance and azimuth specify the position in the "horizontal" or "topocentric" coordinate system.[9]

1.2.2 Rayleigh scattering. The apparent position of the sun on the surface of the skyvault fixes the orientation of direct sunlight for which the rays are (practically) parallel. Figure II-3 illustrates an easily visualized case which corresponds to the sun and the viewed point in the sky lying in the same vertical circle, with their directions defined by radii M and N respectively. In order for a scattered ray R' to be seen by an observer at point O, it must be redirected from its original direction by angle Θ, the scattering angle. As discussed before, in the Rayleigh atmosphere Θ is the dominant parameter determining the characteristics of sky radiation: intensity (radiance), degree of polarization, and indirectly, E-vector orientation. Specifically, scattering angle Θ determines the radiance as seen by an observer looking out into the sky by:

$$I_{total} = k(1 + \cos^2(\Theta))$$

where k is a constant. Thus, as an observer looks away from the sun, scattering angle Θ increases and the intensity of light perceived decreases until a minimum is reached for $\Theta = 90^{\circ}$. Further, for Rayleigh scattering the intensity of light for a scattering angle of 90° is half

9. Such a reference system is obviously subjective because it depends on the location of the observer on the surface of the earth.

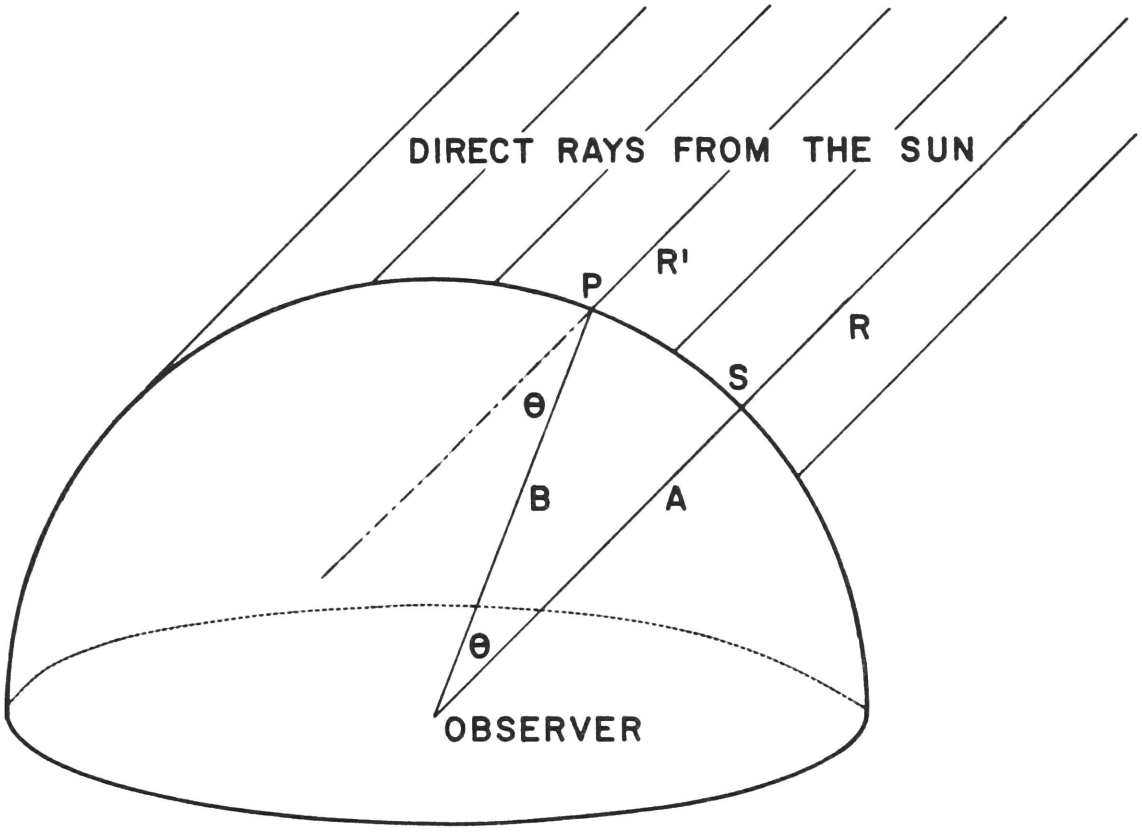

Figure II-3. Geometry of sunlight scattering, as explained in the text.

that scattered at angles of 0° or 180° (looking directly towards or away from the sun). This is easily calculated from:

$$\frac{I_{0^{\circ}}}{I_{90^{\circ}}} = \frac{1 + \cos^2(90^{\circ})}{1 + \cos^2(0^{\circ})} = \frac{1 + 0}{1 + 1} = \frac{1}{2}$$

In the Rayleigh case, the degree of polarization (P) is given by:

$$P(\theta) = \frac{\sin^2(\theta)}{1 + \cos^2(\theta)} = \frac{\text{polarized component}}{\text{totalintensity}}$$

This equation summarizes the observations of skylight radiation described above: as θ increases to 90°, the degree of polarization also increases to a maximum value (100%) for $\theta = 90^{\circ}$. Likewise, when

$\Theta = 0^{\circ}$ or 180° (solar or anti-solar directions), the skylight should be unpolarized.

Finally, in Rayleigh scattering the E-vector orientation is determined by the plane including both the direct rays of the sun and the observer's line of sight and as such, is identical to the plane of the scattering angle Θ. This, of course, is just another way of stating how the E-vector orientation is dependent upon the observer-sun geometry.

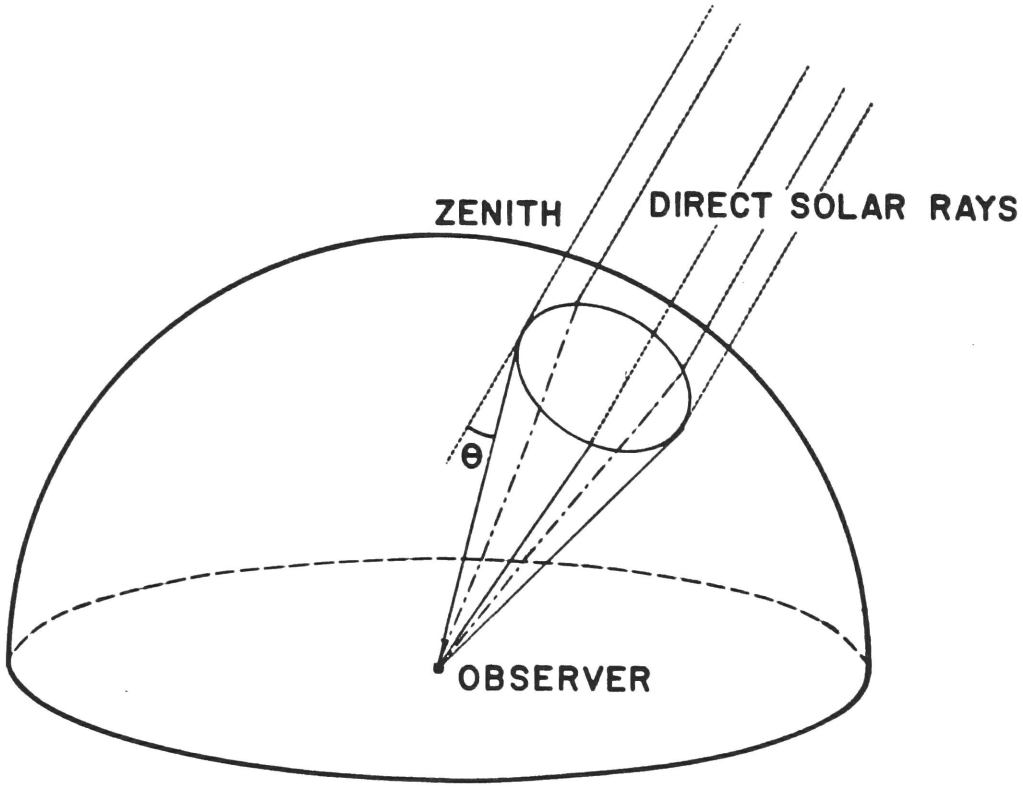

Figure II-4. Circle of constant scattering angle, as explained in the text.

Given the importance of the scattering angle, some general features of the theoretical skylight patterns can easily be appreciated. As

illustrated by Figure II-4, the scattering angle is constant for those points of the sky with the same angular distance from the sun.[10] Because the E-vector is perpendicular to the scattering plane (which is formed by the direct solar rays and the line of sight) and the scattering plane is always parallel to the radius of this circle, the E-vectors are tangent everywhere to the circle. Therefore, an animal able to perceive the E-vector orientation of skylight may observe it as concentric circles on the skyvault, with the sun and anti-solar points as the optical poles, as illustrated by Figure II-1. Since radiance and the degree of polarization also depend (in simple theory) only on the scattering angle Θ, they should also appear to form concentric circles around the solar and anti-solar points.

While this geometrical description may aid in understanding the large scale form of the skylight patterns and be important for animal orientation, it is essential to be able to specify the characteristics of small areas or even single points of the sky. One reason for doing this is that it is not an unreasonable approach to the study of orientation behavior to allow animals to view only small, well characterized parts of the sky, and ask how they use such limited cues. Hopefully, such an approach could provide important information about the mechanisms of their orientation. The next section develops the geometrical relationships between the sun's position on the skyvault and the radiation characteristics of small areas of the sky.

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10. The great circle arc length which appears to form the radius of this circle is equal to the scattering angle.

1.2.2.1 The scattering triangle

The positions of the sun, zenith, and area of the sky observed (skypoint) define three points on the surface of a hemisphere.

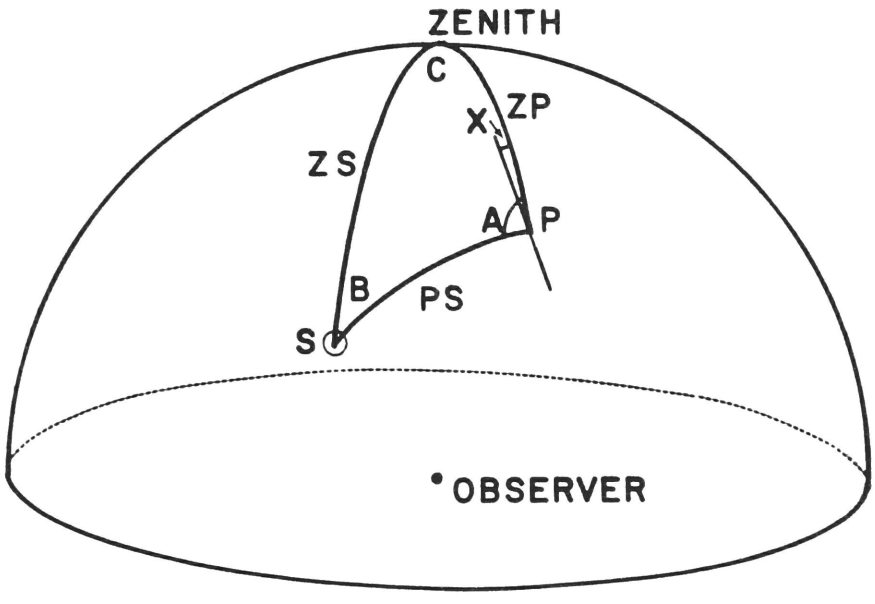

Figure II-5. The Scattering Triangle.

As described above, a spherical triangle is formed if these points are connected by arcs of great circles, as illustrated in Figure II-5, where Z is the zenith, S the sun, and P the skypoint. Such a spherical triangle will be called a "scattering triangle", since the area of the sky is observed by virtue of its scattered light.

Each side or angle of the scattering triangle has a corresponding physical meaning. As just developed, the great circle arc between P and S in Figure II-5 is the angle through which the solar rays have been redirected and thus is the scattering angle Θ. (The plane of Θ also defines the scattering plane.) Arc lengths ZS and ZP correspond to the zenith distances of the sun and skypoint respectively. Since C is the angle between the vertical circles through the sun and the skypoint, it is the relative azimuth. The physical significance of angle A can be understood by considering two facts: (1) The plane of arc PS (the scattering angle Θ) defines the orientation of the scattering plane, and (2) for Rayleigh scattering the E-vector orientation is perpendicular to this plane. Now the E-vector orientation is the angle the principal vibration direction of the electric wave makes with respect to the vertical (i.e.,"X", where clockwise is positive). Since the total angle between the scattering plane and vertical is A, it follows that $A = X \pm 90^{\circ}$, the sign depending on the orientation of the scattering plane with respect to vertical.[11] The important geometrical property is that the observed E-vector orientation determines angle A (with a 90° ambiguity) and so defines the scattering plane. Finally, the physical significance of angle B is of a different sort from the other five elements of the scattering triangle. Since B is formed by the intersection of the scattering plane and the vertical circle through the sun, it does not possess physical attributes to allow it to be identified directly. This is because the sun, as a single point, lacks a characteristic which allows direct determination of the scattering plane orientation. The

11. This is equivalent to saying that the sign of the E-vector depends upon which side of the vertical the sun is located with respect to the point considered in the sky.

situation is completely different from the E-vector orientation at a skypoint which, due to its two dimensionality, specifies the scattering plane orientation. Because angle B cannot be determined by direct observation, we expect that it is not an important parameter in animal orientation. Of course B can be determined by trigonometric measurements or calculation by using other triangle variables. In practice it is used mainly to interrelate the other, more useful variables.

To summarize the physical meaning of each component of the scattering triangle: The sides are:

ZS = solar zenith distance

ZP = skypoint zenith distance

PS = the scattering angle = Θ

Included angles are:

A = $90^{\circ} \pm$ X (X is the E-vector orientation at the skypoint)

B = angle between the solar vertical and the scattering plane

C = relative azimuth between the observed skypoint and the sun

1.2.2.2 Calculating skylight polarization patterns

In this section, the theoretical (primary scattering) characteristics of skypoints for a specific position of the sun are developed. Since horizontal and vertical are two natural reference directions for earthbound observers, skylight parameters are specified here with respect to the horizontal reference system. Given a zenith distance of the sun, the radiation from each point of the sky (specified by zenith distance and relative azimuth) can be determined by trigonometrically analysis of the appropriate scattering triangle. One convenient method is first to

calculate the scattering angle PS by using the law of cosines:

$$\cos(PS) = \cos(ZS)\cos(ZP) + \sin(ZS)\sin(ZP)\cos(C)$$

Then, knowledge of PS allows calculation of the degree of polarization and the relative radiance by using the simple equations:

$$p(PS) = \frac{\sin^2(PS)}{1 + \cos^2(PS)}$$

and

$$I(PS) = 1 + \cos^2(PS)$$

The scattering angle PS can also be used to determine angle A:

$$\cos(A) = \frac{\cos(ZS) - \cos(PS)\cos(ZP)}{\sin(PS)\sin(ZP)}$$

Finally, by using the relation $A = X \pm 90^{\circ}$ and knowing in which half hemisphere (defined by the plane of the solar vertical) the sky point lies, the appropriate E-vector orientation is easily determined.

These methods derive the E-vector orientation X and the scattering angle PS given variables of the horizontal coordinate system, such as zenith distances. Obviously, the <u>reverse</u> procedure is possible: variables of the horizontal reference system can be determined by using the parameters of the sky radiation. The question whether any animals can and do perform such analysis is of central importance to the study of animal orientation. In practice, success would depend both on how well sky patterns match the theoretically predicted conditions and what particular strategies animals adopt for using this geometry in their orientation. These aspects are addressed more fully in Chapter III and Appendix A.

1.3 Stokes Vector Representation.

So far, the patterns of skylight polarization discussed are derived by spherical trigonometry referenced to the vertical and horizontal directions on the surface of the earth. This reference system is used widely in the literature when discussing how the sky appears to earth-bound observers looking out into the sky (e.g., with respect to animal orientation, see Stockhammer, 1959; von Frisch, 1967). But this treatment is somewhat misleading because even though any one particular pattern of skylight polarization obviously has a fixed physical form, the actual intensities measured depend on the relative orientation of the polarization pattern and the reference axes of the detector system. With respect to vision, for example, the number of photons absorbed by a photoreceptor pigment is important. If the incident light is polarized, the actual number of photons absorbed depends strongly upon the relative orientation of the photoreceptor molecules and the E-vector orientation of the incident light. Honey bee compound eyes are polarization sensitive because the visual photopigments are aligned along comb-like microvilli which form the reference axes (Waterman, 1979). Usually, these axes of honey bee eyes constantly change in orientation as the animal moves about and probably only rarely do they happen to correspond exactly to the horizontal reference system. Waggle dances, for example, frequently occur on non-horizontal surfaces while bees can still see the sun or sky. We are interested in what intensities would be measured by the photodetectors under these conditions.[12] This can be accomplished

12. See van der Glas, 1978 for a discussion of probable reference axes, honeybee orientation, and what the sky patterns may look like to bees.

easily by using a general expression of skylight polarization which allows straightforward calculation of the intensities which would be measured by any arbitrary orientation of detectors. This section derives such a general description, again assuming only primary Rayleigh scattering.

1.3.1 The Stokes Vector.

One of the most useful ways to characterize a beam of light is by the four dimensional mathematical vector first devised by G. G. Stokes (1852), which was revived by Chandrasekhar (1950) and used to solve the general problem of radiative transfer (e.g., propagation of light through the atmosphere). A "Stokes vector" consists of four intensity parameters which correspond to the total intensity (of both polarized and nonpolarized components in a beam), degree (per cent) polarization, E-vector orientation, and degree of elliptical polarization. The particular value for any light beam can be experimentally determined by using the intensity measured by instruments in appropriate configurations (see Clarke and Grainger, 1971; Shurcliff, 1962; Cohen, 1958). Any Stokes vector can, of course, be directly related to the electromagnetic description of light (e.g., Chandrasekhar, 1950).

Although there is no universal representation, the symbols I, Q, U, and V are commonly used as the Stokes parameters. These form a four dimensional column vector: $\begin{vmatrix} I \\ Q \\ U \\ V \end{vmatrix}$, where Q, U, and V are intensities of the polarized light. Since the ellipticity of skylight is normally vanishingly small, for all practical purposes the last parameter can be

considered to be 0, so the basic Stokes vector describing skylight polarization is: $\begin{vmatrix} I \\ Q \\ U \\ 0 \end{vmatrix}$. The significance of the first three parameters is clarified by considering a parallel beam of light traveling in the specific direction $\bar{k}$. Any two mutually perpendicular directions $\bar{r}$ and $\bar{l}$ are chosen such that $\bar{r}, \bar{l}$, and $\bar{k}$ are perpendicular (i.e., in vector notation $\bar{r} \times \bar{l} = \bar{k}$, which merely means that the magnetic and electric waves are coplanar.) I_r and I_l symbolize the intensity of the beam along the $\bar{r}$ and $\bar{l}$ reference directions respectively. Now

I_{total} = the total intensity of the light

Q and U = the intensity of the polarized part

so that the total polarized intensity is

$$I_{pol} = (Q^2 + U^2)^{1/2} .$$

Thus, the degree of polarization (percent polarization) is

$$p = \frac{I_{pol}}{I_{total}} = \frac{(Q^2 + U^2)^{1/2}}{I_{total}} .$$

As developed by Stokes and presented in a slightly changed form by Chandrasekhar (1950, pp. 24 ff.) the Stokes parameters can be experimentally determined by the following measurements:

$$I_{total} = I_l + I_r$$

$$Q = I_l - I_r$$

$$U = (I_l - I_r)\tan(2f)$$

$$U = Q\tan(f)$$

where f is the angle between the principal vibration of the light and a reference axis of the detector.

Because the vector is defined by the intensities in two perfectly general, but orthogonal directions, it follows that a specific Stokes

vector can be converted into one appropriate for a different reference system merely by changing the directions of $\bar{r}$ and $\bar{l}$. Obviously, the total intensity (energy) of the beam must be constant, regardless of the orientation of the detector. Similarly, although the numerical values of Q and U depend upon the orientation of $\bar{r}$ and $\bar{l}$, (and therefore on the detector geometry), the degree of polarization must also be constant (i.e., $(Q^2 + U^2)^{1/2}$ must not change). The E-vector orientation, however, is completely relative to the detector geometry. Thus an easy method for transforming specific Stokes vector parameters to correspond to different orientations of $\bar{r}$ and $\bar{l}$ is very important. One way is discussed by Chandrasekhar (1950, p. 34) who showed that for a clockwise rotation of the reference axes $\bar{r}$ and $\bar{l}$ through an angle η to the original orientation, the new Stokes parameters (Q' and U') are determined by:

$$Q' = Q\cos(2\eta) + U\sin(2\eta)$$

and

$$U' = -Q\sin(2\eta) + U\cos(2\eta).$$

Therefore, to determine the new Stokes vector corresponding to a different detector orientation, the relative positions of the new and old reference axes must be known so that new values of Q and U can be determined.

1.3.1.1 Calculation of Skylight Stokes Vectors

The approach used here to determine the Stokes vectors corresponding to specific skypoints is: first the parameters appropriate for a reference system defined by the atmospheric scattering process are calculated. Then these are transformed to be correct for any other specific reference system, such as the horizontal system. This method is reasonable since

Rayleigh scattering, as a dipole process, has as a natural choice for the two perpendicular axes $\bar{r}$ and $\bar{l}$, directions established by the scattering plane (i.e., the plane formed by the incident and scattered rays).

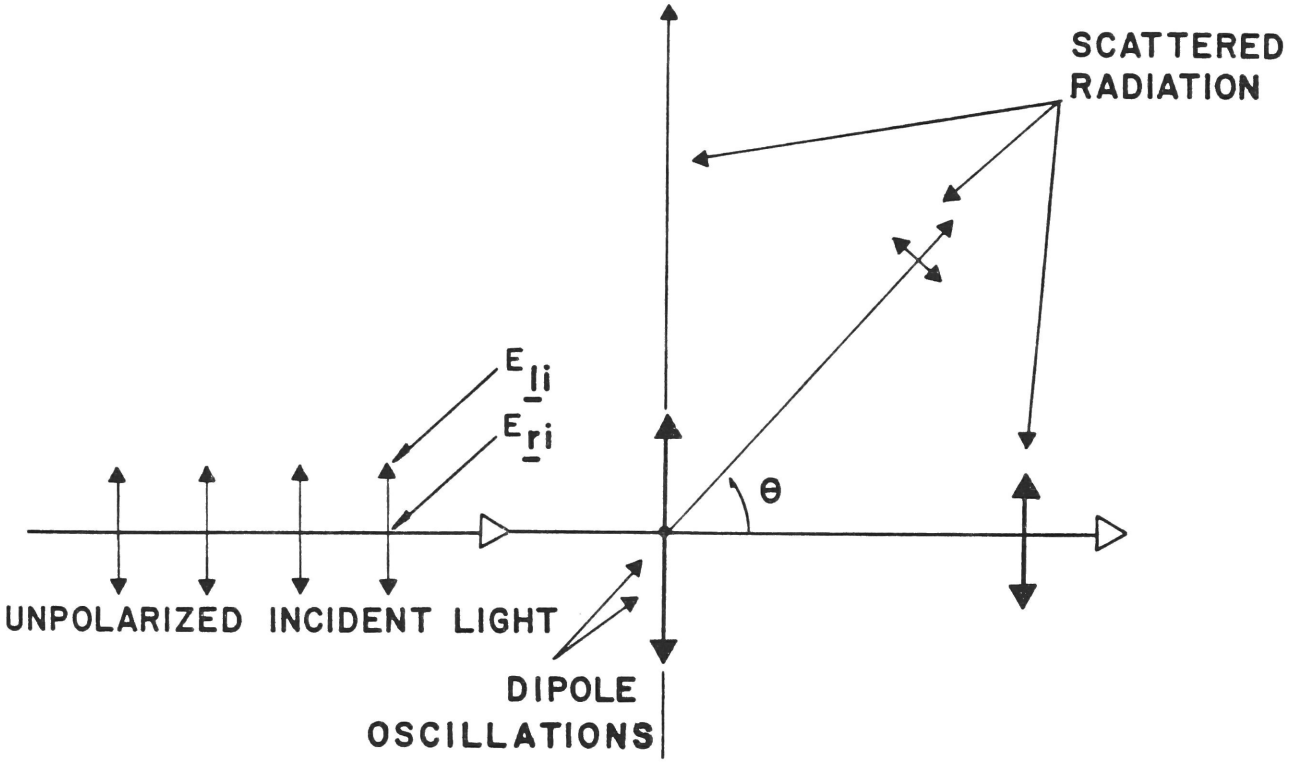

Figure II-6. Schematic representation of Rayleigh Scattering.

The unpolarized wave incident from the left can be represented by two linearly polarized waves vibrating at right angles to each other with equal electric field strengths and random phase relationships. The electrons in the scattering center oscillate in response to the electric component of the incident wave, giving rise to the dipoles represented by the heavy arrow and dot. θ is the scattering angle, equal to arc PS of the scattering triangle (redrawn from Hansen and Travis, 1974).

As illustrated by Figure II-6, if an unpolarized wave meets a scattering center s (such as an air molecule), it induces dipole oscillations which

radiate light into various angles in the plane of $\bar{l}$. (For details, see Hansen and Travis, 1974, pp. 540 ff.) If the electric field components of the incident waves are called E_{ri} and E_{li} (where in the incident unpolarized ray $E_{ri} = E_{li}$), then by geometry the components observed in the scattering plane are:

$$E_{rs} = E_{ri}$$

$$E_{ls} = E_{li} \cos(\theta)$$

where θ is the scattering angle. That is, the two components are in general no longer equal: the component along $\bar{l}$ is always less than or equal to the component along $\bar{r}$: the beam is polarized in the $\bar{r}$ direction. Since $\bar{r}$ and $\bar{l}$ are perpendicular, $f = 90^{\circ}$ and $\tan(2f) = 0^{\circ}$. Therefore, $U = 0$, $I_{pol} = Q$ and P (degree of polarization) $= \frac{Q}{I_{tot}}$. Since $I = E^2$, it follows that:

$$P = \frac{E_{ri}^2 - E_{li}^2 \cos(\theta)^2}{E_{ri}^2 + E_{li}^2 \cos(\theta)^2}.$$

But $E_{ri} = E_{li}$ (unpolarized light), so

$$P = \frac{1 - \cos^2(\theta)}{1 + \cos^2(\theta)} = \frac{\sin^2(\theta)}{1 + \cos^2(\theta)}.$$

Thus, in terms of the scattering angle θ the Stokes vector is:

$$\begin{vmatrix} 1 + \cos^2(\theta) \\ \sin^2(\theta) \\ 0 \\ 0 \end{vmatrix}$$

Although this derivation of the Stokes vector from the dipole geometry is perfectly correct, it does not describe skylight polarization patterns well, since its reference directions ($\bar{r}$ and $\bar{l}$) are defined by

12. This is called the "Rubenson" definition of degree of polarization.

the scattering plane which varies over the entire sky and thus is not appropriate for the reference axes of the horizontal coordinate system. This is easily remedied by realizing that in this case, the orientation of $\bar{r}$ and $\bar{l}$ change over the skyvault exactly as X does (the E-vector orientation seen by an earthbound observer). Because Q and I are easily determined in the theoretical case for the dipole radiator and the scattering angle is identical regardless of the orientation of any detector system (it is defined only by the incident/scattered ray geometry), it is a simple three step procedure to calculate the Stokes vectors for any skypoint which is appropriate for the horizontal reference system. (1) Calculate the scattering angle (Θ) and the E-vector orientation from the scattering triangle and from this (2) calculate the Stokes parameters for the dipole scatterer geometry. It is:

$$\begin{vmatrix} I \\ Q \\ 0 \\ 0 \end{vmatrix}.$$

Since f really gives the orientation of the dipole reference axes ($\bar{r}$ and $\bar{l}$) in the horizontal system, (3) Rotate the reference axes of the Stokes vector found in step (2), so that $\bar{r}$ and $\bar{l}$ are now vertical and horizontal respectively (i.e., rotate by an amount equal to X). This gives a new Stokes vector:

$$\begin{vmatrix} I \\ Q' \\ U' \\ 0 \end{vmatrix}.$$

Of course, both the scattering geometry and horizontal reference system Stokes vectors describe the same beam.

1.3.1.2 <u>One method of Calculation</u>. (Step 1.)

From appendix A, if the zenith distances of the sun and the observed point in the sky and their relative azimuth are known, the spherical triangle can be solved for the scattering angle PS and E-vector orientation X (= A $\pm$ 90°) by using the law of cosines written in two different ways. First, written for the scattering angle Θ = (PS):

$$\cos(PS) = \cos(ZS)\cos(ZP) + \sin(ZS)\sin(ZP)\cos(C).$$

Then, using the value of PS, the law of cosines can be written again for angle A. That is:

$$\cos(ZS) = \cos(PS)\cos(ZP) + \sin(PS)\sin(ZP)\cos(A)$$

and

$$\cos(A) = \frac{\cos(ZS) - \cos(PZ)\cos(ZP)}{\sin(PS)\sin(ZP)}.$$

By knowing that A = X $\pm$ 90° and which half hemisphere (defined by the plane of the solar vertical) the skypoint in question lies, the appropriate value of X can be selected.[13] For the dipole scatterer reference system (reference axes oriented perpendicular and parallel to the scattering plane), the Stokes vector is:

$$\begin{vmatrix} I \\ Q \\ U \\ V \end{vmatrix} = \begin{vmatrix} 1 + \cos^2(PS) \\ \sin^2(PS) \\ 0 \\ 0 \end{vmatrix}$$

(Step 2.)

The Stokes vector appropriate for the horizontal reference system is found by rotating the above vector through angle X. That is:

$$\begin{vmatrix} I \\ Q \\ Q \\ U \end{vmatrix} = \begin{vmatrix} 1 + \cos^2(PS) \\ \sin^2(PS)\cos(2X) \\ -\sin^2(PS)\sin(2X) \\ 0 \end{vmatrix}$$

13. X affects the sign of Stokes parameter U, but not its magnitude.

It is the general form of Stokes vectors in the horizontal reference system. This is a very powerful way to express the form of the skylight radiation because the intensities measured by any arbitrary orientation of a detector system can be directly determined.

2. Skylight navigational cues

Thus far, we have considered only those characteristics of skylight patterns which are visible at a fixed instant (a "snapshot"). This, of course, is not what happens in the natural sky where the patterns of polarization follow the sun in its apparent motion across the heavens. Until now, the possible consequences of the temporal aspects of skylight polarization patterns for animal orientation have been almost entirely ignored. The goal of this section is to develop some some generally unappreciated consequences of the dynamic aspects of sky patterns. As shown briefly below, natural skylight polarization provides important cues not only for sun orientation, but also for true navigation: in theory an animal could fix its position on the earth's surface by using cues visible in the daytime sky.

That navigational cues exist in the patterns of skylight can be easily appreciated by comparing the characteristics of the nighttime and daytime skies. At night, due to the earth's rotation the stars appear to rotate around the intersection of the earth's axis with the celestial sphere (the "pole point"). An observer sees that the linear velocity of individual stars varies widely over the sky: close to the pole point they appear almost stationary (e.g., Polaris) and increase in rate with their distance from the pole point. Navigators have used this characteristic

of the sky for centuries as a compass (the direction toward the pole point), a clock (the relative position of specific stars), and for determining latitude (elevation of the pole point). We already know that animals such as some night migrating birds do use the natural celestial rotation to obtain directional cues (Emlen, 1975).

Since the sun, with its associated patterns of skylight polarization, also rotates around the pole point, similar temporal cues important for navigation exist in the daytime sky, although the skylight polarization characteristics can be used to derive navigationally important variables not possible by observing the stars alone. These can be understood by the following considerations. With respect to the scattering of sunlight the pole point is like any other part of the skyvault. It is geometrically unique, however, as part of the objective reference system used to describe solar position in terms of the earth's equator and axis (the "equatorial" system). Because latitude of the observer, time, solar declination[14], and true solar azimuth are variables in this reference system, the characteristics of skylight polarization at the pole point are directly related to these important navigational variables and can be used to derive them.

The specific relationships can be appreciated by considering the spherical geometry of the observed point in the sky, the sun, and the zenith (points P, S, and Z respectively) from which a scattering triangle (Figure II-5) can be constructed. Here, sides ZS and ZP are the zenith distances (or angles) of the sun and observed point respectively. Side

14. This variable describes the position of the sun relative to the earth's equator and thus is analogous to terrestrial latitude.

PS (the scattering angle) is the angle the direct solar rays have been redirected into the eye of the observer by scattering. We have seen that in the theoretical case, the degree of polarization depends upon the scattering angle, with a maximum occurring for PS = 90°. Likewise, the plane of PS (the scattering plane) also defines the E-vector orientation X. Angle C is the relative azimuth (the angle between the sun and the observed point in the horizontal plane).

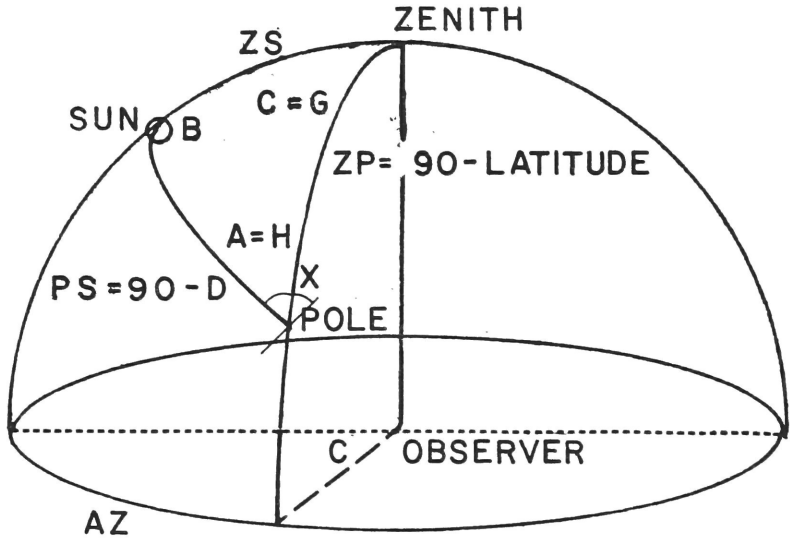

Figure II-7. Correspondence of the scattering and astronomical triangles.

In the special case considered here, since the observed point is at the celestial pole, the scattering triangle is also actually the "astro-

nomical" triangle so important for navigation, as shown[15] in Figure II-7. For purposes here, it is sufficient to realize that in the astronomical triangle H is the "hour angle" (local time from noon), arc PS is the solar codeclination, PZ is the colatitude, ZS is the solar zenith distance, and G is the true solar azimuth.

The importance of this unique correspondence for navigation is that during the day the radiation characteristics of this special scattering triangle can be observed and parts of the astronomical triangle can directly determined. For example, since angle A and angle H in Figure II-7 are identical, the E-vector orientation (X) at the pole point is a direct measure of the apparent local time: it is the complement of the observed E-vector orientation. Thus at noon, $H = 0^{\circ} = A$ (sun on the meridian) and $X = 90^{\circ}$ (E-vector is observed to be horizontal). In sum, since one hour of time equals fifteen degrees of arc, a numerical value for local sun time can be directly obtained by observing the E-vector orientation at the pole point. Accuracy is limited only by how precisely the E-vector orientation can be measured. In addition, it is interesting to note that these observations can be made even if the sun itself is not directly visible, as long as some atmosphere towards the pole point is lighted by direct sunlight.[16]

Obviously, to use this special correspondence between the scattering

15. For detailed consideration of the astronomical triangle, see navigation or spherical astronomy texts, e.g., Smart, 1965.

16. After noting this correspondence, I discovered that Sir Charles Wheatstone (1848) based his "polar clock" on measuring the E-vector orientation at the polepoint. As far as I know, this has been the only practical human use of this unique sky geometry.

and astronomical triangles, an observer must be able to identify the pole point. Although there are at least several relatively complicated methods of doing this, observation of the direct circumpolar rotation would provide it most simply, as Figure II-8 illustrates. Interestingly, some animals may be sensitive enough to motion to perceive the 15°/hour rotation virtually instantaneously. Horridge (1966) demonstrated that certain crabs can perceive solar motion directly and Thorson (1966) found that locusts respond to patterns moving at rates about one tenth that of the earth's rotation. Recent experiments by Whiten (1978) indicate that under some conditions homing pigeons may have the same sort of sensory ability: he found these birds could perceive the motion of small spots of light moving even more slowly than the sun.

Long distance migrants, such as birds or Monarch butterflies, could benefit greatly if they could use these dynamic cues from skylight polarization. Evidence available at present suggests that birds can only marginally detect the presence or absence of relatively rapid rotation of the E-vector (Kreithen and Keeton, 1974) or static E-vector orientation (Delius et al., 1976). This is similar to the ability of many people to perceive that a light is polarized by the presence of Haidinger's brushes. In homing experiments, such as those in which racing pigeons perform so impressively (Keeton, 1974), a bird which detected the dynamic aspects of skylight polarization in the vicinity of the pole point could theoretically determine the extent and direction of his displacement by the experimenter. Displacement in latitude would be straightforward: A bird which sees the pole point lower in the sky than that remembered from the home area should fly towards it and vice-versa. Displacements in

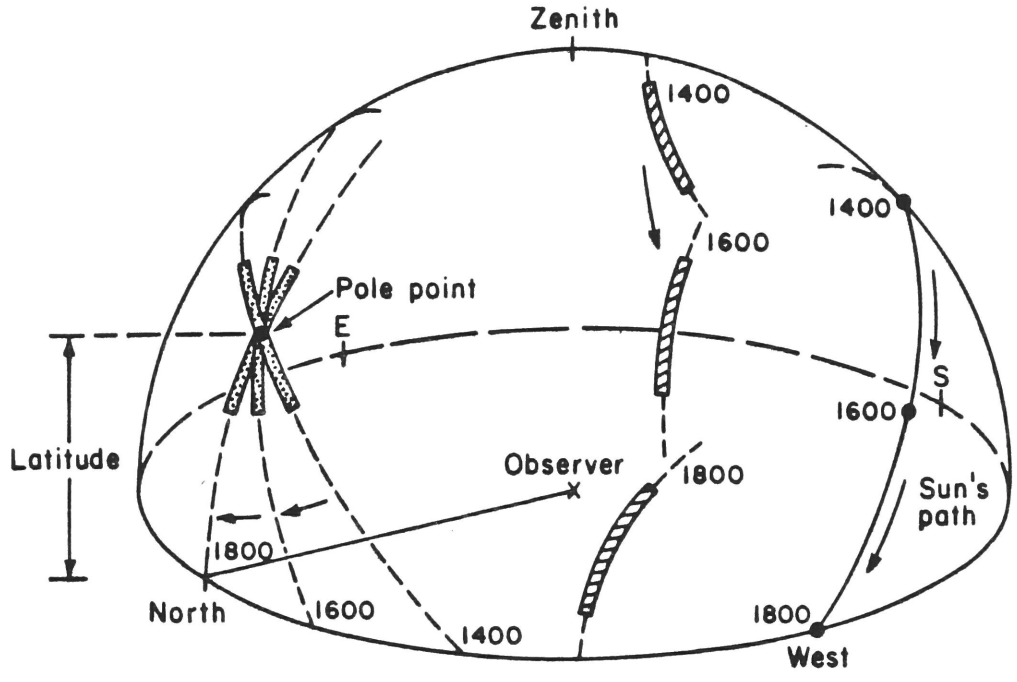

Figure II-8. Polarization patterns as a source of navigational information.

Schematic diagram of the dynamic polarization patterns of the blue sky at the equinox. Each band represents the same part of a circle formed around the sun at the indicated solar time by the polarization parameters. Bands are used rather than lines to symbolize an animal's imprecision in discriminating E-vector orientation or bands of equal per cent polarization. These patterns move counter-clockwise at a constant rate of 15°/hr, but only at the pole point do they rotate without moving in azimuth and elevation. In this way, the E-vector orientation is a direct measure of solar time, as is the orientation of the band of maximum polarization which includes the pole point throughout the day. At other times of the year, it passes within 23.5° of the polepoint. In addition to the E-vector orientation, per cent polarization, and spectral distribution, curvature of the pattern may provide additional optical cues to identify the pole point.

longitude might be detected by differences between remembered time and

the "reading" of the observed "polar clock".

It should be emphasized that an animal need not perceive all of the characteristics of the polarization patterns in order to derive useful information. If, for example, it can detect only the band of maximum polarization present in the sky, information can still be obtained. This is seen in Figure II-8, where considering the pole point, the scattering angle is equal to the codeclination and therefore ranges from 76.5° to 113.5°, depending on the time of year. Since the band of maximum polarization corresponds to a scattering angle of about 90°, at the equinoxes when declination of the sun is 0°, the band of maximum polarization includes the pole point, around which it rotates. At other times of the year, the band rotates around the pole point but is separated from it by an angular distance equal to the solar declination. Further, if the pole point is always between the sun and band of maximum polarization, the solar declination is South. If the band of maximum polarization separates the sun and the pole point, the declination is North.

The band of maximum polarization provides navigation cues in many ways. For example, how could an observer use the inclination of the band of maximum polarization with respect to vertical to determine the direction of North? Figure II-9 illustrates the geometry of the two spherical triangles involved, where D is the declination, H is the hour angle, and A is an angle related to the E-vector orientation. Using the law of sines,

$$\frac{\sin(A)}{\cos(D)} = \frac{\sin(H)}{\sin(90^{\circ})}.$$

But,

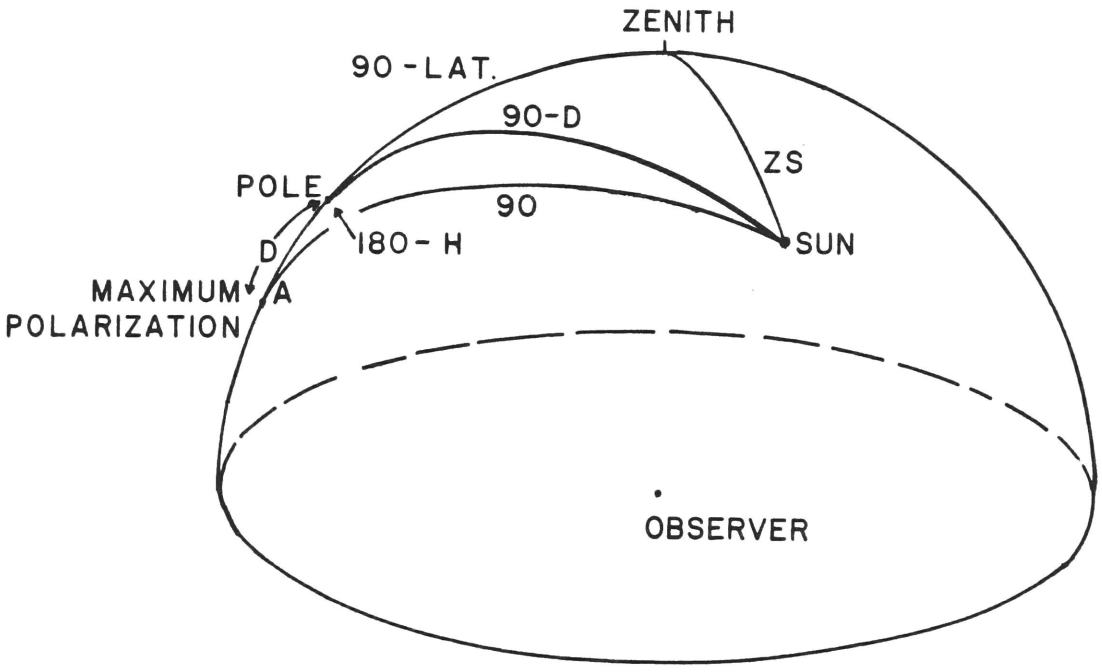

Figure II-9. Relationship of the band of maximum polarization to the celestial pole.

$$A = 90^{\circ} \pm X,$$

So,

$$\cos(X) = \sin(H)\cos(D).$$

Because the E-vector orientation in the band of maximum polarization is parallel to the band at every point, this simple equation summarizes the relationship between the inclination of the band of maximum polarization with respect to vertical and the direction of true North. Thus, perhaps an observer could determine North by finding where in the sky the inclination of the band of maximum polarization matched the predicted value. Furthermore, determination of latitude is just a further simple step

away. Using similar reasoning, many other parameters important for navigation can be determined, and provide theoretical possibilities to test with appropriate behavioral experiments.

Thus, even animals sensitive only the band of maximum polarization may have an excellent compass, clock, and means of determining latitude available to them. For those animals possessing a well developed ability to determine E-vector orientation, even the solar declination might perhaps be derived by observing the distance of the band of maximum polarization from the pole point. This is an important possibility because knowing the declination, latitude, and time, the true position of the sun can be easily determined at any instant. In this regard it is interesting to speculate that the well known insensitivity of the orientation of terrestrial animals to solar elevation may exist because for them the solar elevation and azimuth are dependent variables obtained by use of latitude, time, and declination. In addition, the exceptions to this general rule of insensitivity to solar elevation are interesting: aquatic animals. For example, Hasler and Braemer (1963) found that solar elevation (or some related variable) is important in the compass orientation of sunfish, perch, and salmon. In this regard, it is important to understand that sky polarization patterns do not penetrate very deeply into water: other patterns, characteristic of an aquatic environment are established. (For details, see Waterman, 1979.) Although it is possible that even these aquatic patterns have temporal aspects which can be used as navigation cues, the demonstrated unimportance of solar elevation in the orientation of these animals may constitute strong negative evidence.

This is not to argue that skylight patterns around the pole point are the only cues used in navigation or that they are even used directly. In fact, they are probably frequently unreliable because of heavy cloud cover alone. Also, vertebrates may require substantial time in order to perceive changes in the sky pattern (although the actual position of the band of maximum polarization could itself serve as an important directional cue). In view of these factors, perhaps the sun is the principle compass which is frequently calibrated by information derived from the changing sky patterns. For example, although honey bees have the best analyzed behavior for orienting by patterns of polarization--they can detect and use specific E-vector orientations with relatively high precision under some circumstances (see Chapter V), as far as we know they use sky polarization patterns only to determine the sun's position. In experiments up to now, they clearly use the constantly moving sun as the reference of their dances, not the fixed pole point.

Some of the most interesting and important studies of animal navigation are based on experimental shifts of an animal's time sense and subsequent homing tests. The results of these experiments have shown that for birds the sun itself is not used in true navigation, although it ordinarily serves as an excellent compass. Clock shifted birds leave release sites in directions which imply they know the direction of home and use the sun as a compass to get there (reviewed by Keeton, 1974). If their clocks have been reset, however, birds often fly off in approximately the predicted direction away from home. Yet most return to the loft, many of them amazingly soon. Do they accomplish this feat through a recalibration of a solar compass by observing the dynamic sky patterns?

If the idea that animals use the rotation of patterns around the pole point for calibration is correct, one specific prediction is that ordinary clock shifts may be ineffective if the animal can see the natural, blue sky around the pole point. Keeton and Alexander (1974) have already shown that the internal clock is still easily changed even if pigeons can see the sun directly while they are undergoing the shifting. However, it is unclear from the description of these experiments whether the pigeons were able to see blue sky around the pole point. Further, we might expect that the effects of clock shifts could be quite different if the tested animals could see the blue sky for a period before being released.

In addition to the problem of explaining the effects of clock shifts, there are at least two other difficulties with this theory of goal-directed homing. Most normal releases of homing pigeons which show accurate initial homeward headings have involved displacements of at most only a degree or two in latitude and longitude and yet homeward direction is selected almost immediately after release. Furthermore, pigeons sometimes demonstrate accurate homeward orientation under clouds sufficiently thick to conceal the sun's position (Keeton, 1974) and therefore almost certainly thick enough to conceal patterns of skylight polarization as well.

This section has developed only a few of the major consequences of the dynamic aspects of skylight polarization patterns which may prove to be important factors for understanding certain aspects of animal orientation and navigation. While there are other ways in which information can be obtained from these patterns, most are more complicated and it is

premature to discuss them here, especially since as rich in information as the sky polarization patterns are, there is as yet no direct evidence demonstrating that any animal actually uses them. One possible factor is that until now our insensitivity to the porization of light has prevented us from appreciating how important these cues may be. However, the potential usefulness of such information in orientation (and perhaps even for bicoordinate navigation) is so great that this possibility deserves critical investigation.

A preliminary but necessary step of evaluating these possibilities is to understand how well animals can detect and use static patterns of polarization as orientation cues. This constitutes a major goal of this thesis. Here, honey bees were shown small, polarized artificial light sources and the results are reported in Chapter V. First, however, Chapter III compares the measured characteristics of the natural sky with the predictions of Rayleigh theory, and discusses various ways animals could possibly use the skylight information.

CHAPTER III.

Skylight polarization measurements.

1. Introduction.

Honey bees and a host of other animals orient themselves by using the sun as a compass. Since the sun is frequently hidden behind clouds, trees, or the horizon, an ability to infer its position by other means or to replace it altogether with some other compass system is crucial. Von Frisch (1948; 1949; 1967) demonstrated that when the sun is not visible, bees can orient their flights and communication dances by means of the extensive patterns of polarized ultraviolet (UV) light in the sky. These patterns, in theory at least, are quite regular and depend so strongly on the position of the sun that the idea that animals come programmed to use them to calculate the sun's location is tempting. This chapter will deal with the measured physical characteristics of the sky patterns which could be useful as cues for animal orientation. As a specific example, I consider what bees can actually see in the sky, and why evolution should have chosen the UV wavelength band for polarization orientation.

As discussed in Chapter II, according to the simplest (Rayleigh) theory (Strutt, 1871), when unpolarized sunlight scatters from molecules in the atmosphere a polarization is induced which depends on the scattering angle--the angle between the incoming (direct solar) and outgoing (skylight) rays. In review,[1] if simple Rayleigh theory were sufficient to describe sky radiation (i.e., if light scattered only once and all

1. For details, see Chapter II and Appendix A.

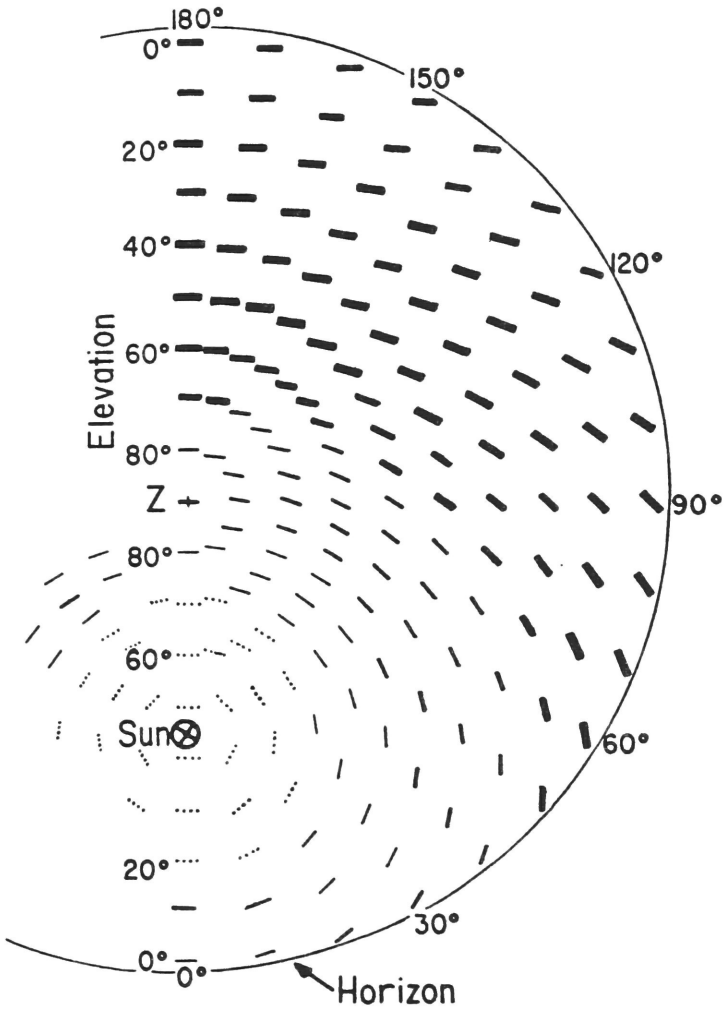

Figure III-1. Theoretical E-vector orientation for the sun at 45° elevation.
The half-hemisphere of the sky measured is collapsed into a plane. The solar vertical is toward the bottom of the figure (azimuth 0°) and azimuth increases uniformly counter-clockwise at 0° to 180°. Only data from 10° intervals are displayed. At each point in the sky shown here, the E-vector has the orientation which would be observed in the sky if primary scattering theory were completely appropriate. For example, horizontal E-vectors would be seen as horizontal at the corresponding place in the sky. The thickness of the E-vectors indicates qualitatively the degree of polarization. Dotted lines indicate that the polarization is below the known perceptual threshold of honey bees.

atmospheric constituents were of the proper dimensions and isotropic), the sky pattern observed would be geometrically simple (Figure III-1, III-2, III-7). After scattering, skylight would be partially linearly polarized (p) by an amount depending on the scattering angle Θ:

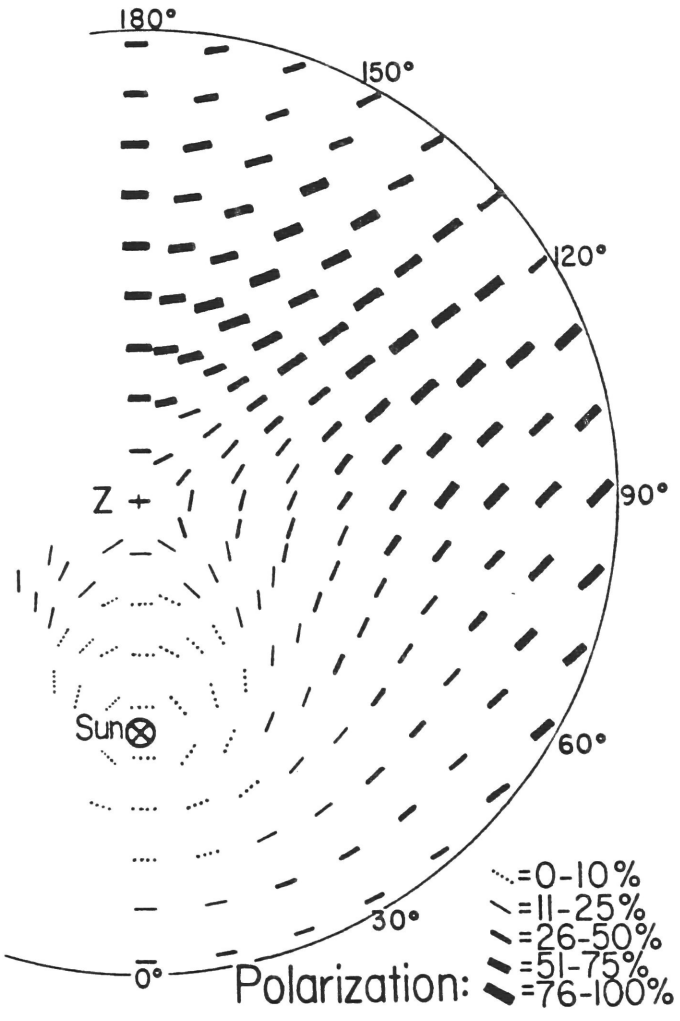

Figure III-2. Theoretical E-vector orientation relative to the horizon for the sun at 45° elevation. The same data used for Figure III-1 are plotted here with the E-vector orientation drawn relative to the horizon at each azimuth. The result is comparable to a fish-eye view of the patterns, and, though less useful for direct calculations, more effectively illustrates the symmetry and dependence of the sky patterns on the position of the sun.

$$p(\theta) = \frac{\sin^2(\theta)}{1 + \cos^2(\theta)}$$

Thus toward the sun ($\theta = 0^\circ$) the light should be unpolarized, while the maximum degree of polarization should occur for scattering angles of 90° (Figure III-7). In addition, each partially polarized skylight ray would exhibit a predominant vibration direction (E-vector orientation) perpendicular to the plane of the scattering angle, and together would produce

a well-defined pattern (Figures III-1 and III-2). Because scattering occurs inversely proportional to the fourth power of the wavelength, UV wavelengths are scattered about 16 times more effectively than red. This, of course, is the reason why the sky appears blue to us: more short-wavelength photons on their way through the atmosphere are scattered down towards us than long-wavelength photons.

Honey bees behave as though they are capable of inferring the position of the sun with information obtained from the blue sky: they can orient their dances when allowed a view of 15° or more of the sky (von Frisch, 1948; 1949; 1967; Zolotov and Frantsevich, 1973), and under some conditions even smaller areas may be sufficient (Rossel *et al.*, 1978). The ability of bees to orient themselves when only a very restricted part of the sky is visible is crucial since they live in cavities in trees where they must often fly with most of their view of the sky obscured by vegetation. In addition, they commonly dance outside the hive or on the surface of a swarm cluster. The tropical honey bees, from whom they evolved, live on exposed comb built on tree limbs in forests (Wilson, 1971; p. 266) and so always dance outside with, at best, only restricted patches of sky available for orienting their dances.

Bees are also capable of using artificial polarized sources for orientation (von Frisch, 1949; 1967; pp.395 ff.; Rossel *et al.*, 1978) and under some conditions can accurately use sources subtending less than a degree in visual angle (Edrich and von Helversen, 1976; Chapter V). Because simple Rayleigh scattering predicts a pattern which is symmetrical with respect to the sun, it is possible that bees use some regularities to "place" the sun with respect to any visible patch of sky. For

example, the sun should be located at the intersection of the great circle perpendicular to the E-vector orientation seen at a point in the sky and the horizontal circle defining the solar elevation. This type of solution of the orientation problem would be practical only if the Rayleigh pattern (or some other useful geometrical form) actually exists in the natural sky. A number of theoretical possibilities, some non-geometrical in nature, have been suggested (Kirschfeld and Lindauer, 1975; Rossel et al., 1978; van der Glas, 1977), and each depends on the exact information which exists in the sky. But, to evaluate what aspects of sky information might be used as cues by animals in their orientation, the patterns of the entire sky at any given instant must be known under a variety of conditions. Since any biological orientation system presumably reflects a nearly optimal use of the available cues, a detailed knowledge of how various atmospheric and ground conditions affect the sky pattern could provide useful insights about the likely mechanisms of animal orientation.

We already know some of the biological factors. Von Frisch (1967; pp. 401 ff.), for example, showed that only light which stimulates the ultraviolet receptors (hereafter called UV) is important to honey bees, and then only if it is above a certain minimum of per cent polarization. He also demonstrated that E-vector information is the most important parameter for orientation. These observations have been confirmed for bees (Zolotov and Frantsevich, 1973; von Helversen and Edrich, 1974) and ants (Duelli and Wehner, 1975; reviewed by Wehner, 1976), and are probably valid for a wide variety of insects. While only UV wavelengths have been demonstrated to provide information for polarization orientation in

bees, longer wavelengths are not unimportant since they often determine whether the polarization information is used (Kirschfeld, 1973; van der Glas, 1977; Chapter V). Although we do know of cases in which longer wavelengths mediate polarization sensitivity, these generally involve aquatic animals and may be special because UV wavelengths are strongly attenuated by transmission through water (for review, see Waterman, 1979). I will present and discuss the results of my physical measurements in the broadest sense because we do not yet know what factors are important for an understanding of later discoveries about the capabilities of animals for orientation.

The exclusive use of UV receptors by insects to derive information for polarization orientation is puzzling. For some of their other visual orientation, many insects are differentially sensitive to UV light, but judged by sensory physiology, potent UV sensitivity seems an anomaly. For example, although a 350 nm (UV) light is about 4.5 times more attractive to honey bees than a 550 nm (green) one in a phototaxis experiment (Bertholf, 1931), direct physiological measurements demonstrate that the green receptors are actually about 5 times more sensitive than the UV receptors (Goldsmith, 1960). Presumably, these animals are wired to amplify the UV light behaviorally about 22 times because it is somehow advantageous for them to do so: in phototaxis, a potent UV sensitivity may help animals move into "open space" (Mazokhin-Porshnyakov, 1969). This seems physically plausible for several reasons since the sky, as "open space," is the only extensive natural source of UV, and many natural surfaces, such as soil and vegetation, strongly absorb UV. Animals relying primarily on UV light as a sign of open space would not

be likely to be misled by inappropriate reflections. I will develop similar analyses to consider possible reasons why short wavelengths are so important as orientation cues.

Considering skylight polarization patterns, one important question is whether UV sensitivity arises because of physical or biological factors. The physical aspects are difficult to analyze since UV wavelengths have been largely ignored in experimental investigations of skylight polarization, and as a result virtually no relevant data exist. The important physical variables are total intensity, degree of polarization, and E-vector orientation of each part of the sky as a function of wavelength. Even though until now we did not know how the entire sky looks in UV compared to longer wavelengths as a function of atmospheric conditions, basic physical considerations make it difficult to imagine any selective advantage to using UV wavelengths for polarization orientation since many features of these patterns are <u>poorest</u> in the UV. For example, in honey bees, differential UV-wavelength sensitivity cannot be explained by visual receptor thresholds, since the daylight photon flux is enormous for all wavelengths to which the strictly diurnal honey bee is sensitive. In fact, considering the sensitivity of the honey bee's eyes, the photon flux is <u>smallest</u> in the UV, constituting from about 8% of direct sunlight to a maximum of about 30% for some parts of the blue sky (energy data of Hess, 1938, converted to relative photon flux with respect to the honey bee visual sensitivity spectrum). One conceivable advantage of using short wavelengths for polarization orientation has already been mentioned: by using only short wavelengths animals would be fairly sure that they were using <u>sky</u> information and not polarization

patterns produced by reflection from vegetation and other natural surfaces, which generally are not strongly dependent on the sun's position. But since there are other ways such a separation might effectively be accomplished (e.g., von Frisch [1967; pp.409 ff.] has shown that for orientation bees only use polarization information coming from above them), there probably are other specific advantages for using UV wavelengths.

A principal consideration is that the pattern in UV should diverge most from simple theory if only because UV photons scatter so greatly in the atmosphere, diminishing the extent of usable sky pattern by reducing the per cent polarization and causing the radiance and spectral distributions to depart from theoretical predictions. In principle, these sources of "noise" are well known and were central factors in von Frisch's conclusion that the honey bee orientation system could not be based on analysis of patterns of per cent polarization or radiance. As von Frisch (1967; p. 391) has shown, the E-vector orientation alone seems essential for honey bee orientation.

Might honey bee UV sensitivity be explained by some unknown property of the E-vector orientation in this wavelength band? Von Frisch, relying on the suggestions of Sekera (cited by von Frisch, 1967; p. 382) postulated that UV-polarization patterns might be advantageous to use for orientation not only because the UV E-vector orientation most precisely approximates simple theory, but also because they might be most stable during marginal sky conditions, while patterns in longer wavelengths may be easily disrupted. These ideas seem to have become widely accepted in the literature. Although the evidence for this conjecture seems very

slim, any strategy which could extend the conditions under which successful orientation is possible would certainly constitute a major selective advantage.

To provide data to evaluate how UV sky information might be advantageous for orientation, I designed and built a precision polarimeter which measured quickly and accurately the skylight radiation parameters in narrow and white spectral bands for half of the sky under diverse atmospheric conditions. My goal was to provide "snapshots" of the actual sky. Ultimately I hope to be able to correlate these snapshots with behavioral data gathered simultaneously.

2. Materials and Methods.

2.1 Polarimeter.

I recorded the "Stokes vector" of each point of the sky, which is a conveniently succinct description of polarized light since it completely specifies a beam, and also simplifies computation of any effects created by optical devices (see Chapter II, and Shurcliff, 1962). Use of Stokes vectors also has the advantage that the results are perfectly general and thus easily applied to any detector configuration. This is especially important because we do not yet know precisely how the biological detector systems are arranged and thus, in effect, do not know how the sky patterns actually appear to animals.

My polarimeter determined the Stokes vectors by using the principle that a "retardation plate" (="waveplate") has a net observable effect only on polarized light passing through it. I rotated the waveplate

around its center so that it modulated only the polarized component of the light beam analyzed and left the unpolarized part unaffected. The optical principles of various kinds of such "active" polarimeters are described in a general way by Serkowski (1974). In operation, a 40 Hz sine wave superimposed on a DC component was generated from any partially polarized beam. From this wave, a Stokes vector completely describing linearly polarized light was derived almost instantaneously since the DC component was directly proportional to the total intensity, the amplitude of the 40 Hz component was directly proportional to the degree of polarization, and the phase was directly related to the E-vector orientation. A device described by Sekera (1955; pp. 2 ff.; 1957a; pp. 311 ff.; 1957b; pp. 487 ff.) provided the original inspiration for my instrument, although in its final form my polarimeter was very different in how quickly and extensively it measures the sky, and other substantial details.

Skylight first entered a collimator tube 100 mm long (Figure III-3). Only parallel skylight rays were analyzed since baffles effectively eliminated oblique rays. A linear iris diaphragm located at the distal end of the tube limited the area of the sky analyzed to between 8.5° and 4°. The field of view could be increased to 19° by removing the collimator. Sky measurements reported here always corresponded to about a 6° area of the sky, approximately equal to the area viewed by a typical honey bee ommatidium (which has an acceptance angle of about 6°, [Laughlin and Horridge, 1971; Emheim and Wehner, 1972]).

The polarization modulator was a high-quality, half-wavelength retardation plate. The optical properties of typical plates are so

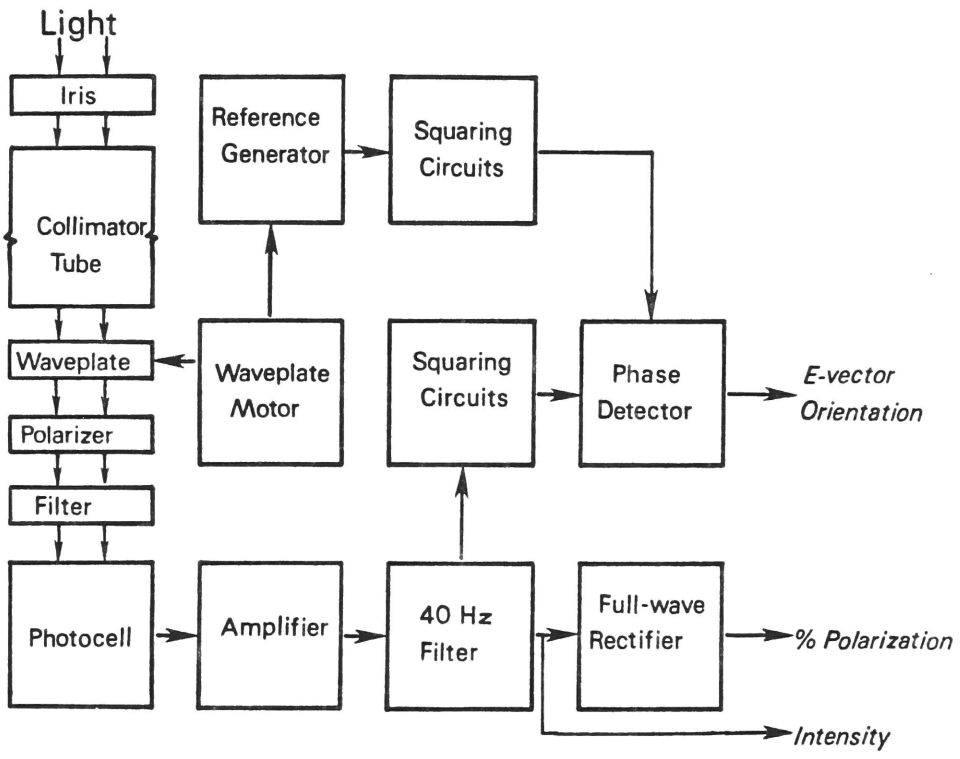

Figure III-3. Principle components of the scanning polarimeter. Incoming light passes successively through an iris, collimator tube, rotating waveplate, polaroid filter, one of four interchangeable spectral filters, and falls on the photocell. Electrical output from the photodetector possesses an AC voltage (polarized part) superimposed on a DC level (proportional to the total intensity). The difference in phase of the AC signal and the internal reference specifies the E-vector orientation. Other circuits derive the precise Stokes parameters from this complex wave.

wavelength dependent that measured values of degree of polarization would be accurate only when wavelength-specific correction factors are applied or when only known E-vector orientations are measured. To eliminate this problem I used an achromat which yielded better than 90% accuracy between 330-700 nm. It was constructed from optical quartz and magnesium fluoride by Karl Feuer Optical Associates, Montclair, New Jersey. The

waveplate was rotated about its center at 10 Hz by a precision synchronous motor. Because of the two optic axes, any incident polarization was modulated at 40 Hz, while the unpolarized component remained unaffected.

After emerging from the retardation plate, the skylight beam passed through a fixed, UV-transmitting linear polarizer (Polaroid Corporation HNP'B) cemented between two very thin optical quartz plates with UV-transparent optical epoxy (Epotec #500). Specific wavelength bands were analyzed by inserting precision analytical interference filters into the beam after the polarizer. Since the polarizer remained fixed, any possible deleterious effects due to the polarization sensitivity of the detector were eliminated because the E-vector orientation was constant with respect to the photodetector. To allow selection of wavelength bands during operation of the machine, three filters were accommodated inside the instrument and could easily be moved into the beam. The four spectral ranges used in these measurements were derived either by using very narrow (9 nm half-maximum bandwidth) filters centered on 350 (UV; Karl Feuer Optical Associates), 500 (blue/blue-green), and 650 nm (red; Ditric Optics, Inc.) or a Corning Glass Works #3965 ("white") filter which passed UV and visible light, but absorbed near-infrared. The white measurements correspond most closely to the wavelength band commonly reported in the literature. Secondary transmission regions of the narrow filters were blocked to a minimum optical density of four and an average optical density of seven. Special care was taken to eliminate near-infrared radiation, to which the photodetector was quite sensitive. The narrow filters were selected to provide data representative of the entire visual/UV spectrum as well as values specifically for: 1) the

behaviorally determined (von Helversen and Edrich, 1973) sensitivity maximum of polarization orientation of honey bees (the 350 nm filter); 2) the approximate, broad maximum of the energy distribution of skylight (the 500 nm filter); and 3) wavelengths close to the maximum photon flux of daylight (the 650 nm filter). Obviously, the actual photon flux as well as the information content of each of the spectral bands are important variables to consider while evaluating different possible strategies for polarization detection.

The photodetector was a large, UV-optimized photovoltaic cell (E.G.& G. #UV4000B) which was highly linear over seven decades of irradiance. Current produced by incident skylight was converted to voltage by a very high input impedance (FET) operational amplifier and the gain was further increased by other high-quality operational amplifiers, which made the polarimeter extremely sensitive. The voltage from the photovoltaic cell was the electrical analog of the optically modulated beam of skylight, and was processed by the electronic circuits schematized in Figure III-3. The outputs of these circuits were DC level, 40 Hz amplitude, and phase, which were directly related to the Stokes parameters of total intensity, degree of polarization, and E-vector orientation.

The polarimeter was enclosed in a light-tight aluminum box, coated on the inside with flat black paint, and mounted on a modified equatorial telescope mount with principal axes corresponding to the zenith and horizon directions. Conventional setting circles enabled the polarimeter to be directly positioned in the horizontal coordinates corresponding to any point of the sky. Precision potentiometers attached to each axis provided easy and accurate electrical specification of position. The two

voltages corresponding to the azimuth and zenith distance and the electrical correlates of the Stokes parameters were continuously available to an analog-to-digital converter of a Digital Equipment Corporation PDP-11 minicomputer which acquired, stored, and manipulated the data.

For the data reported here, the polarimeter was manually moved while the computer automatically acquired data at programmed intervals of 5° in elevation and azimuth over the sky vault (total of 630 points). Each stored sky value was the arithmetic average of 25 separate measurements. To minimize data acquisition time, only one half of the sky was measured, since the plane of the solar vertical theoretically divides the sky into two halves which are mirror images of each other. With this procedure the intensity, degree of polarization, and E-vector orientation of an entire half hemisphere could be measured within eight minutes. By comparison, an outstanding study by Coulson et al. (1974) using photon counting techniques required 15 minutes to measure the sky only in the plane of the solar vertical.

Since the general, wavelength-dependent features of skylight polarization were of interest, especially as a function of atmospheric conditions, the sky radiance (photon flux) is expressed here in relative units, while the degree of polarization and E-vector orientation are in absolute units. Due to the non-ideal achromatic waveplate, the largest errors (about 10% too low) involved measurement of the degree of polarization for 500 nm. Because of the high linearity of the photodetector system, relative intensities have only very small errors over almost the entire sky.[2] E-vector orientation was determined by digital methods and

2. Depending on the prevailing conditions a small, variable area

was the most accurate of the three Stokes parameters. Phase varied linearly over a 178° E-vector orientation change (the final 2° were undefined because of unavoidable time delays in the electronic circuit). Under most circumstances, this 2° ambiguity did not pose a serious problem since its position could be arbitrarily selected at any time. E-vector orientation could be accurately determined within 0.25°.

2.2 Methods.

Through the courtesy of James L. Gould, all sky measurements were taken from the roof of Eno Hall, Princeton University Campus, Princeton, New Jersey. By selecting the time of day, most of the field of view was unobstructed, especially high in the sky. Appropriate notes appear in the figure legends whenever terrestrial features disturbed the sky measurements.

Except for a few completely overcast conditions, azimuth 0° of the measurements always corresponds to the plane of the solar vertical. When the sun was visible (even through fairly heavy cloud cover) the polarimeter could be accurately oriented by setting a special viewfinder on the sun's disc. On completely overcast days, the instantaneous azimuth of the sun was calculated by spherical trigonometry and the polarimeter oriented as precisely as possible using a magnetic compass. Once the reference axes of the instrument were established, azimuth 0° was readjusted before each new series of sky measurements to correct for the

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around the sun was frequently so bright as to saturate the amplifiers. This produced a constant measured E-vector orientation which had to be considered when evaluating the data.

sun's movement since the last setting. In addition to subjective records of sky conditions, color photographs of the sky were taken through a fish-eye lens (about 170° field of view) during each series of measurements. With practice, points at every 5° of elevation and azimuth of an entire half hemisphere of the sky could be measured within 7-8 minutes. This minimum time was established by the temporal restrictions of the computer system. Thus, the sun moved about 2° along its arc over the course of a complete set of measurements. Changes resulting from this movement could be easily detected by the polarimeter, and also some errors occurred (less than 2°) in setting the axes of the instrument. Such assumed limitations, while probably too severe, are a necessary consequence of measuring large areas of the sky quickly. To determine how closely skylight characteristics matched theoretical predictions as a function of wavelength, single points of the sky could be serially analyzed at different wavelengths. Such measurements could be accomplished within 10 seconds and directly compared.

Although specific Stokes vectors were determined for each sky point, it is difficult to use these to compare various measured and theoretical values for large areas of the sky. Thus, for most data the differences between theoretical and observed skylight characteristics are graphically summarized. Here, the theoretical values expected from <u>primary</u> Rayleigh scattering were calculated by spherical trigonometry (Chapter II), and for some, the absolute value of the differences between measured and theoretical values are shown in three dimensional plots of azimuth, elevation, and deviation from theory, as specifically described for each figure. Since data exist only for every 5° in azimuth and elevation,

intermediate points are determined by linear interpolation. Other features are explained separately as needed in the respective figure legends.

3. Results of measurements.

For convenience, the results of sky measurements under a variety of atmospheric conditions are presented in three main sections: radiance and spectral distribution, degree of polarization, and E-vector orientation as a function of wavelength and atmospheric conditions.

3.1 Radiance and spectral distribution.

The radiance distribution of a clear sky possesses three main characteristics: 1) the greatest radiances occur at points in the sky close to the sun; 2) radiance decreases steadily until about 90° from the sun, and then increases again to the antisolar vertical; 3) radiance diminishes as the zenith distance of the point of the sky observed decreases. These three characteristics can be easily appreciated by examination of the representative data presented in Figure III-4. Although the first two of these features are similar to the predictions of simple Rayleigh theory, even under the most favorable atmospheric conditions encountered during these measurements, the measured relative radiance never approximated the predictions of Rayleigh theory, especially for points in the sky with large zenith distances.

The radiance distribution was observed to depend strongly on wavelength: the longer the wavelength used for observation, the larger

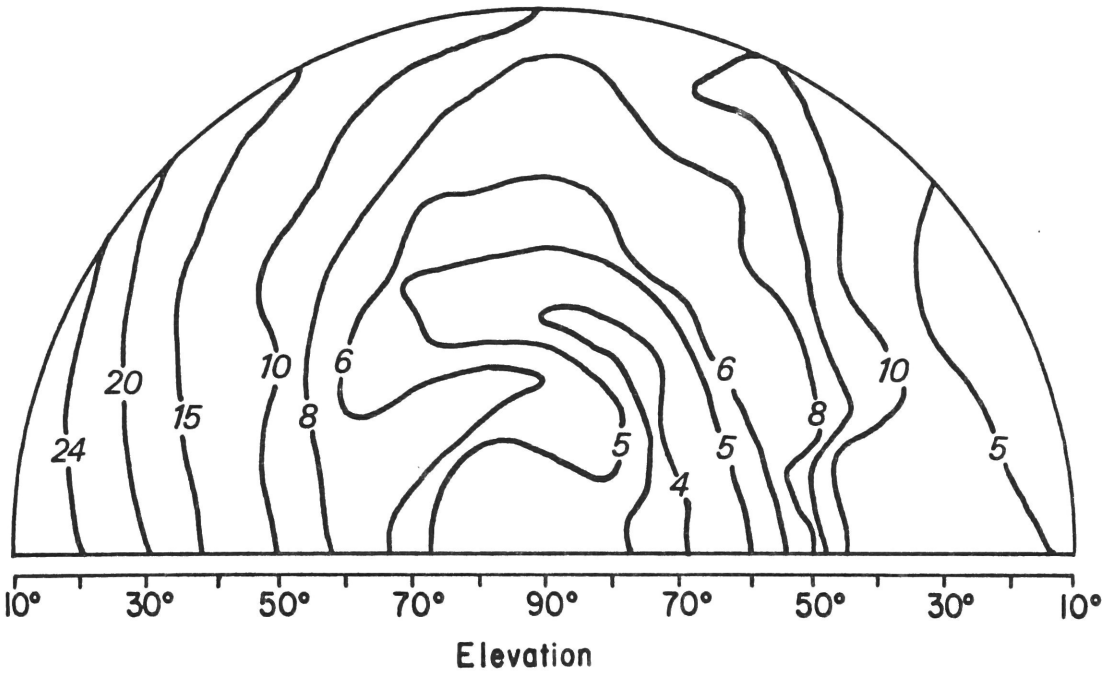

Figure III-4. Relative sky radiance of a virtually clear sky measured at 500 nm.

The measured half-hemisphere of the sky is collapsed into a plane. The solar elevation is 5° and is located on the left of the figure. Azimuth is 0° at the sun and increases to 180° clockwise. Isopleths connect points of equal relative radiance. This typical example shows that for a clear sky, the radiance is lowest at the zenith and monotonically decreasing elevation so that, except for parts of the sky close to the sun and opposite to it, points near the horizon exhibited the largest radiance. The irregular nature of this pattern close to the zenith was produced by very thin, wispy cirrus clouds. (Compare to the overcast conditions in Figures III-5 and III-6.)

the differences between the greatest and smallest radiances observed. That is, the radiance distribution of UV light always appeared much more uniform than that of red. At the same time, the geometrical distributions of radiance predicted by Rayleigh scattering theory were more

closely approximated by the pattern at longer wavelengths. But even for these cases, it did not match well.

The radiance flux from a clear sky exhibits other wavelength-dependent characteristics. For example, close to the sun the sky color is always the same as that of the sun itself, and looking away from the sun, the sky color becomes increasingly rich in short wavelengths to a maximum for points in the sky about 90° from the sun. In general, the radiance and short wavelength composition of sky light were observed to possess opposite characteristics: when one was large, the other was small. For example, the point in the sky with minimum radiance usually occurred at a moderate zenith distance in the antisolar vertical. This point also usually appeared to be the most nearly saturated in short wavelengths.

Under complete overcast, the total level of radiance was, of course, much reduced (typically only 5-10% of the radiance of a clear sky) and the radiance relationships were reversed from those of a clear sky: radiance was greatest at the zenith point and least along the horizon. In addition, complete overcast appeared to obliterate the wavelength-dependent aspects of sky radiance and the pattern was generally symmetrical around the zenith point. As expected, uneven overcast produced irregular patterns of sky radiance which were difficult to categorize.

For uniformly overcast sky conditions, sky radiance appeared to be independent of solar position, as summarized by the data of Figure III-5, where the radiance can be seen to be at a minimum at the horizon and at a maximum at the zenith. To determine whether the sun could be located at

any wavelength behind complete cloud cover (solar disc not visible to the naked eye or in later analysis of visible light photographs), radiance measurements were taken around the solar vertical. The results of these observations show that regardless of the wavelength used for analysis, when the sun could not be seen by the naked eye it was not detectable by the polarimeter. Figure III-5 illustrates a typical result for radiance measurements taken at 350 nm in which the asterisk indicates the position of the sun behind the unbroken cloud cover, and no obvious features in this three-dimensional radiance plot indicate the sun. By comparison, when the sun's disc could just be detected by eye, instrumental measurements always showed its presence, as Figure III-6 illustrates for another set of radiance measurements obtained for 350 nm relatively soon after those in Figure III-5. During both of these radiance measurements, honey bee dances on a vertical comb surface were well oriented. On horizontal surfaces, on the other hand, complete overcast can result in disoriented dances (von Frisch, 1967; pp. 395 ff.).

In summary, the relative radiance distribution is characterized by large variability in both magnitude and geometrical form. Even when the sky appears clear, there are usually large deviations from the expected magnitude, and sometimes in the angular dependence of the radiance. There are two conditions for which the sky radiance distribution can be described with some degree of confidence: 1) for clear sky, the radiance distribution decreases as scattering angles of 90° are approached and as the zenith distance decreases. Far from the sun, the greatest radiances occur for points along the horizon. 2) Under complete overcast, the radiance is symmetrical around the zenith and decreases to a minimum at

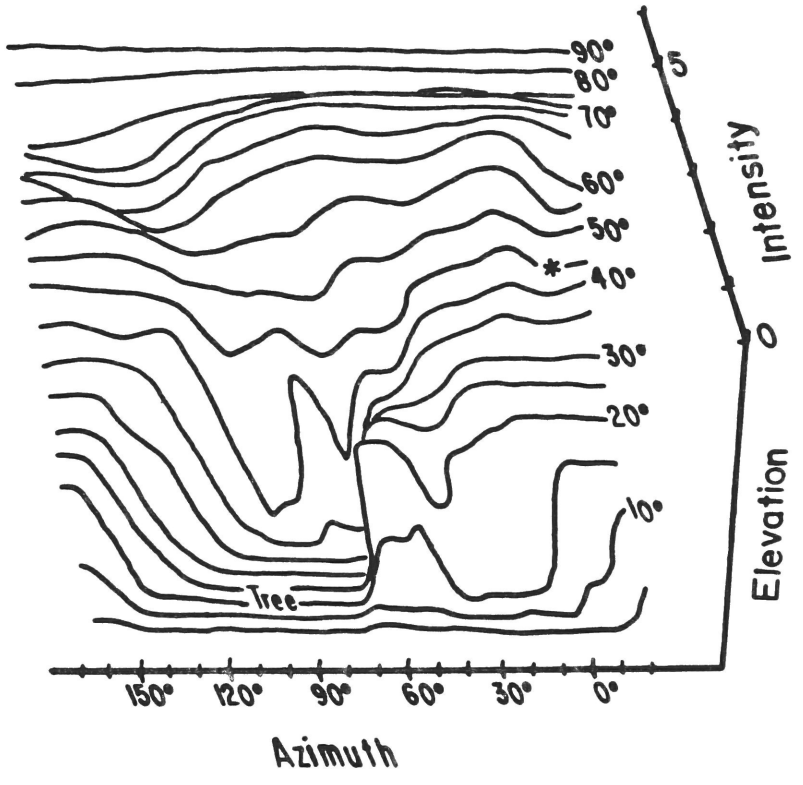

Figure III-5. Relative ultraviolet sky radiance for complete overcast measured at 350 nm.

A three-dimensional plot of relative UV radiance of a relatively uniform, dark sky covered with altostratus clouds. For overcast conditions, all measurements showed that the radiance relationships are reversed--the greatest radiance occurs at the zenith and the least at the horizon--and that the sky pattern is quite symmetrical about the zenith. Elevation is the ordinate, azimuth the abscissa, and the relative intensity is out of the page. During the measurements, the solar disc was not visible to the naked eye or in subsequent analysis of photographs. The sun's position behind the clouds (elevation of 45°) is indicated by the asterisk. Although an increase in radiance around the position of the sun is not obvious, simultaneous observations of the vertical dances of honey bees trained to forage from an artificial feeding station showed that the bees were still precisely oriented. A large tree produced the small radiance low in the sky, as indicated in the figure.

the horizon.

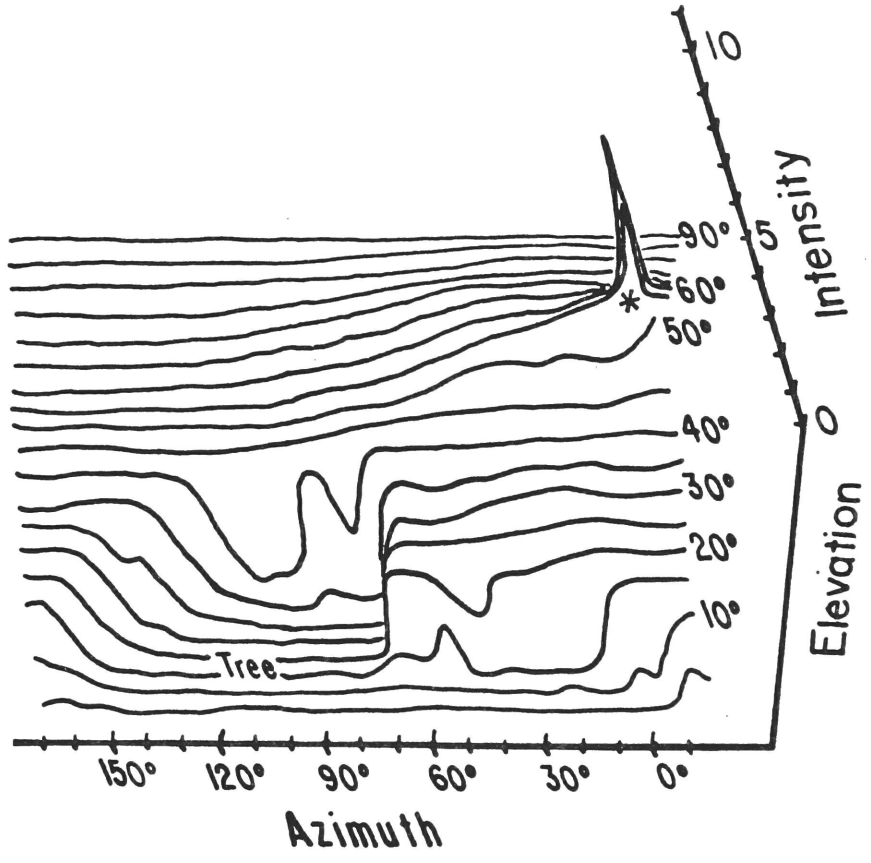

Figure III-6. Relative ultraviolet radiance (350 nm) when solar disc was just visible.
Typical radiance measurements of uniform overcast when the sun's disc (elevation 57°) was visible to the naked eye. These data were collected later the same day as those shown in Figure III-5. Such measurements always showed the solar position clearly by a fairly large aureole. The small radiance measured low in the sky at large azimuth angles was caused by an obscuring tree which rose over the roof.

4. Degree of polarization.

For clear sky, most measurements of per cent polarization exhibit the general geometrical form predicted by simple Rayleigh theory: very low values are observed toward the sun, and an increase to a relative maximum at scattering angles of 90°. For scattering angles greater than 90°, the

degree of polarization gradually decreases to the plane of the solar vertical. However, the magnitude of per cent polarization is generally quite different from theoretical predictions and is highly dependent on wavelength. Of the four spectral bands used in this study (UV, blue/blue-green, red, and white), per cent polarization was always smallest in the UV and frequently greatest in blue/blue-green. For example, Table III-1 gives the conventional quartile percentiles for a series of measurements in three wavelength bands gathered on an exceptionally clear summer day within 45 minutes of each other. The theoretical Rayleigh maximum was rarely approached as closely as in this example. And even for these data, measured patterns poorly matched the entire range of predicted values. Figure III-8 illustrates that the actual magnitudes of per cent polarization and the geometrical symmetry are generally substantially lower than Rayleigh theory (Figure III-7) predicts.

Another manifestation of the wavelength dependence of per cent polarization was that, unlike those at longer wavelengths, the deviations in UV as a function of position on the sky vault constituted a smoothly varying function. Average deviations for 500 nm were intermediate in form between red and UV wavelengths. Thus, like radiance measurements, per cent polarization is predictably diffused.

Another general characteristic of the distribution of per cent polarization was observed: with increasing zenith distance of the point in the sky, the per cent polarization generally decreased, although the radiance increased. This relationship was especially obvious for those points in the sky with scattering angles of about 90°, as shown by the representative data of Table III-2.

Table III-1. Quartile distribution of per cent polarization for an exceptionally clear summer day. (Total of 630 points of the sky.)

wavelength	sun's elevation	(min) 0%	25%	(mean) 50%	75%	(max) 100%
350 nm	67°	0	16	28	33	41
500 nm	60°	0	22	45	56	64
650 nm	63°	0	18	39	50	58

Table III-2. Per cent polarization measured in the band of maximum polarization (scattering angle = 90°).

	zenith distance									
wavelength	5	10	15	20	25	30	35	40	45	50
350 nm	28	33	37	41	41	39	39	37	35	32
500 nm	53	51	58	58	59	57	57	56	57	54
650 nm	42	52	56	55	56	53	52	52	52	49

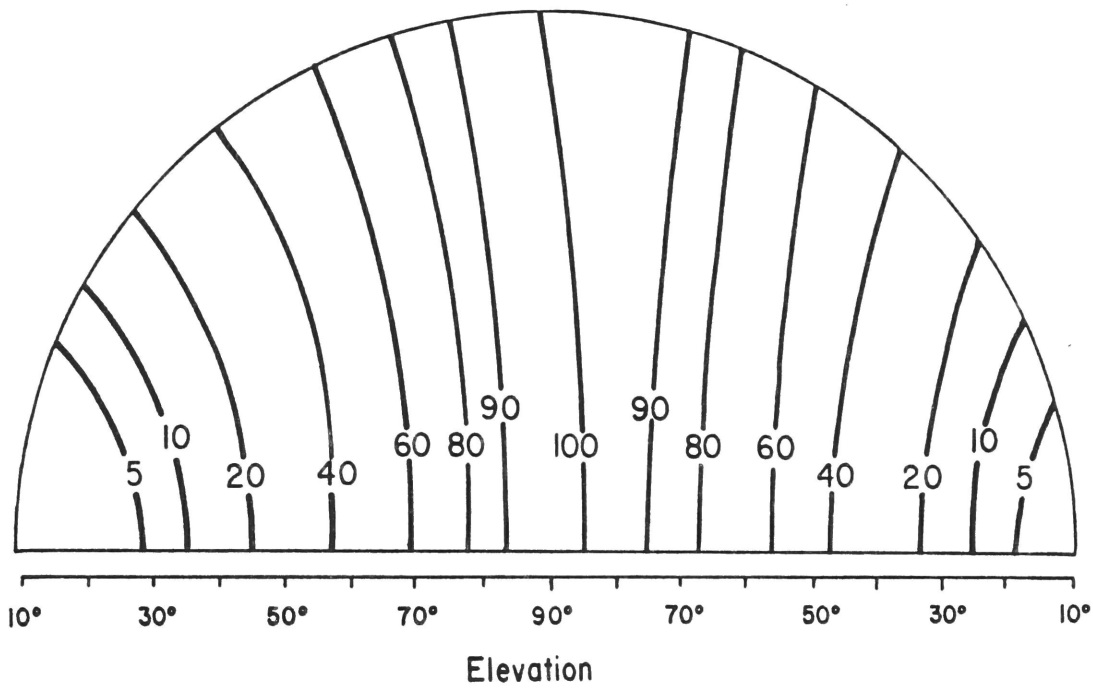

Figure III-7. Theoretical distribution of per cent polarization for a solar elevation of 5°

Isopleths connect points in the sky which are expected, on the basis of simple Rayleigh theory, to possess equal per cent polarization. The sun is on the left side of the figure. This form demonstrates the striking symmetry of the pattern which depends on a single, dominant geometrical parameter: the scattering angle (the angle between the incident direct sunlight and the scattered skylight rays). Minimum (0%) polarization is expected to be observed toward the sun and antisun, and maximum (100%) along the arc 90° from the sun.

On several occasions, anomalously high per cent polarization values were measured close to the horizon for sky points with azimuths between 90° and 160°. Although this phenomenon was not investigated in detail, observations were always associated with obvious, heavy layers of dark haze at the horizon.

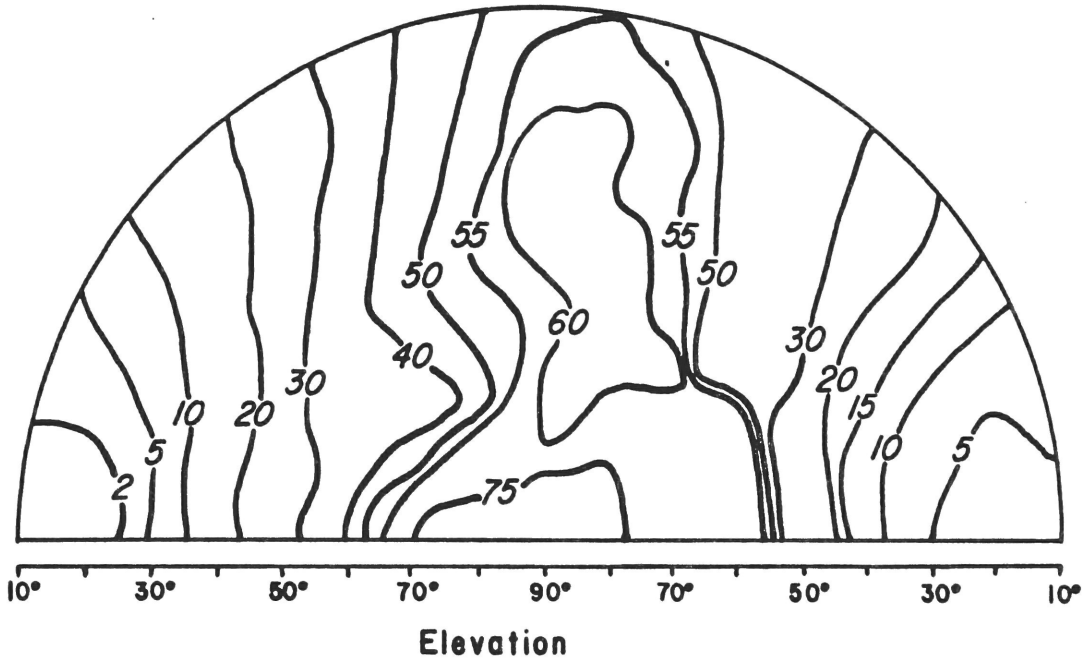

Figure III-8. Per cent polarization of a clear sky measured at 500 nm.
Even under the most favorable atmospheric conditions encountered, the actual magnitude of degree of polarization is generally much lower than theoretical predictions. Solar elevation is 5°, and data were collected simultaneously with those of Figure III-4, illustrating that the theoretical predictions occur only approximately in the sky.

When the sky was completely overcast (neither sun nor blue sky visible) the measured degree of polarization was usually less than 1% for most points on the sky vault, especially those with small zenith distances. Larger amounts of polarization were frequently measured close to the horizon, but for some cases these could be attributed to the reflection of light from features on the earth's surface.

In summary, the magnitude of per cent polarization was observed to be a highly variable parameter which only rarely approached the theoretical maximum values of primary Rayleigh scattering, even under the clearest atmospheric conditions. The geometrical distribution of varying degrees of polarization approximated Rayleigh theory better, but was also quite variable and divergent. Deviations from the predictions of Rayleigh scattering were found to be strongly wavelength dependent, with short wavelengths deviating most. For complete overcast, the amount of linearly polarized skylight was virtually zero. Under intermediate sky conditions, variable and small amounts of polarization were observed. The characteristics of these conditions in connection with the E-vector orientation are discussed in detail below.

5. E-vector orientation.

For most parts of the clear sky, the measured E-vector orientation corresponded reasonably closely to the geometrical predictions of first order Rayleigh scattering. Figure III-9 illustrates how well a typical set of measurements at 350 nm matches the theoretical expectations of Rayleigh scattering. Here, the absolute values of the angular deviation of the observed from the expected are plotted as a function of azimuth and elevation of the point in the sky. It is clear from these data that the only place in the sky where large divergences from theoretical expectations regularly occur is near the solar vertical.[3] Of the points measured in the sky, 75% diverged less than 6° from theoretical predictions,

3. The small deviations at low elevations arose from surface-reflected light.

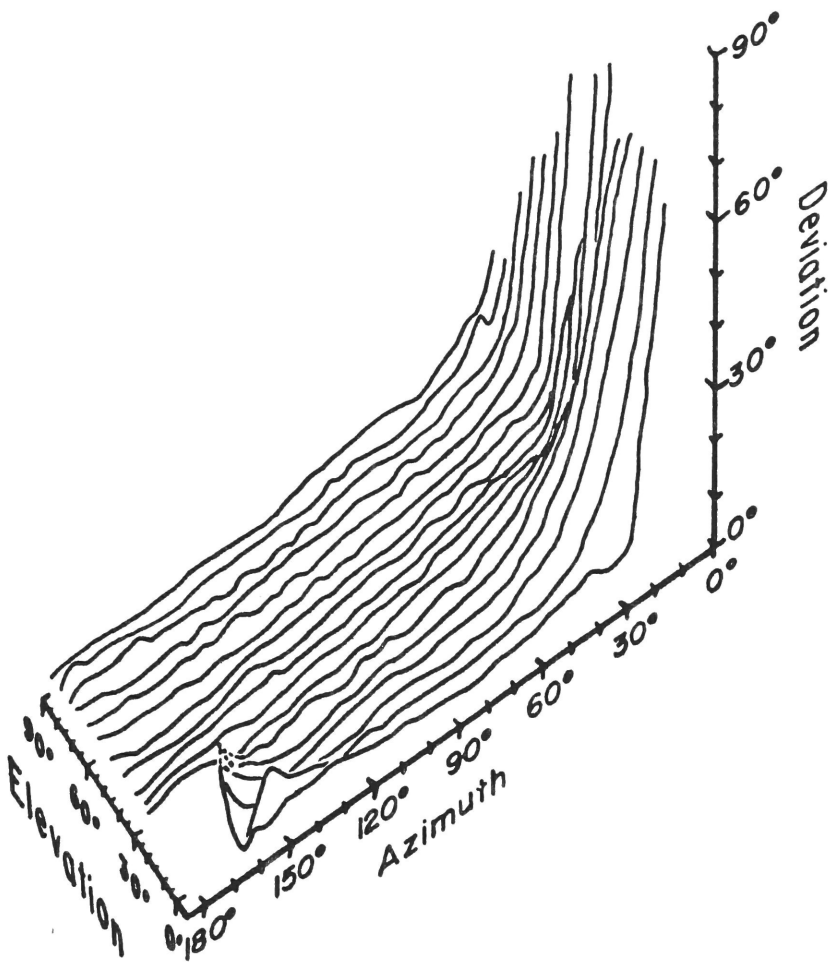

Figure III-9. Deviation of E-vector orientation from theoretical expections measured at 350 nm. Magnitude of the differences between the E-vector orientation measured in the UV (350 nm) for a clear sky and the expectations of primary Rayleigh scattering are plotted. Azimuth, elevation, and deviation form the labelled axes. The solar vertical corresponded to azimuth 0°. The sun's elevation is 4°. Except for points in the sky close to the solar vertical, the measured E-vector orientation matched theoretical predictions well. (Of the measured points of the sky, 75% possessed deviations less than 6°.) The small deviations at low sky elevations arose from light reflected from a building.

and most of the large divergences occurred close to the solar vertical. When the sun was low, substantial deviations were also regularly observed near the antisolar point.

For points in the sky far from the sun, small but significant differences were consistently measured in the E-vector orientation as a function of wavelength. Generally, red wavelengths diverged least and UV most from theoretical predictions. Wavelength analysis of single points of the sky confirmed this observation. Occasionally, much larger deviations occurred, and were associated with light haze. For example, for one very clear sky, 75% of the measured sky points possessed divergences less than 5°, with practically no differences between UV and red. With increasing haze (sky becomes whiter, but no clouds) the wavelength differences increase dramatically. For one series of measurements, I found that 75% of the measured sky points diverged less than 10° from theoretical expectations at 650 nm, while measurements at 350 nm (15 minutes later) exhibited divergences up to 20° for the same portion of the sky. Then a large change in the sky brightness was observed (within a half hour) and subsequent measurements in the UV showed deviations of up to 28° for 3/4 of the sky measured. With these kinds of atmospheric changes, the dependence of E-vector deviation on wavelength was very striking.

The E-vector orientation of points in the sky close to the sun always exhibited a strong wavelength dependence regardless of atmospheric conditions I measured: deviations at UV wavelengths always extended farther from the solar vertical than those at longer wavelengths. This can be seen by comparing Figure III-9 (for UV) with Figure III-10 (for 650 nm). In these figures, the deviation of 75% of the sky was about the same, and differed less than 5° from the predictions of simple Rayleigh theory. At long wavelengths, however, the large deviations around the

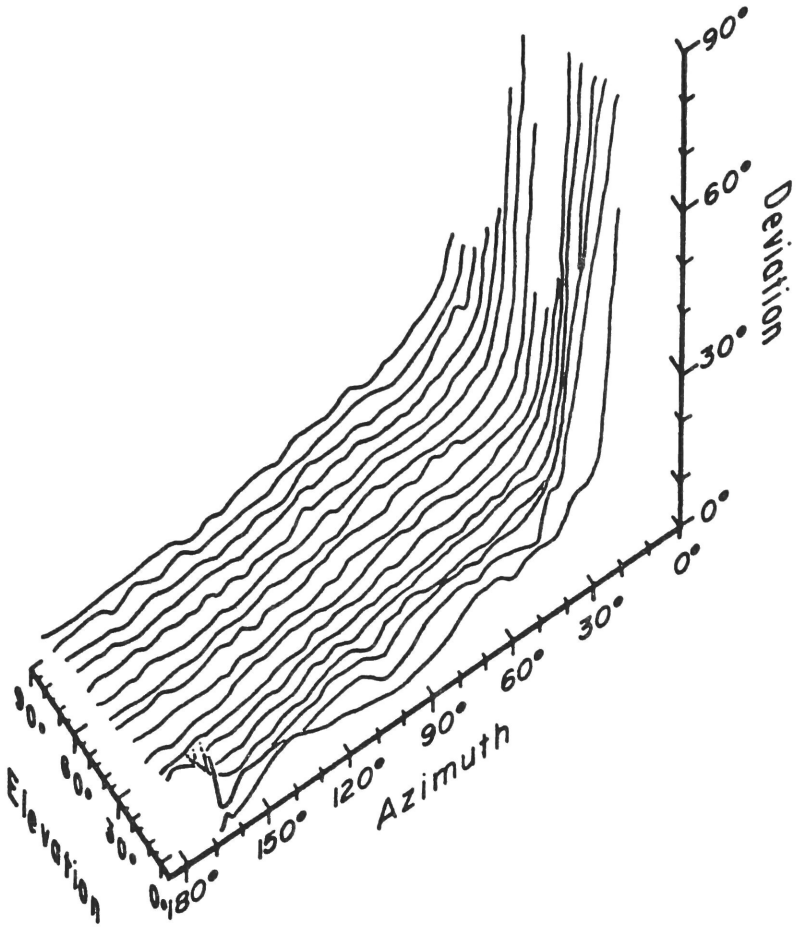

Figure III-10. Deviation of E-vector orientation from theoretical expectations measured at 650 nm.

These data for 650 nm were collected immediately after the UV data shown in Figure III-9. Solar elevation was -4°. Like data for UV wavelengths, the measured E-vector orientation of parts of the sky far from the sun agreed fairly well with theoretical predictions. Notice, however, that the E-vector orientation at these long wavelengths is closer to theoretical over a larger area of the sky: the large deviations extend for a smaller distance out from the plane of the solar vertical. Similar sky measurements at 500 nm. produced plots of deviation intermediate in form and magnitude between those for UV and for red. These examples summarize the results for measurements of the clear sky: the E-vector orientation was better at red wavelengths and worst in the UV. With increasing light haze, the deviations as a function of wavelength increased strikingly.

solar vertical extended over a smaller area than those at UV wavelengths.

For blue/blue-green wavelengths, the circumsolar deviations of E-vector

orientations extended over an area intermediate in size between those of the shorter and longer wavelengths. These observations were well supported by a comparison of E-vector orientation over a wide variety of clear skies.

For light, irregular cloud cover, the measured E-vector orientation pattern was quite close to theoretical expectations. For example, 11 separate measurements in the UV showed that 75% of the sky deviated less than 14° from Rayleigh theory, compared to 75% of the sky deviating less than 10° for typical clear sky measurements.

For completely overcast skies no wavelength-dependent differences were ever observed: the sky pattern seemed equally poor, irrespective of wavelength. (Measurements were difficult because per cent polarization was usually less than 1%.) Figure III-11 illustrates a typical example for data taken at 350 nm, while the accompanying absolute per cent polarization plot illustrates that the measured degree of polarization was virtually zero over most of the sky, reaching a maximum of only 3%. It is interesting to note that even under these poor conditions there are some places in the sky with appropriate E-vector orientation.

For non-uniform overcast, especially when the sun's disc was visible, the E-vector orientation over at least part of the sky was usually quite close to the theoretical predictions of simple Rayleigh theory. Figure III-12 illustrates a representative example of this, again for data from measurements at 350 nm. This example demonstrates especially well that the visibility of the sun is an important factor in whether or not appropriate E-vector orientations exist, since data was collected

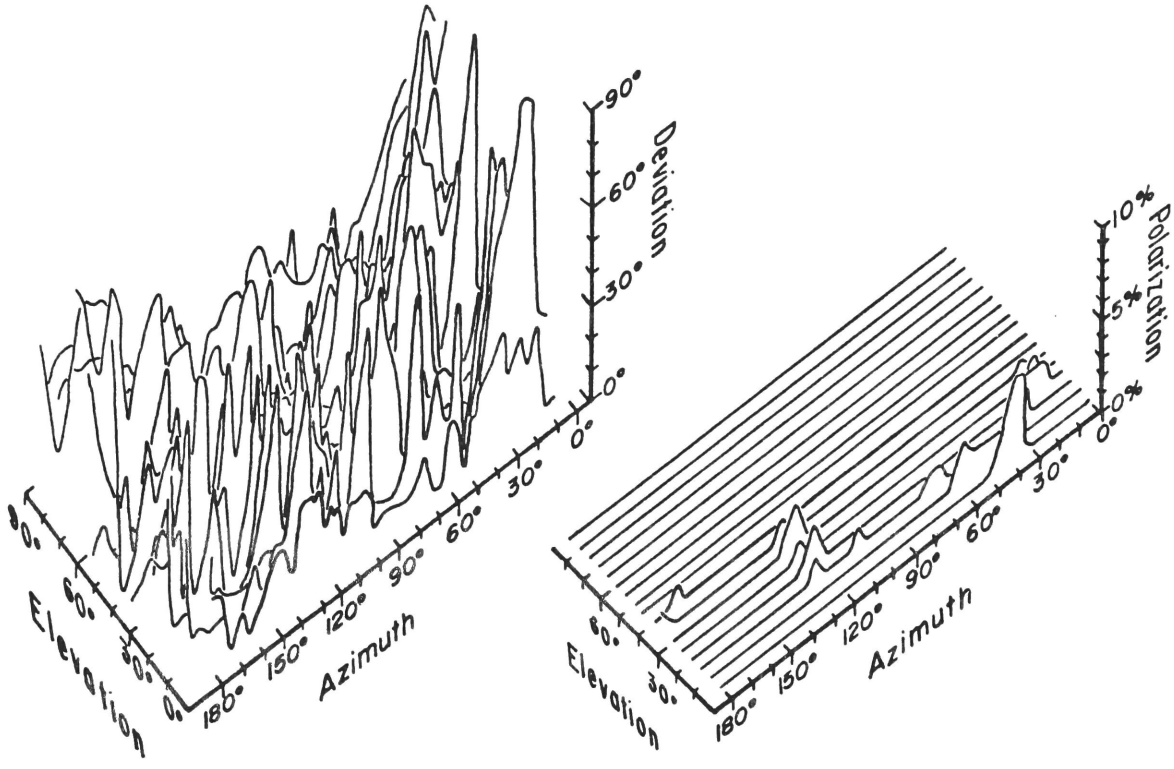

Figure III-11. Absolute per cent polarization and deviation of E-vector orientation for a completely overcast sky measured at 350 nm.
As summarized by this representative example of data taken at 350 nm., when the sky was completely overcast (sun's disc never visible during measurements) the E-vector orientation diverged widely from theoretical expectations. The fluctuations are probably not significant anywhere. Large deviations occurred regardless of the wavelengths used for the measurements. At the same time, the measured per cent polarization was virtually zero over the entire sky, as shown in the accompanying plot of absolute per cent polarization as a function of position on the sky vault.

under both conditions. When the sun's disc was visible (for data up to 75° in elevation), the deviation of measured E-vector orientation from theory was quite small far from the sun, even though the per cent polarization reached only 12%. When, however, the sun was obscured by heavy clouds during the data collection for elevations 80°-85°, the deviations

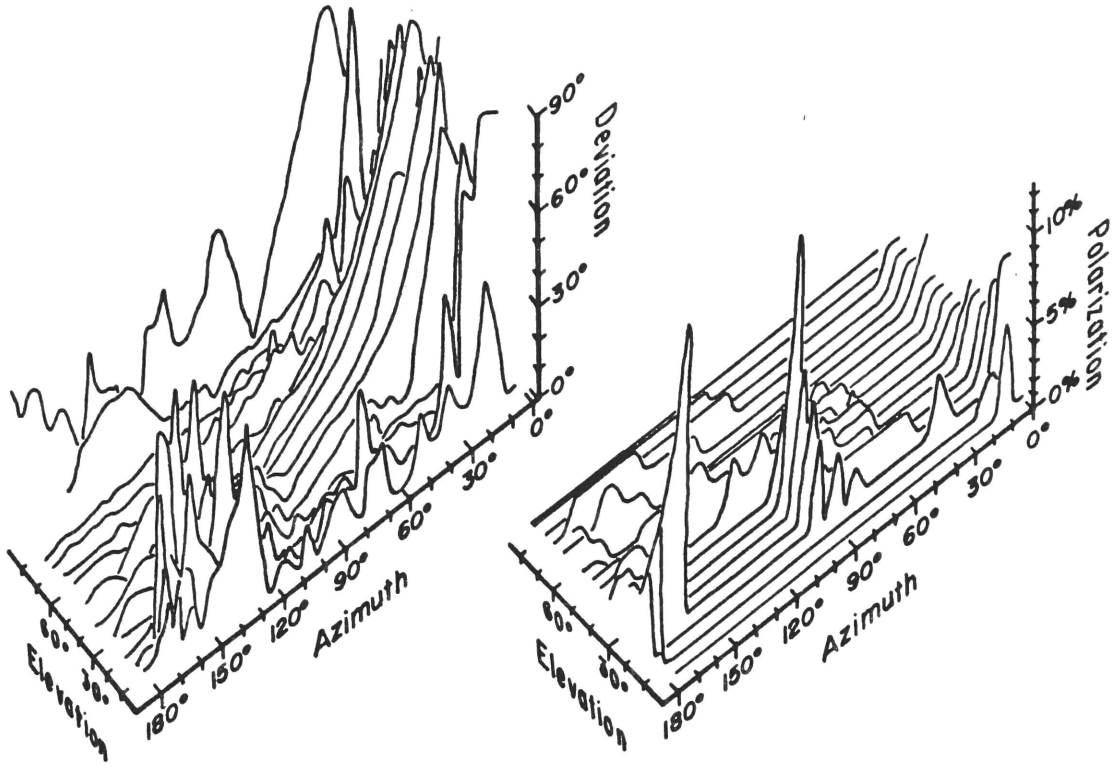

Figure III-12. Absolute per cent polarization and deviation of E-vector orientation for an overcast sky with the sun's disc barely visible measured at 350 nm.

When the sun's disc was just visible through cloud cover, some appropriate polarization patterns existed, as illustrated by this example for data at 350 nm. During data collection, the sun's disc was visible until points in the sky with elevation 80°-85° were measured. Notice that far from the sun the E-vector orientation is close to theoretical expectations. When the sun disappeared behind clouds, the E-vector deviation dramatically increased as the per cent polarization decreased. I frequently observed that as long as some direct solar rays were present (due to breaks or thin sections in the cloud cover), the observed E-vector orientation was close to that predicted by Rayleigh theory. At the same time, the per cent polarization, although generally very low, was greatest in those sky areas where the E-vector existed in an appropriate form. Conversely, where the E-vector diverged greatly, careful analysis of the results of a series of measurements revealed no clear wavelength dependence, although frequently the per cent polarization was somewhat higher in the UV. However, well-developed, enhanced polarization patterns in the UV were generally measured against isolated cumulus clouds, as discussed in the text.

increased tremendously.

The agreement of observed E-vector orientation with theoretical expectations can be shown in another way: for overcast conditions, the per cent polarization was measured to be virtually zero, except in those parts of the sky which exhibited E-vector orientations generally adequately predicted by theory. Although all examples of partial Rayleigh patterns were carefully examined to determine whether the pattern was better at any wavelength measured, no clear relationships could be discerned. True simultaneous measurements as a function of wavelength were not available, however, and thus sky conditions changed in various unpredictable ways between measurements. Frequently, however, the per cent polarization was slighter greater at UV wavelengths than at other, longer wavelengths.

In summary, the results of my measurements of E-vector orientation confirm that this polarization parameter is relatively insensitive to atmospheric conditions. For clear sky, the longer the wavelength, the larger the area of sky for which the observed E-vector orientation matches the theoretical predictions well. For uniformly overcast skies, the E-vector orientation appears equally disturbed for all wavelengths. For uneven overcast, especially when the sun's disc is visible, substantial areas of the sky often possess appropriate E-vector orientations, although the degree of polarization is ordinarily very low. Frequently, the per cent polarization is slightly greater at UV wavelengths than at longer wavelengths, though not always clearly so.

6. Discussion.

My measurements of skylight polarization parameters provide extensive data about those features of skylight radiation which might be used as orientation cues by animals. Since Sekera (1951,1956,1957a,b), Hansen and Travis (1974), and Coulson (1974) have published comprehensive reviews of many of the physical aspects of skylight polarization and since Waterman (1979) has just summarized the present state of understanding of many biological aspects of animal polarization sensitivity, I will concentrate here on three main aspects. First, how do my data compare with those previously reported in the literature? This is relatively difficult to determine since, as far as we know, I am the first investigator to measure such extensive areas of the sky in a short time at those UV wavelengths (350 nm) known to be important in the orientation of a number of organisms, including the honey bee. Second, what are the possible physical bases of the measured divergences of skylight patterns from the predictions of simple Rayleigh scattering? Third, how reliable would the observed skylight parameters be if they were used as orientation cues, and especially, might there be advantages in using specific parameters?

6.1 Radiance and spectral distribution.

6.1.1 Clear Sky My observations demonstrate that the radiance and spectral distribution of a clear sky depend on the angular distance of the part of the sky observed from both the sun and zenith. This characteristic of clear sky radiation arises mainly from three interacting factors: Rayleigh scattering from air molecules, aerosol scattering from large

particles, and the great increase in optical thickness of the atmosphere close to the horizon.

Specifically, light coming from the sky around the sun arises from the mainly forward scattering of direct sunlight by aerosols. This process, rather than Rayleigh scattering, creates the bright aureole around the sun. Like previous investigators (e.g., Coulson, 1971), I found that the solar aureole was the dominant contribution by aerosols to the radiance of the clear sky. The fact that I always observed an aureole indicates that aerosol particles were never entirely absent from even the clearest atmosphere in central New Jersey during the summer. The usual white color of the aureole demonstrates that this type of scattering does not depend strongly on the wavelength of light. Such a lack of wavelength dependence is expected because of the relatively large size of the scattering particles with respect to UV and visible wavelengths. For areas of the sky farther from the sun, the aerosol scattering no longer contributes much sky radiance and Rayleigh scattering from air molecules predominates. This qualitatively explains my observation that skylight is increasingly rich in small wavelengths for points of the sky further from the sun, but also decreases in total radiance up to 90° from the sun. On the basis of simple Rayleigh theory, points in the sky 90° from the sun should have half the radiance of the sky measured near the sun. Because of the enormous flux from the aureole, however, my measurements never even remotely approximated this prediction.

A third major contribution to the radiance and spectral characteristics of skylight is the interaction of light with optically thick parts of the atmosphere. Briefly, skylight reaching an observer from

directions close to the horizon must travel through extremely thick layers of air. Everywhere along this path, short-wavelength photons are scattered differentially out of the beam. Thus, longer-wavelength photons reaching the observer tend to have been scattered a great distance from the observer, while short wavelengths arise from scattering relatively close by. The whitish color at the horizon of a clear sky is explained by the fact that for such extremely thick atmospheric paths, long and short wavelengths contribute to the beam in almost the same proportion as they occur in the incident sunlight, and as a result the sky appears white. When any part of such long atmospheric paths becomes shaded from direct sunlight, as by patchy clouds, dramatic color effects can arise from the relative distribution of photons left in the beam.[4] Areas of the sky at high elevations are different, however, because atmospheric paths are relatively short, so that only small amounts of long-wavelength photons are scattered into the beam. Thus the sky appears to be a saturated blue, relatively poor in long-wavelength photons. The characteristics of scattering and the structure of the atmosphere allow for equal contributions of long- and short-wavelength flux only for paths close to the horizon, and calculation of the dependence of dominant spectral flux on the length of the path through the atmosphere provides some interesting cases.

The very high probability that short wavelengths will scatter explains my observation that the simple geometrical pattern predicted by the theory of primary Rayleigh scattering was best approximated by long wavelengths, which possess the smallest component of multiple scattering

4. Minnaert, 1954; pp. 248 ff., advances similar arguments and discusses some unusual cases.

to dilute the pattern. The same factor makes the short-wavelength sky radiance much more uniform than for longer wavelengths. Washed-out short-wavelength patterns have been recorded by many observers (reviewed by Fritz, 1966).

The chief characteristic of the radiance and spectral distribution of even the clearest sky I observed was variability. Profound changes occurred over even short periods of time, especially just preceding cloud formation. I can confirm the discussion of Rozenberg (1960; pp. 5 ff.) and also the great divergences of measured sky radiance from theory which have even been recorded by investigators from airplanes at high altitudes where the aerosol contributions are greatly reduced. For example, the results of measurements of sky radiance obtained at 18,000 feet by Tousey and Hulburt (1947) and up to 38,000 feet by Packer and Lock (1951) demonstrate that only points in the sky far from the sun possess radiances close to theoretical expectations and then only after corrections for surface reflections and multiple scattering.

Because they depend so strongly on the vagaries of the atmosphere, I conclude that the magnitude of sky radiance and spectral distribution per se would not constitute good orientation cues. The relative relationships of very large areas of the sky may, however, be useful, since they generally match qualitatively the simple geometry of Rayleigh scattering. But the necessity of using large areas of the sky to make these determinations seems to me to be a rather severe constraint on the general utility of these characteristics as cues, and behavioral experiments clearly show that large areas are not essential for animal orientation.

6.1.2 Overcast sky. When the sky was partially or heavily covered by clouds, the measured radiance (typically only about 10% that of clear days) generally agreed even less well with the predictions of Rayleigh scattering. Since partly cloudy skies are so difficult to specify, I can only compare my results with other records of radiance for completely overcast conditions. Even though none of my measurements corresponded to "uniform" overcast, my data seem typical (e.g., compared to review by Walsh, 1960 pp. 44 ff.; Coulson, 1971). In all cases, the radiance distribution is symmetrical around the brightest point in the sky--the zenith--and at the horizon radiance is generally only about half of the zenith value. This characteristic radiance distribution (reversed when compared to clear sky) is easily understood qualitatively when we consider that the minimum optical density of an overcast sky occurs toward the zenith, while a maximum is towards the horizon. I found no obvious wavelength dependence in overcast radiance distribution, but because I only measured in three narrow wavelength bands, I cannot be sure that this is true in general.

While the radiance distribution of a cloudy sky is greatly different from the simple geometry expected from Rayleigh scattering, until now it was not clear whether the sun itself is entirely obliterated. Obviously, since the relative position of the sun is a central cue for the orientation of many animals, the answer to this question is important. That the sun may not, in fact, be completely hidden was suggested by the results of the behavioral experiments correlated with physical measurements performed by von Frisch et al. (1960, reviewed von Frisch, 1967; pp. 366 ff.). They concluded that for at least some types of complete

overcast (uniform altostratus), honey bees were able to see and orient to the sun's disc through the clouds. Strangely, the bees seemed to be able to do this only at UV wavelengths.

6.1.2.1 Is the sun visible under overcast? Von Frisch's studies were prompted by his observations that the communicative dances of honey bees were still well oriented even under complete overcast (von Frisch 1948; 1967; pp. 366 ff.). By transporting bees to unfamiliar territory, he sought to determine whether the bees could orient themselves independently of local landmarks. Even though von Frisch and his colleagues could not see the solar disc themselves, both forager and recruit bees were still well oriented. However, if a mountain obscured the sun, the bees were said to have been disoriented. For more direct orientation experiments, they used honey bees dancing on horizontal surfaces. Deprived of gravity, to which they normally reference their dances, the bees need to see some solar orientation cues directly. Von Frisch et al. reported that the bees were correctly oriented only when they could see that part of the clouded sky, never less than 15°, behind which the sun stood. This ability was said to depend on UV light, because only when UV wavelengths were removed from the beam did the bees become incorrectly oriented.

To determine whether the sun might be differentially visible at UV wavelengths, von Frisch and his colleagues made UV photographic measurements of the clouded sky while simultaneously observing the precision of orientation of horizontal honey bee dances. Generally, their data demonstrated that as long as there was an increase in radiance around the sun (average of only 5%), the bees could still orient themselves. When the

dances were disoriented, photographic analysis of the sky demonstrated no increase in radiance around the sun's position. In von Frisch's opinion, differential transmission of UV light through the clouds around the sun was the basis of the bees' perception. However, a later series of similar measurements were viewed by von Frisch as negative, since they demonstrated UV radiance differences around the sun of less that 2% (reviewed by von Frisch, 1967; p. 377). Because the bees were still oriented, von Frisch speculated that since the cloud cover was not uniform in these cases the bees might have been using other cues, such as bright patches in the sky. This is a very tenuous argument at best, but no better explanation comes to mind.

None of my radiance measurements during overcast, taken while I observed well-oriented vertical honey bee dances, clearly demonstrated the position of the sun. There are several differences between the techniques of the measurements, however, which may prevent them from being directly comparable to the data of von Frisch et al. (1960). First, their data suggested increased UV radiances only for very small areas of the sky around the sun: typically about 3°-5°. It is possible that my 5° measurements were too coarse to determine the solar disc. But this is unlikely because I specifically tested for this possibility in several cases by measuring the sky manually at very small angular intervals with only negative results. A second possible source of divergence between the two sets of data is that von Frisch's measurements correspond only to "uniform and not very heavy" cloud cover; and although I tried to measure the same, I possibly never duplicated their sky conditions exactly. Third, the typically small changes in radiance measured by von Frisch may

not have been obvious in my data. Careful analysis, though, failed to show any such small changes, and the linearity of my instrument combined with my methods should have allowed me to detect differences of less than 1%. A fourth reason may constitute a substantial methodological problem: I could only observe vertical dances in the hive and so can not be absolutely certain that the bees were not using some other cue to determine direction. This is important because the bees were not transported to an unfamiliar area and therefore may have used their knowledge of local landmarks to orient themselves.

Unfortunately, there seems to be little independent material in the literature with which to consider further the problem of the sun behind cloud cover. The only notable example of which I am aware is part of a series of measurements by Coulson (1971) of radiation patterns produced in a polluted atmosphere. Because UV wavelengths are important promoters of photochemical reactions, he fortunately included them in his series of narrow spectral measurements, which were centered on 320, 365, 451, 552, 652, and 795 nm. The results of his radiance measurements for uniform overcast stratus sky are very similar to mine, and show the characteristic darkening of the horizon, with the zenith generally showing the greatest radiance. He found that only for substantial cloud thinning did radiance increase in the solar aureole, and over the wavelength range measured, little wavelength dependence was exhibited. In fact, unlike von Frisch's observations, Coulson found that when the sun was instrumentally visible, the increase in radiance around the sun (contrast) was more pronounced at <u>longer</u> wavelengths. For my measurements taken when the sun was barely visible, careful examination confirmed this wavelength

characteristic of the transmitted radiation field. Coulson points out that this is probably not a result of the transmission properties of the clouds. Instead, he suggests that the radiation entering the tops of the clouds is much more directional at longer than at shorter wavelengths, so that the difference between the aureole and the rest of the sky was maximized at longer wavelengths. Conversely, shorter wavelengths have much larger components of multiple scattering which produce a more extensive radiance distribution from the clear sky above the clouds minimizing the contrast of the aureole with the rest of the sky.

What about physical aspects of wavelength-specific differences in the transmission of light through clouds? This is an exceedingly complicated field, since the optics of a cloudy sky are much more varied than those of a clear sky, and also are difficult to measure. For example, because of their great optical thickness, light penetrating clouds usually has undergone multiple scattering and this adds a large diffuse component to sky radiance. Bauer (1964) has compiled a survey of general aspects of light scattering in clouds, which is quite useful even though limited to infrared wavelengths.

As McCartney (1975; p. 299) points out, any cloud or fog selectively scatters at some wavelength (dependent on its droplet size distribution). Since cloud water droplets are always much larger than the wavelength of light, fundamental physical principles predict that the scattering for UV, visible, and near infrared would be independent of wavelength (van de Hulst, 1957; p. 423). The problem can not be resolved easily, however, because more sophisticated theoretical models, such as those by Deirmendjian (1969) predict that the scattering of visible light very

slightly decreases with decreasing wavelength. In addition, theory predicts that there would be strong forward scattering which would decrease with increasing wavelength (as reviewed in McCartney, 1976; pp. 303 ff.), and both visible and UV wavelengths are expected to produce strong aureoles.

The optical properties of clouds have not yet been extensively measured. In addition, those studies which do exist have frequently concentrated only on infrared rather than on visible wavelengths. Although extensive data on the transmission of solar rays through clouds was collected by the early actinometrists, much of it seems unreliable today. One notable modern example is the study of Bocharov (cited by Fiegel'son, 1960; p. 51) who measured the spectral transmission of light through clouds and found that it was virtually independent of wavelength. However, he only measured at wavelengths as short as 500 nm. Many more measurements have been made on convenient ground fog. In general, investigators have found that short wavelengths are often attenuated slightly less than longer wavelengths (e.g., Arnulf et al., 1957; Eldridge, 1966; reviewed by McCartney, 1975; pp. 299 ff.)[5] But again, these depend strongly on the prevailing conditions during the measurements.

Several interesting related phenomena reported in the literature may be important. For example, under special circumstances a sharply defined solar disc without a perceptible aureole has been observed through clouds. This "sun effect," described by Deirmendjian (1969 a,b), occurs from a suppression of multiple scattering inside the cloud and makes the

5. This is not true of haze for which the transparency increases until it is almost complete for 10^4 nm (Arnulf et al., 1957).

sun appear to have about the same radiance as the surround. But this case does not depend strongly on wavelength, since the sun's disc appears essentially as white. There are, however, also instances of true wavelength-dependent transmission through clouds of very specific droplet size distributions. These cases give rise, for example, to observations of a blue sun or moon (Paul and Jones, 1951; Lothian, 1951; Porch et al., 1973). Perhaps von Frisch's measurements of the cloudy sky correspond to exceptional circumstances which are just right for UV wavelength transmission. But even though such special conditions have been observed, they are presumably quite rare and they seem unimportant on the whole to the orientation problem.

6.1.3 Summary for radiance measurements. In summary, even under the best conditions the aerosol content and optical depth of the atmosphere greatly disturbed the radiance patterns. In spite of this, large areas of the clear sky often have the qualitative geometry predicted by Rayleigh scattering. However, it is difficult to imagine even in these cases how small sections of the sky could be used to derive orientation cues, since their absolute values are much different from theory and are temporally variable. It seems clear that the radiance and spectral distribution of small areas of even clear sky would be of minimal use for deriving the sun's position. Furthermore, my results clearly indicate that bees ought not to be able to perceive the sun through an overcast at any wavelength, including the UV. I suspect that my honey bees were able to orient themselves under completely overcast conditions (sun's disc not instrumentally visible at UV or longer wavelengths) by relying on the relative position of landmarks or other non-solar cues. An attempt

should be made to duplicate von Frisch's remarkable behavioral evidence that bees can perceive the sun through uniform cloud cover since, assuming both sets of data are correct, the bees may have some more subtle orientation strategy than we suppose at present.

6.2 Degree of polarization.

6.2.1 Clear sky. For a Rayleigh atmosphere with primary scattering alone, the maximum polarization should be practically independent of wavelength and solar position and be located 90° from the sun, as described in Chapter II. In the real atmosphere, Coulson (1952) found that the polarization maximum reached its greatest value (never 100%) for both large and small solar zenith distances. A broad minimum occurred for solar zenith distances of 50°-60° and increased 1% for zenith angles greater than 80° and 4-5% for small zenith angles. Coulson's measurements also showed that the polarization maxima were less than 90° from the sun for small wavelengths and farther than 90° for longer wavelengths. The radiation parameters actually observed depend upon many optical effects (Coulson, 1974; pp. 450 ff.). Detailed theoretical calculations by Fraser (1955) showed that the location of the maximum polarization increasingly deviates from 90° from the sun with decreasing wavelength and should be as much as 5° off in the UV. Actual observations show that the deviations of the position of the maximum polarization at short wavelengths often exceed the predictions of theory, while those of longer wavelengths do not agree well either (Sekera, 1955; pp. 57 ff.).

When higher order scattering occurs, Sekera (1955; p. 59) has pointed out that for a pure Rayleigh (molecular) atmosphere the degree of polarization theoretically increases with increasing wavelength. His measurements of the natural sky demonstrated, however, that the maximum degree of polarization occurred at about 460 nm and decreased for both longer and shorter wavelengths. Extensive recent measurements by Coulson et al. (1974), collected at the Mauna Loa Observatory from an elevation of 3 km overlooking the ocean, showed a maximum degree of polarization between 500-600 nm. The better approximation of these results to the predictions of simple Rayleigh theory is not unexpected since the Coulson measurements were derived from much clearer sky than we (and most animals) are able to use. However, the results of measurements by Gehrels and Teska (1963) taken in the desert show that the maximum polarization (75%) occurred at about 550 nm. Finally, the results of theoretical considerations by de Bary and Bullrich (1964) show that the maximum can occur in any part of the visible spectrum, depending on the local conditions.

My measurements of degree of polarization generally compared better with the observations of Sekera: I found that the maximum polarization of the clear sky generally occurred for the 500 nm data. But since I employed only widely separated, narrow spectral bands, I cannot be specific about this point. I found, like other researchers, however, that for clear sky the degree of polarization at UV wavelengths was always much lower than that for longer wavelengths.

6.2.2 Factors of deviation. Specific factors which contribute to the deviation of degree of polarization from the Rayleigh predictions are multiple scattering, molecular anisotropy, aerosol scattering, and reflection from the earth's surface. A comprehensive and outstanding theoretical and experimental study of sky radiation by Bullrich (1964) illustrates that the various phenomena of sky radiation can be understood only by a thorough understanding of these interrelated parameters. I therefore consider briefly here the physical influence of each of these factors on radiation from the clear sky.

Multiple scattering is mainly responsible for the observed highly wavelength-dependent magnitude of the degree of polarization, just as it is for the deviations of the radiance distribution. Multiple scattering decreases the degree of polarization because the light reaching an observer is a combination of both singly scattered and multiply scattered components. That is, multiply scattered photons entering an observer's eye can come from any direction and thus may possess scattering angles of any value. In contrast, direct sunlight or singly scattered radiation reaches the observer only from specific, well-defined directions. The variable scattering angle associated with multiple scattering means that both the degree of polarization and the E-vector orientation can be of any magnitude: the exact values are of a statistical nature. The precise contribution of multiple scattering to skylight parameters can be calculated exactly for a molecular atmosphere by an extension of the methods developed by Chandrasekhar (1950). Extensive calculations have been performed and tabulated by Coulson et al. (1960). Dave (1964) and de Bary and Bullrich (1964) have specifically compared the first few orders of

multiple to primary scattering components. They show that for a molecular atmosphere, over much of the sky multiple scattering usually has a different E-vector orientation than primary scattering and thus has components parallel to the scattering plane, and is called "negative" polarization (see also Strong, 1958; p. 108, and Coulson, 1974). Close to the sun or antisolar point, the multiply scattered components are more highly polarized than the primary and thus the E-vector is perpendicular to the predictions of simple Rayleigh scattering (i.e., perpendicular to the plane of the scattering angle).

If the primary scattered component equals the multiply scattered, the positive and negative polarization forms cancel each other, producing no net polarization. Such areas of the natural sky are called "neutral" points (see Coulson, 1974; pp. 449 ff.). Because the relative contribution of multiple scattering to the sky radiation increases with decreasing wavelength, the negative polarization usually extends to larger angles around the sun and antisun for smaller wavelengths and the neutral points are located farther from the sun or antisun. (Theoretically, in a few special cases it may not, as shown by de Bary and Bullrich, 1964.) The E-vector deviation data shown in Figure III-9, for example, show the effect of multiple scattering around the sun by the existence of the deviant negative polarization. Even for the clearest sky, I always measured a larger angular extent of these areas for small wavelengths. My polarimeter could easily and accurately measure the position of the neutral points, and I likewise found these to have the largest angular deviation from the sun for UV wavelengths. On the basis of these results, I conclude that if total area of the sky available for orientation is

important, animals should use longer wavelengths as cues.

Although Rayleigh theory predicts two neutral points--one in the direction of the sun and the other in the antisolar direction--the effects of multiple scattering move them from the expected positions, although they do generally remain in the solar or antisolar vertical. Occasionally, neutral points have been observed at other places in the sky. Such exceptional circumstances can arise, for example, by directional reflection of sunlight from underlying surfaces such as bodies of water (e.g., Soret, 1888). Since the behavior of the neutral points is intimately involved with prevailing atmospheric conditions, comprehensive studies of neutral point behavior are numerous. The point above the antisun (the "Arago" neutral point) has been particularly studied since it is easily observed by visual methods. Interesting summaries are given by Sekera (1955,1957a), Coulson (1974), and Neuberger (1940, 1951, 1957).

A small source of the deviation of the measured degree of polarization of natural skylight from theoretical expectations is the fact that air molecules are not completely electrically neutral and therefore do not satisfy a principal assumption of simple Rayleigh theory. Adjustments to this non-ideal behavior can be made easily by introducing a "depolarization" factor amounting to 6%.

Scattering from aerosols is responsible for depolarizing a larger amount of skylight, and disturbs the expected Rayleigh spectral and radiance distributions of the atmosphere profoundly. These large particles, which occur mainly in the lowest levels of the atmosphere and usually make the sky appear grey, are frequently the limiting factor in visibil-

ity. Their distribution may be easily and quickly changed by a number of factors and thus constitute a major source of "noise" in the sky patterns. Sekera (1957b), for example, noted that a rapid change in wind resulted in fluctuations of measured per cent polarization as large as 30% over very short times (and absolute deviations of 50-60%). Coulson et al. (1974) have made similar observations. It is important to note that modern industrial activity is not the sole source of the highly variable particulate suspensions in the atmosphere. Large forests are perpetually shrouded in "heat haze" consisting of tars and resins formed by photoreactions of hydrocarbons released by leaves (Went, 1955). Such hazes are common, for example, in tropical rain forests--just the environment in which honey bees are thought to have evolved (Wilson, 1971; p.266). Thus the optically disruptive characteristics of aerosols do not constitute orientation problems of recent origin.

Three further optical properties of aerosols are worth considering: 1) they tend to shift the neutral points closer to the sun, in contrast to the effects of multiple scattering (Coulson, 1971; 1974; p 452). 2) The small amounts of elliptical polarization produced in the atmosphere arise from the multiple scattering of linearly polarized light from aerosols. Dave (1970) has calculated that under some conditions the ellipticity of skylight may reach 4%. 3) My observations of anomalously high degrees of polarization at low elevations in the sky for scattering angles greater than 100° may be explained in part by the fact that scattering from aerosols often has a pronounced minimum for these very scattering angles (see summary in McCartney, 1975). Such an area of the sky would therefore have less aerosol-produced flux to depolarize the

skylight and the radiation observed would be closer to the predictions of Rayleigh scattering. This idea is especially compelling because my observations of these anomalous phenomena seemed correlated with the presence of very obvious, thick layers of haze along the horizon. Because the concentration of aerosols greatly increases close to ground level, aerosol scattering probably also accounts for my observations that the per cent polarization of points in the sky 90° from the sun decreases with increasing zenith distance, and confirm a large series of measurements by Russian workers which have been partially summarized by Stamov (1970).

One interesting aspect of the behavior of particulate suspensions is that they often act as condensation nuclei and thus their size depends on humidity, which is frequently a characteristic of a particular air mass. For example, sometimes the first visible indication of the approach of warm air is that the sky becomes much whiter as the size of the aerosols greatly increases and Rayleigh scattering of sunlight gives way to aerosol scattering. In this sense, the blueness of the sky can be a measure of atmospheric turbidity (Neuberger and Neuberger, 1943). Van de Hulst (1957; pp. 420 ff.) has reviewed the basic physics of some of these situations. At the same time, the positions of the neutral points of the sky frequently move drastically with atmospheric changes (Neuberger, 1951). I have observed these phenomena often during my measurements and have wondered whether the form of the skylight polarization patterns might also occasionally be useful to animals as signs of imminent weather changes. Indeed, Sekera (1955; p. 64) reported that occasionally skylight polarization patterns fluctuate greatly long before any clouds

actually appear. It is interesting to note in this regard that honey bees are said to sense weather changes well in advance, and to adjust their foraging behavior accordingly (von Frisch, 1967; p. 245).

A final consideration in this greatly simplified discussion of possible sources of deviation from theory in the degree of polarization, is the effect of reflection from the earth's surface by which light is rescattered by the atmosphere back towards an observer. Coulson et al. (1974; pp. 40 ff.) discuss some of the possible geometries. One important factor is that highly reflecting surfaces increase the contribution of multiple scattering to the total sky radiation. For example, de Bary and Bullrich (1964) point out that without surface reflection the multiply scattered component of the entire sky is about 1.5 times that of the primary component. For high surface reflectance, the multiply scattered component increases to 4 times the primary, especially for the sky close to the horizon. Although much light is reflected diffusely and thus only depolarizes the sky patterns (Chandrasekhar, 1950; Chandrasekhar and Elbert, 1954; Gehrels, 1962; Coulson 1968), under some conditions, e.g., reflection from water or soil, strong polarization of light can occur (Soret, 1888; Jensen, 1942; Sekera, 1961; Chen and Roa, 1968; Roa and Chen, 1969). It is interesting to note that theoretical calculations by Sekera (1961) for reflection of light from the surface of the sea predict an increasing deviation of per cent polarization for longer wavelengths. Other interesting studies have been reported by Coulson et al. (1965), Coulson (1966), and Fernald et al. (1969).

Other wavelength dependent effects of reflection have been demonstrated in the measurements of per cent polarization by Gehrels and Teska

(1963). Their results show a decrease in the maximum polarization for longer wavelengths, especially the near-infrared, and is explained by differential reflection from the ground, especially from vegetation, of long wavelengths. For example, just before sunrise the per cent polarization in infrared was 84%, which decreased to 64% in only twenty minutes. Unfortunately, the physics of reflection is understood only for a few idealized situations (see Coulson, 1974; pp. 463 ff.), and how the sky patterns are changed is known even less. Thus, the general characteristics of this potentially important source of deviations from Rayleigh theory are relatively uncertain.

One important parameter not yet investigated is how E-vector orientation changes for certain types of reflection. Studies such as Coulson's (1968), however, which concentrate largely on measuring reflected light without regard to polarization may still be useful because in general the greater the reflectance from a surface, the less polarization is produced and vice versa (the 'Umov' effect). It is interesting to note in this regard that since short-wavelength light is reflected only poorly by many natural surfaces, the degree of polarization may be relatively large. But since surface-reflected flux is normally so small compared to the sky-produced flux, the effects are probably often only minor. This topic deserves detailed experimental investigation.

6.2.3 Summary of degree of polarization measurements. The major conclusion from my per cent polarization data is that over a variety of environmental conditions the quality and magnitude of the patterns in the natural sky are never very close to theory, but are best at relatively

long wavelengths and worst at short ones. That the maximum polarization occurs for moderate visible wavelengths can be understood by considering the effects of very great multiple scattering in the UV and high reflectivity of long red wavelengths by the ground, especially vegetation. To complicate matters, the magnitude of these parameters often changes dramatically in a very short time, depending on local conditions.

6.3 E-vector orientation.

My repeated observation of the relative insensitivity of E-vector orientation to disturbing atmospheric factors is expected from the basic physical characteristics of atmospheric scattering. Since the E-vector orientation depends only on the plane of the scattering angle, any primary-scattered radiation must possess the appropriate E-vector orientation. Processes which greatly disturb other Rayleigh parameters--such as multiple scattering and diffuse reflection--can produce scattering angles of practically all magnitudes and orientations. For highly polarized parts of the sky, multiple scattering is ordinarily of such small radiance that it merely 'dilutes' the simple geometric patterns established by primary scattering, but does not greatly affect the net E-vector orientation. Conversely, as already noted, for those areas of the sky in which the degree of polarization of primary scattering is very small, (e.g., close to the sun and antisolar point), the Rayleigh scattering pattern is overpowered and slight amounts of negative polarization (defined above) can be observed.

My observations of the wavelength dependence of relatively small E-vector deviations are explained by a multiply scattered component. Thus,

my observations that increasing light haze produces greater deviations, especially in the UV, are not surprising, since any atmospheric condition which increases multiple scattering will also tend to increase the magnitude of the deviation of E-vector as a function of wavelength. These observations agree well, qualitatively, with calculations of Rayleigh scattering (including multiple scattering) derived by Coulson et al. (1960) who present extensive tabulations of the Stokes vectors for selected points in the sky. In addition, theoretical data for multiple scattering have been calculated by Dave (1964) for a molecular atmosphere and were more extensively compared to the predictions of single scattering by de Bary and Bullrich (1964). As expected, for points in the sky outside of the solar vertical they found that multiple scattering most affected the E-vector orientation of short wavelengths, which deviated as much as 13° (at 371 nm) for a specific elevation of the sun from the predictions of primary scattering. Similar comparisons at 644 nm showed maximum deviations of only 5°. De Bary and Bullrich discussed the expected relative magnitudes of small deviations for different parts of the sky and should be consulted for further details. The results of my measurements are qualitatively the same and constitute experimental confirmation. It is essential to realize that even these small E-vector deviations can produce large errors if used in a strict geometrical orientation system to locate the sun. For example, these errors would affect a forager's ability to return to her hive, and would cause dances to indicate locations far from the actual goal.

In considering the accuracy of E-vector orientation possible for a animal, we must look not only at how well each individual point in the

sky matches primary theory by also at how extensive usable polarization patterns are in the natural sky. As discussed above, the sharply increasing proportion of multiply scattered light at shorter wavelengths means that appropriate E-vector patterns are most extensive at longer wavelengths and least in the UV.

6.3.1 Overcast sky. The inappropriate patterns observed on completely overcast days are understandable considering that the great optical density of clouds makes it highly probable that all skylight is multiply scattered when it emerges. Since virtually no direct sunlight exists to establish primary Rayleigh patterns, the resulting range of scattering planes produced by multiple scattering means that the light is thoroughly depolarized.[6]

The areas of the sky with appropriate primary E-vector patterns which can be measured on days when the solar disc is visible depend on how much direct sunlight penetrates the clouds or passes through holes and scatters from the air beneath. I expect that only in exceptional circumstances would the polarization patterns produced in the atmosphere above the clouds be transmitted through even relatively thin sections of cloud cover.

Coulson (1971) has also collected some sky measurements under marginal overcast conditions. As far as I know, there are no other reliable measurements similar to these available in the literature. Under com-

6. However, an anomalously high degree of polarization is sometimes seen. For example, Waterman reports (in Sekera, 1961) that he has observed highly polarized light with a horizontal E-vector orientation near the horizon on completely overcast days.

plete overcast, Coulson measured very small amounts (less than 1%) of positive polarization, which compares very well with my observations. He found that as cloud thickness decreased, the usual patterns of the clear sky--including even neutral points--started to emerge from the virtually unpolarized background. When the solar disc was visible through the cloud cover, he measured 4%-6% polarization. My measurements under overcast gave similar results, and so constitute important verification. However, Coulson's measurements led him to conclude that the sky patterns depend little on wavelength under these circumstances.

There are, however, other minor divergences between Coulson's observations and mine which may be partially explained by methodological differences. First, Coulson noted that the sun's position was obvious in the radiance measurements before detectable polarization features emerged. Since my measurements were of half the sky, I probably never duplicated exactly the conditions pertaining to his measurements. He was able to continuously monitor a much smaller range of skypoints since he concentrated on the plane of the solar vertical. Second, Coulson did not specifically examine whether the E-vector orientation of the weak polarization patterns matched theoretical expectations. Third, he concentrated most of his measurements in the UV and thus had very few observations at long wavelengths from which to compare wavelength characteristics. On the other hand, my measurements required substantial amounts of time to acquire and I was not able, in general, to compare sky conditions directly on the basis of wavelength. In view of the possible importance of these different factors, the details of overcast versus marginally overcast skies should be more systematically investigated.

6.4 Which cues should animals use?

Considering the results of my sky measurements and other factors discussed above, which skylight parameters would constitute the best cues for orientation? This problem depends on a number of variables. One is how large a part of the sky is available to animals: the requirements for larger areas seem much less stringent than for smaller ones. For example, considering the results of radiance, spectral distribution, and degree of polarization measurements for clear sky, the patterns I measured for large areas of the sky were clearly related to the sun's position. Such cues presumably could be used straightforwardly for orientation. In these cases, numerical deviations of these patterns from the predictions of simple Rayleigh theory might not constitute a severe problem since even if the patterns of skylight polarization over the entire sky are degraded, the obvious sun-related patterns still exist in a "weaker" form. But if only restricted views of the sky are available, a situation with which animals must often deal, deviations in magnitude can constitute a very serious problem in orientation since it is then impossible to determine the relationship of the area of the sky viewed to the entire pattern. For example, how could an observer know whether the particular degree of polarization measured for a small area of the sky corresponded to a part close to the sun for clear sky or further away from the sun under poorer atmospheric conditions? Obviously, similar problems exist for radiance and spectral distributions. A severe problem for E-vector orientation may also exist since any analytical calculation will produce errors due to the usual small deviations from theory. In sum, the values of polarization characteristics arising for non-ideal

conditions cannot be used in any orientation system based on theoretical scattering geometry without introducing serious errors (see Chapter II).

6.4.1 Are corrections for divergences possible? Is it possible to use characteristics observable in the sky to correct somehow for the non-ideal nature of the sky patterns? Pyaskovskaya-Fesenkova (1958; 1960) has developed and Stamov (1970) has extended the idea that the magnitude of the maximum degree of polarization may be a useful index of the effects of all divergent atmospheric factors on the sky patterns. Using a large collection of sky measurements (mainly visual) along a circle of elevation including the sun (an almucantar), these Russian investigators empirically determined that the maximum polarization actually observed in the sky could adequately and simply predict the magnitude of the polarization for other parts of the sky by using a modified Rayleigh theory. It is interesting that the quality of fit of the relationships seems quite independent of general atmospheric conditions, even though the magnitude of the maximum polarization itself depends greatly on prevailing conditions. (Other investigators have attempted similar empirical fits with varying degrees of success--e.g., Coulson et al., 1974; pp. 30 ff.)

With the empirical formula of Stamov (1970), I examined my data on degree of polarization and found that for areas of the sky far from the sun and horizon, the predictions agreed only fairly well with the measured values. However, even these fairly close agreements would give rise to large errors if used to determine the relative geometry of the sun by geometry. Near the sun and the horizon, the deviations of measured values from the predictions of the empirical equation were generally very large.

Another factor seems important in determining whether skylight polarization parameters could be used in an analytical orientation mechanism by appropriate corrections: large areas of the sky would have to be measured in order to determine the normalization parameters. Again, such a requirement would considerably reduce the usefulness of such an orientation system. In addition, the frequent variations due to changes in prevailing atmospheric conditions would require a continuous recalibration. On the basis of physical considerations alone, I doubt that a normalization scheme could be successfully employed by animals in their orientation.

6.4.2 Importance of skylight parameters in animal orientation. Experiments using artificially produced polarization stimuli have demonstrated that for honey bees (von Frisch, 1967; pp. 387 ff.; von Helversen and Edrich, 1974; Edrich and von Helversen, 1976; Rossel et al, 1978; Chapter V) and ants (Duelli and Wehner, 1975) the absolute radiation parameters such as radiance, degree of polarization, and spectral distribution are of minor importance over a wide range of magnitudes. The results of my measurements show that this skylight parameter is stable over a wide range of atmospheric conditions and, for large areas of the sky, it is acceptably close to the predictions of primary Rayleigh scattering theory, and may, therefore, constitute a "best" parameter. One contributing factor is that the largest divergences of the E-vector pattern occur only relatively near the sun and antisun where the degree of polarization is below the known perceptual thresholds of animals so far studied. Thus, not only are animals unlikely to be confused by these anomalous patterns since they do not perceive them, but

these areas of the sky are often so close to the sun that other cues, such as radiance, would reliably indicate the sun's position. However, the small deviations measured (which are a function of atmospheric conditions) would constitute a limit on the precision obtainable by their use. I therefore suspect that bees may not use a strict analytic method for reducing polarization information. In this regard it is interesting to note that Rossel et al. (1978) suggest that their behavioral data could be accounted for by a general, approximate rule for dealing with sky information. However, their rule seems often to be less precise than the dance orientation of bees, and their supporting data do not completely agree with those reported in Chapter V. Further experiments will be necessary to determine the biological details. In any case, my measurements greatly reinforce von Frisch's physical reasoning that honey bee polarization orientation should depend primarily on E-vector orientation alone.

6.5 Why should animals use the UV?

The question of why short, UV wavelengths are most important for honey bee polarization orientation still remains to be answered. Radiation characteristics of a clear sky cannot be the reason since geometrical information in the UV is generally worse than in longer wavelengths, especially in terms of degree of polarization, stability of E-vector orientation, and the spatial extent of sky patterns. In fact, considering these factors it seems obvious that detection systems should be limited to longer wavelengths. The fact that animals are sensitive to polarization only in narrow, short-wavelength spectral bands strongly

suggests, though, that for some reason longer wavelengths are less useful. One possible factor, already mentioned above, is that by using UV wavelengths, an animal would be fairly sure to analyze the sky and not other polarization patterns such as those generated by reflection. My behavioral experiments (reported in Chapter V) give some support to this idea and illustrate that the spectral distribution of a light can be of great importance in determining how honey bees interpret a source. For example, a small, polarized light with long-wavelength components is used as if it is the sun: only if it is large enough will such a source be used as part of the polarized sky. The profound interaction of source size and wavelength distribution leads me to believe that there are probably other reasons underlying UV sensitivity than just making certain that the source of an orientation cue is properly identified.

A second possibility has been postulated by Wehner (1976): bees may use UV wavelengths for polarization orientation so that information can be analyzed <u>separately</u> from motion and form detection which are mediated by longer-wavelength receptors. While independent systems are attractive because in some sense they simplify central nervous system processing, I do not think such a "parsimonious" view is necessary. For example, the "honey guides" of flowers (reviewed by von Frisch, 1967; pp. 481 ff.) constitute one important form-detection role of UV receptors, and Stockhammer (1956) has shown that at least a crude type of form vision based on polarization exists for honey bees. In fact, it is not clear whether polarization orientation may itself be a type of form detecting system. Although experiments by Edrich and von Helversen (per. comm.) and the anatomical evidence of Menzel (per. comm.) give support to the idea of

separate visual functions mediated by specific receptor types, it seems likely that there are two classes of UV receptors, only one of which is dedicated to gathering information for polarization orientation. Obviously, it ought to have been just as easy for evolution to put blue- or green-sensitive pigments in this special class of cells, and, as we have seen, under clear-sky conditions, the information gathered by such a system would be slightly better. In addition, as discussed above, longer wavelengths can "mask" the effects of polarized UV light for bees if the source is small (Chapter V). Kien and Menzel (1977) have discovered color opponent neurons which may be important for this effect. Also, Kirschfeld (1973) has found similar "masking" aspects of long wavelengths in optomotor experiments. These results demonstrate that UV receptors are not always involved alone in polarization detection and orientation.

Another possible reason short wavelengths are used for orientation may be that when polarization sensitivity evolved in bees there were great advantages for using UV even for the clear sky. For example, the UV flux may have been much larger than it is today. Of course central to such a hypothesis is the idea that use of UV today constitutes no liability. Such ideas are hard to evaluate because of the the lack of good data about atmospheric and solar conditions of long ago.

I was intrigued by the results of my measurements under overcast skies. My usual observation was that when the sky was completely covered by heavy clouds only very small amounts of polarization were detected and the E-vector orientations were not correct, while appropriate E-vector patterns existed for large parts of the sky when the solar disc was just visible through the clouds. The difference between these two conditions

must depend mainly on the presence or absence of direct solar rays. Specifically, if some direct sunlight is incident on the air surrounding the observer, scattering occurs beneath the clouds, producing patterns with the same E-vector orientation seen in a clear atmosphere. The radiance, spectral distribution, and degree of polarization, however, are very different from those of a clear sky because a background of virtually unpolarized, diffuse light from the clouds exists on which the Rayleigh light is superimposed. This under-the-clouds effect is responsible for the small but reliable magnitudes of per cent polarization which may be measured, and the process is similar, in some respects, to what happens in areas of the sky close to the sun where the patterns due to Rayleigh scattering are superimposed on haze-scattered light, producing far smaller degrees of polarization than predicted by simply scattering theory. As a result of the background flux, the spectral distribution in both cases is much whiter.

In view of my data which indicate that the polarization patterns for some types of overcast contained higher per cent polarization in the UV compared to longer wavelengths, it is important to consider why wavelength effects might be expected under some circumstances. One possible factor may be that UV wavelengths are differentially transmitted through some types of clouds as reviewed in Waterman (1979), and as anyone who has been sunburned on a cloudy day will agree is a real possibility. If this is true, and if the directionality of the rays is largely preserved in the transmission process, one would expect a more extensive E-vector pattern in the UV as a result of the larger number of photons scattering from the air beneath the clouds. As discussed above, both my

example, as the sky becomes overcast the E-vector orientation in the UV probably remains stable the longest (even though it approximates theoretical geometry the least), which may be what Sekera meant in his communication to von Frisch (1967; p. 382) when he claimed that UV wavelengths were the least sensitive to "atmospheric disturbances." Coulson's (1971) measurements, however, lead him to comment that there were no obvious wavelength dependencies for diminishing overcast. But since he did not actually examine the precision of the E-vector orientation, more specific measurements must be made to evaluate this possibility in detail.

If my expectation that a very high probability of the scattering of UV may differentially establish patterns in short wavelengths is correct, one prediction is that under the proper geometrical conditions, measurable polarization patterns should exist against clouds when the sky near the sun is relatively clear. Again, if direct solar rays can illuminate at least some air between an observer and the cloud, polarized light geometrically related to the sun's position should be produced by scattering. This possibility was strongly suggested during the course of my measurements, since I was constantly impressed by the fact that isolated clouds rarely disturbed the patterns of E-vector orientation at that point in the sky to any great extent.

To test directly whether this idea is correct, and also to obtain measurements of degree of polarization as a function of wavelength for patterns produced by scattering from short optical paths, I pointed my polarimeter at a series of typical summer cumulus clouds. Because the instrument was stationary, direct comparison of the polarization parameters on the basis of wavelength was possible by quickly interchanging the

narrow-band interference filters. Unfortunately, all of my measurements were collected on days when large amounts of haze brightened the sky to a very unsaturated blue. Thus, I feel the results of my measurements do not correspond to optimum, clear sky conditions. Nevertheless they are very suggestive.

Typical measurements for a hazy summer sky are summarized in Table III-3, in which sky patterns measured against isolated clouds are compared to those from blue sky nearby. Clouds used for these data had an elevation of 35°-60°, a relative azimuth of 100°-150°, and were estimated to be about 2 km distant from the polarimeter. My results demonstrate several factors clearly. First, although the observed cloud radiances were always greater than for adjacent clear sky at all wavelengths, the cloud-reflected flux was still wavelength dependent. This loss of short wavelengths probably arises in the beam's transmission to and from the cloud, during which it differentially loses its short-wavelength photons because of scattering (e.g., Minnaert, 1954; p. 240; Feigl'son, 1966; p. 102).[8] Second, in all cases I could measure polarization patterns against the clouds, for which the measured E-vector orientation matched the predictions of Rayleigh scattering closely. Measured degree of polarization in these patterns was <u>greatest</u> for UV, least for red, and moderate for blue/blue-green, which differs greatly from measurements of the blue sky where UV wavelengths typically exhibit the <u>smallest</u> degree of polarization. The small levels of polarization measured for adjacent blue sky are indicative of the extent to which multiple scattering degraded the

8. Alternately, if clouds really are differentially transparent in the UV, a smaller proportion of UV light would be reflected from clouds towards the observer.

Table III-3. Average per cent polarization measured against 15 different small cumulus clouds at 35-60° elevation in the antisolar half of the sky, ratio of cloud radiance to nearby blue sky, and per cent polarization of the surrounding blue sky. These measurements were typical for very hazy summer days in 1977.

wavelength	per cent polarization ±10%	cloud/sky radiance ±2%	per cent polarization of sky
350 nm	10	1.2	17
500 nm	7	1.7	28
600 nm	6	2.7	24

sky patterns, as are the unexpectedly small differences between the cloud and sky radiances. I think that under better atmospheric conditions, UV patterns against clouds would possess even larger degrees of polarization. What these results mean for insects (if they could detect polarization at all wavelengths) is that on typical, bright, partly cloudly summer days, there would be large "blank" spots in the pattern at visible wavelengths resulting from the strong reflectance of unpolarized light from the clouds at those wavelengths, which would drive the per cent polarization below the perceptual threshold; while in the UV the pattern would tend to be continuous over the sky. Hence, in the UV virtually any isolated patch of sky which happened to be visible would provide useful orientation information to flying or dancing bees.

One possible source of deviation in the E-vector patterns measured against clouds is that under some conditions light may be partially polarized by reflection. Although a few theoretical studies have been undertaken (e.g., Kattawar and Plass, 1971), apparently no extensive measured data appropriate for earthbound observers have been collected. It would be interesting to determine whether monitoring UV wavelengths minimizes anomalous polarization patterns produced in this way.

While my measurements demonstrate advantages for using short wavelengths under patchy cloud cover, vegetation which obscures parts of the sky may produce an even greater differential enhancement of polarization information in short wavelengths. Such a situation is encountered, of course, very frequently by foraging and dancing honey bees. For these cases, the volume of air available for scattering is <u>very</u> short--between tree leaves and a bee, for example--making the scattered flux

extraordinarily rich in UV photons relative to visible light; while the absorption of UV by vegetation would so reduce the unpolarized background that the per cent polarization in the UV would be well above threshold.[9] At the same time, the enormous flux of reflected green and near-infrared photons from vegetation would tend to obliterate any polarization patterns at visible wavelengths. Hence, bees flying or dancing under a canopy of vegetation might well be able to see perfectly good patterns of UV-polarized light against the leaves overhead. A differential reflectance is already well known. For example, Krinov's (1960) widely quoted data show a relatively large peak at about 550 nm and huge increases for longer wavelengths. Also, it is interesting to note that measurements by Gehrels (1962) and Gehrels and Teska (1963) show a large decline in the degree of polarization at long wavelengths because of the reflection from vegetation surrounding the analyzing instrument.

7. General Conclusions

My sky measurements demonstrate that: 1) E-vector orientation is the most useful and stable cue in the sky although it generally does not match the predictions of simple theory exactly. 2) Any visible wavelength will serve quite well under clear skies for polarization orientation, although the pattern is slightly better at longer wavelengths. 3) Under overcast skies, no wavelength band provides useful polarization information. 4) Under partly cloudy skies, the proportion of the sky with usable polarization information is greatest in the UV. 5) Under many circumstances,

9. Of course the total flux level would be much smaller, and it remains to be determined whether bees' UV receptors are sensitive enough.

typical and biologically significant Rayleigh scattering patterns may exist against overhead vegetation at UV wavelengths. Therefore, I propose that the UV sensitivity of animals is primarily an adaptation for detecting skylight patterns under limiting conditions when useful scattering can occur only relatively close to an animal.

CHAPTER IV.

Methods.

1. General Rationale.

Von Frisch's classic experiments described in Chapter I established without a doubt that honey bees can detect and use for orientation the polarization of even fairly small areas of the blue sky. But his experimental techniques were not accurate enough to show more than the general direction and form of the dances and individual waggle runs were not studied (von Frisch, 1967; pp. 385 ff.; pp. 397 ff.). In most of his experiments von Frisch drastically changed the interrelationships of the skypoints by providing a view of the sky through a polarizing filter. This severely alters the natural pattern, because every point on the skyvault now has the same E-vector orientation. This procedure was useful for showing that bees used polarization of skylight for orientation, but it also changed the sky patterns in many other ways, such as the total intensity and per cent polarization. A better alternative is to limit the area of the sky viewed to include only the point of interest so that independent manipulation of various radiation parameters can be accomplished.

Considering these factors, one reasonable method of study is to limit the number of cues available to the animal and study the importance of individual variables. This approach generally requires using artificial rather than natural cues, and it has been followed extensively in the experiments reported here and to a lesser degree in those of Rossel

et al. (1978). How characteristics of artificial polarization sources correspond to the natural sky has already been discussed in detail in Chapter II: the relatively simple geometry of primary Rayleigh scattering is mirrored in the values of a number of the physical parameters of polarization sources--e.g., E-vector orientation, degree of polarization, and color. For clear, natural sky, of course, the radiation coming from each point on the skyvault is related because of their common geometrical dependence on the scattering of direct sunlight.

It may seem that there is a basic limitation in this "single skypoint" approach, because von Frisch and others have concluded that honey bees require areas of the natural sky subtending at least 10°-15° of visual angle to orient themselves precisely. This area certainly cannot be considered as a single point, because the E-vector orientation is not constant across areas of this size. In preliminary experiments, however, I found that honey bees can orient to very small (less than 1°) spots of polarized ultraviolet light. On the basis of polarization cues, such small spots can probably be considered as single points.[1] With such isolated, small spots of polarization one can analytically predict how honey bees might orient their dances. How well the dance directions match the predictions constitutes a good test of the importance of each possible type of information. However, to do this successfully individual waggle dances must be observed in detail.

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1. Edrich and von Helversen (1976) found that bees could successfully use very small spots in their orientation. However, these spots were projected from the zenith, which constitutes a special case. See Chapter V, section on zenith stimuli, for a comparison of the differences between my experiments and theirs.

My behavioral experiments were based on observations of the precision and direction of honey bee dances on the comb of horizontal two-frame observation hives. Honey bees, trained to forage from distant, artificial feeders, returned to the hive inside the laboratory, and for ease of study were constrained (by the structure of the hive) to remain in a limited, specific "dance area". As discussed in Chapter I, for horizontal dances, gravity can no longer act as a reference cue as it usually does for dances on the vertical comb of the normal hive. To orient horizontal dances, bees must actually be able to see a light source or detect some other cue. (Sometimes bees are able to use rather surprizing features as cues, as for example, perhaps the earth's magnetic field. See Appendix B.) The visual environment surrounding the horizontal hive was modified so that the bees could only see a "point" source of light (generally a maximum of 5° in diameter) against a diffuse background as they danced over the surface of the comb. Such small light sources stimulated only a few ommatidia of a honey bee's eye at any instant.

In my experiments, the bees always viewed artificial light sources while dancing. Except for their foraging flights outside the hive, dancers never saw any part of the natural, blue sky. In the simplest case, such a "point" source is interpreted by a dancing bee as being the sun, and the angle between the dance direction and the light source is the same as that between the feeder and the sun itself outside the hive. For many experiments, it is convenient to designate this direction as the control direction. Changing characteristics of the light source (e.g., E-vector orientation, color, zenith distance, apparent visual size and less frequently the degree of polarization) often induced specific

changes in the waggle dance orientation from the solar direction (control). The possibilities are best illustrated by examining a specific case.

As discussed in Chapter II, in the natural sky there are ordinarily two points of identical E-vector orientation on the skyvault at the same elevation.[2]

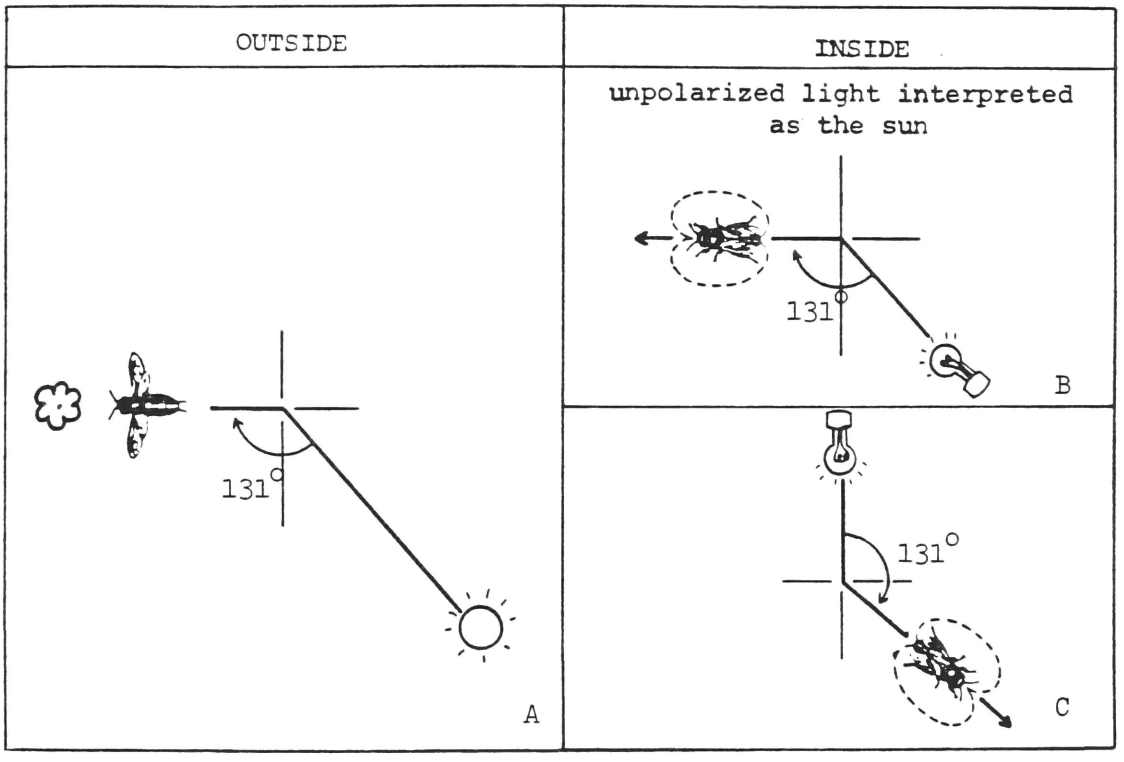

Figure IV-1. A honey bee is foraging from a feeder located 131° to the right of the sun (A). Upon her return to the horizontal hive inside the laboratory, she sees a white light in the same position as the sun outside. She points her waggle dances directly toward the goal (B). If the artificial light is moved in relative azimuth, the bee always points her dance 131° to the right of the light source (C).

If a dancing bee is shown a source of polarization with this E-vector orientation, how is it interpreted? For example, suppose a honey bee is foraging from a feeder due West from the hive, as illustrated by Figure IV-1. When the solar zenith distance is 21° and the sun's azimuth is 139° (i.e., on June 11, at local time 1100 for latitude 40°N), as she flies out from the hive towards the goal, she will see the sun 131° on her left. That is, the relative azimuth of the feeder is $+131^{\circ}$. If the sky is clear, she can simultaneously observe the patterns of skylight polarization (Figure IV-2). She will see, for example, an E-vector orientation of $+70^{\circ}$ (i.e., 70° clockwise from vertical) at a zenith distance of 50° at <u>two</u> places on the skyvault: 32° and 122° to the right of the solar vertical (skypoints I and II respectively). Thus, the feeder is located 99° and 9° to the right of these two points in the sky with equal E-vector orientation and elevation.

When she returns to the hive inside the laboratory, the forager attempts to point her horizontal dances directly toward the feeder. If she uses only the experimental light source as an orientation cue, her dance directions indicate how she interprets the stimulus. If, in the example above, she uses it as the sun, her dances will point 131° to the right of the light source (control direction). If, however, the dancing bee interprets the source as skypoint I, her waggle dances will point 99° to the right of the source: the same angle she observed on her outward flight to the feeder. Similarly, if she uses the experimental stimulus as skypoint II, she will dance 9° to the right.

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2. Generally, other parameters, such as degree of polarization, are different.

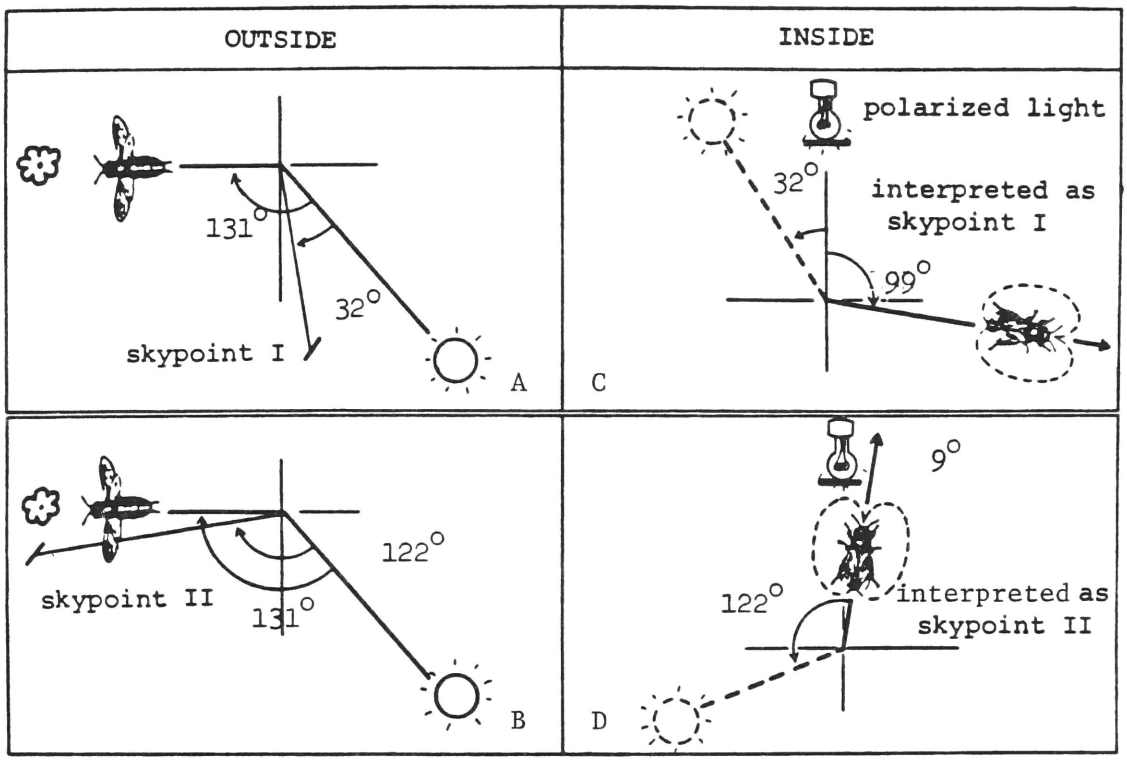

Figure IV-2. Honey bee flying to the goal sees two point in the sky with an E-vector orientation of +70°, skypoint I 32° (A) and skypoint II 122° (B) to the right of the sun. Back in the hive she is shown a stimulus polarized at +70°. If she interprets it as skypoint I, she will dance 99° to the right of this light (C). If she interprets it as skypoint II, she dances 9° to the right (D). Both 99° and 9° would be correct.

Notice that the angular difference between the waggle dance directions using the stimulus as the sun or part of the sky equals the relative azimuth between these points. That is, for solar orientation the relative azimuth is 131°, for skypoint orientation it is 9° and 99°. So 131° - 9° = 122° and 131° - 99° = 30° which equal the relative bearing of each of the skypoints from the sun.

Thus for experiments with a light source of fixed position, the absolute orientation of the waggle dances do not need to be measured to determine how the bee interprets the stimulus. If the control direction (solar orientation) is arbitrarily called zero and the bees interpret the source as a part of the sky, the waggle dances will deviate from the control an amount equal to the relative azimuth between the skypoint and the sun, but in an opposite sense. That is, bees interpreting a stimulus as the skypoint to the right of the sun will exhibit dances to the left of the control direction. In this way, the deviation of dance orientation from control indicates how the bees interpret the light source. Obviously, other orientations are also diagnostic of how the bees perceive the stimulus. These rules apply regardless of the relative orientation of the goal, sun, and skypoints. Thus, in these experiments solar orientation establishes a variable reference system for analyzing the dances.

2. Materials and Methods.

For each experiment, an artificial feeder (Gould, 1975) which provided a scented, 2 molar sucrose solution was opened at a station where the bees had foraged previously. By introducing a few drops of solution containing the same scent into the hive, foragers were quickly induced to visit this feeder. After a few successful foraging flights, these bees generally danced when they returned to the horizontal observation hive. A returning forager (usually individually marked) was selected and centered in a small stimulus light with specific polarization parameters. Her resulting dance orientation was then analyzed.

As a honey bee carries out successive waggle runs she often moves over relatively large areas of the honeycomb. To assure that a bee always had the same orientation relative to the stimulus light during her dance, the horizontal hive was mounted on two sets of perpendicular rollers so that any area of the honeycomb could be centered in the stimulus without rotating the hive. With such an arrangement, any bee could be kept in the same relative orientation to the test light quite easily, even if she moved widely over the dance floor.

Since an observer's presence often affects the orientation of dances (e.g., von Frisch, 1967, reports that bees can orient their dances to light reflected from an observer's face) and because the positions of the UV stimuli used extensively in these experiments were invisible to me, dancing bees were observed by a video camera, and each dance was recorded for further detailed analysis. The reference system for these experiments was fixed with respect to the camera and the hive. The camera viewed the dances from a distance of about 3 meters through a zoom lens (f = 16-64 mm), and was regularly moved to assure that the bees were not using it as an orientation cue. Appropriate experimental information, such as source polarization, time, and the sky conditions, were simultaneously recorded on the audio track of the tape. Video records were analyzed by drawing the orientation of each waggle run direction directly on a television monitor, and measuring the angles (within 0.5^{o}) with respect to gravity by a special level and protractor. These video records proved especially advantageous because individual dances could be reanalyzed many times. Multiple analyses was often essential in order to study those bees exhibiting poor orientation, since then they typically

danced in a very hesitant manner.

2.1 Hive construction.

The hives used in these experiments consisted of two standard frames of honeycomb modified so that returning bees could enter only on one side of the bottom frame. The hive communicated with the outside through a flexible plastic tube (inside diameter 2.5 cm) which allowed extensive movement of the hive but still permitted easy entry and exit of foraging bees. The hive population was quite small throughout most of the experiments so that the bottom frame was frequently deserted. Under these conditions dances tended to occur in other, more populated locations of the hive, and returning foragers could be induced to dance on the lower comb only by increasing the number of bees stationed there. This was easily accomplished by covering the upper comb with a dark cloth, shining a light on the bottom frame, and relying on the bees' strong phototactic behavior to attract many of them to the bottom frame. Even low wattage incandescent bulbs were extremely effective in this. Even though such a light was extinguished before beginning the experiments, many bees remained on the bottom comb once foraging began, and they induced dances in this "dance area". Although bees still occasionally danced on the upper comb, these were usually pollen foragers.[3]

To eliminate any possible changes in polarization form or spectral distribution of the stimulus light, the usual glass walls of the bottom comb was replaced by thin, ten-mesh (2.5 mm spaces) nylon screen (the

3. Pollen collectors generally danced many times before leaving to forage again: first on the bottom frame, and then on the upper comb where the pollen was stored.

strands were opaque). This mesh interfered minimally with both the presentation of stimuli and the observation of waggle dance directions. By comparing dance orientation under both nylon screen and glass, it was my impression that those under glass, (especially if the glass was dirty with wax or condensation) frequently were quite different from dances under the mesh, and these differences were especially evident with polarized stimuli. A principal factor probably was that the apparent source size increased when viewed through dirty glass (see Chapter V). For example, dancing bees tended to orient to the polarization of a small white stimulus only when viewed through glass but not the nylon screen. Another factor is that light may be modified in its polarization and spectral distribution by differential reflection through glass. In sum, glass sides modified the stimuli in diverse and unpredictable ways and therefore were eliminated.

Most of the results reported here correspond to measured waggle dance directions observed from a carefully leveled horizontal hive, which was frequently checked. Such horizontal hives, although so different from natural ones, did not seem to greatly affect the bees' activities. In 1977, a hive was horizontal for 3.5 months, except for a one week period, and in 1978 several exceeded 5 months. Nonetheless, the deposition of eggs, storage of food, and other hive activities appeared quite normal on both sides of the comb.[4] There was, however, evidence of much decreased recruitment efficiency when these hives were darkened. This is not unexpected because of the importance of gravity for dance orientation inside normal, dark hives. To obviate this problem, a small,

4. Chauvin, 1960, also did not observe any obvious, unusual changes in hives he kept horizontal for several months.

unpolarized light was present during those days in which the hive was not used for experiments. The bees easily oriented themselves by using this artificial sun.[5]

2.2 Locale.

Except for 12 October 1977, all experiments were performed on the campus of Princeton University, Princeton, New Jersey (40°29'N latitude, 74°39'W longitude) where the elevation is 52 m. The hives were mainly located on the second floor of the Vivarium of the Department of Biology, but some were also kept on the roof of Eno Hall. From the hive entrance, bees were trained to fly in two principal directions: South, where athletic playing fields extended for about 350 m to a large stand of trees, and the East, where a main feeding station was located on the northeast corner of an athletic field about 700 m distant from the the hive entrance, at true azimuth 60° (measured clockwise from North). To reach this location, bees had to fly over or around several tall buildings. On 12 October 1977, a hive was moved to the sixth floor of Smith Hall on The Rockefeller University campus, New York City and the feeder was located 150 m horizontally from the hive, at an azimuth of 300°.

2.3 Training honey bees to forage.

5. This procedure was not a complete solution since the bees exhibited unusual difficulties in leaving the horizontal hive. This is because any stray light visible to them interferes greatly with their departure, due to phototactic reactions which are unmodified by the negative geotaxis which prevails in vertical hives. This problem has been observed by others using horizontal hives (e.g., von Frisch, 1967), and under some conditions is quite severe.

2.3.1 Typical training methods. A common method for training honey bees to forage from artificial feeders depends upon leading them gradually away from the hive as they collect sugar solution from a feeder (e.g., Gary and Witherell, 1971; Gould, 1975). This is usually accomplished by distributing drops of high quality (2 Molar) scented sugar water directly at the hive entrance so that any departing bee tends to step into them and then drinks reflexively. Once a bee discovers a drop of sugar water, she will actively search for others. By judicious application of the syrup, bees can be quickly led to a feeder dispensing the same solution, which has been placed as close as possible to the hive entrance hole. Bees learn very quickly to forage (by walking) from the hive to such a feeder. The sugar source can then be gradually moved away along a board directly attached to the hive, just below the entrance hole. A good rate is about one-third of the distance between the feeder and the hive every ten minutes. At short distances from the hive, the bees abandon walking and start to fly. Then the feeder can be shifted farther in each move.

These techniques ultimately work well because when a group of well established foragers is led far enough from the hive, they perform waggle dances which recruit new bees to the feeder. Until this distance is reached, relatively few new bees appear because the round dances of the foragers send recruits out in all directions. Besides the factor of distance, other problems are associated with this training method. 1) If the feeder is moved from the hive too quickly, even the established foragers do not follow and the sugar source must be returned. 2) If the movement is too slow, the bees can get "stuck" at previous feeder positions and again substantial time can be lost by enticing them to the new

feeder location. 3) The visual environment often profoundly influences the efficiency of training. If characteristic landmarks are visible, such as a large group of trees, bees readily become entrained to feeder positions close to such obvious features (e.g., von Frisch, 1967; pp. 331 ff.). All of these factors, of course, do not ordinarily pose a problem of inefficiency in recruitment process because flowers do not move in nature.

The entrances to my hives were not at ground level. Since von Frisch and his colleagues (von Frisch et al., 1953; reviewed by von Frisch, 1967; pp. 163 ff.) have clearly shown that "up" and "down" as directions are not communicated in the dances, recruitment is often not nearly as efficient as in other circumstances and conventional training is very difficult. Von Frisch et al. (1953) discovered that an effective method of training consists of gradually lowering or raising the feeder with its associated foragers until the desired level was reached, where the normal training procedures could be resumed. While the method works, it is generally very time consuming. In addition, the Eno Hall rooftop location required that the bees be enticed down the side of an office building. During the hot summer weather, many searching bees entered open windows, bothering the occupants.

2.3.2 Training bees by transport. Considering these factors, I thought it was worth trying to transport bees feeding around an elevated hive entrance in a single step to a ground level location at a sufficient distance to elicit waggle dances. Theoretically, this technique should work only if the bees are familiar with the hive environment, and are able to return by using familiar landmarks. Hopefully, if the transported bees

drank the sugar water, they would dance upon their return.

Such one-step transports of bees from the hive entrance was almost always successful if they continued to drink undisturbed while carried to the desired feeder location. If for any reason a bee was not feeding when this position was reached, she always departed never to return to the feeder. If, however, she continued to feed until leaving of her own accord, she performed a characteristic "orientation" flight around the feeder as she departed to the hive. This flight consisted of very tight circles with her head pointed towards the feeder, gradually increasing in diameter, which changed to semi-circles centered around the general direction back toward the hive until she disappeared from sight. After 5-10 minutes (for a move of 200 m), most bees would return to the feeder, and proved to be established foragers. When this method worked, it not only eliminated the problem of differing altitudes, but also increased the number of recruits much earlier in training.

Several other interesting aspects of this behavior were observed by individually numbering bees as they drank. 1) A large number of transported bees (perhaps all) when leaving the hive after the first transport, searched close to the hive at the former position of the feeder. Only after a few minutes did they disappear from the hive vicinity and then quickly appeared at the feeder. Thus, the 5-15 minutes before the first transported bees returned seemed to result from a searching for the old feeder. 2) Bees departing in groups from the transported feeder tended to return in the same groups. Thus the observed behavior was probably a general characteristic of bees. Subsequent single-step transports were routinely and successfully carried out to as far as 200 m

from the hive. The distance limit seems to depend only on the length of time the bees feed and how fast the feeder, with its bees, can be gently carried to its desired location.

This training procedure even worked if I caught bees that were flying out from the hive and transported them to a feeder. This was accomplished using an inverted glass beaker covered with red plastic around the sides. If this device was placed over the hive entrance, bees flew upwards towards the white light, but were stopped by the glass. Because of their positive phototactic behavior, they kept trying to escape through the clear end. After a number of bees were captured in this way, they could be slowly carried to the desired feeder location. When the inverted beaker was placed over a feeder and the clear bottom covered with an opaque sheet, the bees soon discovered the sugar solution, from which they drank reflexively. (The red filter over the side walls of the beaker allowed the bees to be observed but did not induce phototactic behavior.) As soon as bees drank, the beaker was removed, the bees marked and allowed to depart at will. These bees generally performed the very characteristic orientation flights around the feeder as they departed. There were, however, several major differences not observed when bees were moved on a feeder close to the hive. 1) Some bees <u>never</u> returned to the hive and continued to fly around the feeder. These bees probably were inexperienced foragers and not familiar enough with the hive environment to return. This conclusion was strongly supported by the observation that if these bees were recaptured at the feeder and released much closer to the hive entrance, virtually all returned quickly to the hive. 2) Fewer bees returned to the feeder when transported this way.

Two observations seem significant. First, many of the bees which returned could be observed inside the hive and they acted quite agitated. Second, even bees which did return to the vicinity of the feeder had very obvious difficulties finding the feeder itself. It seemed that these bees really did not know the configuration of the feeder. For example, although they flew around its general location, they did not land. This observation confirms in another way the studies of Menzel (1967) which showed that honey bees learn the shape and color of a food source only a few seconds before and after they first begin to drink nectar. Also, Opfinger (1931, 1949) has shown that the orientation flights after leaving the feeder for the first few times allow the bees to determine the location of the feeder with respect to the immediate surround and do not function to identify the form of the feeder per se. She found that features within about 50 cm of the feeder itself proved unimportant to a bee upon her return. These factors explain some of the differences observed between the transport of bees captured while leaving the hive and those feeding close to the hive. In the first case, the feeder configuration during the first few seconds of drinking did not correspond to the one seen by the bees upon their return. This probably explains their trouble in locating the feeder upon their first return, although they returned to the general area. However, if a dozen bees are transported in this way, eventually a few do find the feeder; and once they begin to forage from it, many of the other bees soon discover it. In many circumstances, capturing the bees on wing is better than transporting a feeder itself, since the move is not limited by how long the bees drink. Under proper conditions, bees can be quickly trained to forage from a feeder located 200 m or more from the hive, even if the hive entrance and

feeder are not at the same level.

Such transport procedures also provide opportunities for interesting experiments. For example, is the flight to or from a food source important for the determination of direction and distance to the goal? Obviously, by transport the outward flight can be eliminated. Also, some bees captured while leaving the hive are flying to another goal and it is interesting to ask whether they will change their foraging pattern and how well they dance upon their return. Will these bees indicate the former goal, the new goal, or a combination of the two? The results of some of these experiments are discussed in Appendix D.[6]

2.4 Actual training procedures used.

For final positions within 200 m from the hive, training was accomplished in the following manner: a high quality (2M) sucrose syrup scented with lemon, anise, or vanilla was applied in drops to the hive entrance and used to lead the bees to a feeder.[7] The feeder (located as close to the

6. It is interesting to speculate further that the observed differences in the number of bees which returned to a new feeder when transported may depend on whether they had been foraging close to the hive versus those captured leaving the hive, and may depend upon the fact that bees which were foraging around the hive were always experienced foragers. In contrast, some bees caught leaving the hive probably were inexperienced bees. In fact, I observed that the number of bees which did not return to the hive after transport greatly increased during early afternoon. We know from the work of Schricker (1957) that this is the time that many inexperienced bees perform "play" flights. This idea was further supported by the observation that those bees which tended to fly straightaway from the hive entrance, returned after transport much more readily. Bees which departed the hive entrance hesitantly (e.g., by walking) generally did not. Bees of this second group were probably inexperienced.

7. Most of the time my hives required food and thus the bees foraged readily. However, transport tests on well-fed hives

hive as possible) was marked by large blue or yellow cards and connected to the hive entrance by a small bridge along which the bees could walk. When many bees were vigorously foraging, the bridge was eliminated, forcing the bees to fly about 0.3 m. A relatively large number of foragers were frequently lost at this point: principally those not actually on the feeder when the bridge was removed. When the bees flew readily from the hive to collect the sugar solution (usually after a few minutes) the feeder was removed. Any bees remaining on the feeder were gently blown away. Within 5 minutes, a large number of foragers were searching eagerly around the hive entrance for the sugar solution. Then the feeder was returned to its previous position.[8] Almost all searching foragers immediately settled on the feeder and began to drink. At this point, an opaque cover (e.g., a large aluminum photoreflector) was placed over the entire feeder which was then gently moved with its feeding bees to the desired location (usually by an easy jogging) and the cover carefully removed. This cover prevented wind or light from disturbing the bees.[9]

During relatively long moves, usually some bees had already finished drinking by the time the cover was removed. They departed immediately without performing orientation flights. Most bees,though, finished feeding at approximately the same time. When the last bee departed towards

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were also successful. This demonstrates that success does not depend only on the nutritional state of the hive.

8. Caution must be exercised under some circumstances: bees often react aggressively when a food source is removed, especially around the hive entrance when the food stores are low.

9. It is also important to keep the feeder meticulously clean, since the bees will stop to groom themselves if they become covered with syrup. Whenever this happens, bees fly straightaway to the hive when finished and do not return.

the hive, another identical feeder was placed in the old feeder position (close to the hive), which attracted many foragers which had not been moved. It was then moved in an identical way. This proved feasible only because the transported bees flew directly back and remained inside the hive for roughly 3-5 minutes. Since it generally took only about 10-15 seconds to attract the bees searching for the feeder close to the hive, a second group of bees could be easily moved in this way. Since the foraging groups quickly lost their relative synchrony, only two moves could be easily accomplished.

For training to feeders farther than 200 m, a transparent inverted red beaker with clear bottom was used to capture the bees departing the hive and transported in the manner described in detail above. Using either of these techniques, bees from a hive on the roof of a 6 story building could be trained in about 15-30 minutes to forage from a feeder below them located at a horizontal distance of 150 m.

After developing and using these techniques extensively, I discovered that direct transportation of bees to the final goal while they fed on sugar water or honey was apparently a common practice of earlier observers (e.g., Maeterlinck, 1901). Also, capturing foragers outside the hive, inducing them to feed, and observing the direction of their departing flights has been used by "bee hunters" in their attempts to find the location of wild hives (e.g., Rout, 1907; Gibbons, 1962).

3. Visual environment of the hive.

The experiments were performed in a large room with white sheets

completely surrounding the hive at a distance of several meters. Diffuse illumination was provided by 40 watt incandescent bulbs (located below the surface of the comb) which were adjusted until the dances were disoriented.[10]

4. Polarization sources.

Two principle light sources were used as stimuli in these experiments. 1) A standard, 150 watt xenon arc (Hanovia, Inc.) projection system (Schoefield, Inc.) with quartz optics. Physical measurements showed that its output was virtually unpolarized. 2) a 150 watt quartz-halogen lamp (General Electric FCS quartzline lamp) in a high intensity projection system (modified microfilm projector; Edmund Scientific Company #71,985). The condensing system consisted of pyrex aspheric and planoconvex lenses (which transmitted near-UV light) at right angles to each other. The beam was bent by a "cold" mirror (i.e., it transmitted infrared and reflected UV and visible light). Unless a cold mirror was used, the beam overheated the comb. However, the mirror reflection produced a slight elliptical polarization in the beam. This was not ordinarily a problem because it was converted to completely linearly polarized light with a polarizing filter. This lamp housing was partially open in the rear and was arranged to cast relatively diffuse light over most of the room, and this light was supplemented by other lamps to make the lighting as even as possible. The infrared beam transmitted through the cold mirror was redirected by a conventional mirror toward the floor so bees on the

10. Under these conditions, the bees were not, however, always completely disoriented: they sometimes oriented themselves quadrimodally, perhaps to the earth's magnetic field. See Appendix B for details.

surface of the comb could never observe it while dancing. The light was operated from an adjustable, fairly well regulated direct current power supply with a maximum ripple of about 200 mv. When used in experiments, the lamp voltage was increased 15-20% above its rated voltage to increase the UV content of the lamp's spectral output. Although this procedure was very effective, it dramatically decreased the bulb life.

Both sources used a UV transmitting (to 200 nm) polarizing filter (Polacoat, Inc. #105-UV), which could be oriented in the light beam to produce any desired E-vector orientation. With a special protractor it could be adjusted to a specific orientation within about a 1° error. An adjustable iris diaphragm allowed the aperture of these sources to range between 2 and 50 mm. At typical operating distances (0.6 m) the apparent source size could be continuously varied between about 5° (0.006 steradians) to about 0.2° (0.00001 steradians) of visual angle.[11] By comparison, the solar and lunar discs subtend about 0.5° (0.00006 steradians). The cross-section of the beam was usually adjusted so that the source subtended about 5° of visual angle for the bee, so that a dancer could be easily centered. The beams possessed divergences of about 0.2 steradians/meter.

Because the quartz-halogen source produced slightly elliptically polarized light when the UV linear polarizer was removed, this projection system could not be used as an unpolarized source. Although the xenon arc source was generally used for this purpose, some experiments required

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11. The solid angle corresponding to specific visual angles can be calculated by using the small solid angle approximation from Keitz (1971, pp. 21 ff.). Specifically,
$$W = \pi \alpha^2 \quad \text{(steradians)}$$
where α is the cone apex half angle in radians.

several sources, and therefore a conventional microscope illuminator was also used (General Electric #1493). Physical measurements showed that it was unpolarized. This illuminator was always operated well above its rated voltage (in most cases about 50%) from either an unregulated alternating current supply or a fairly well regulated direct current supply depending upon the specific experiment. Except for the xenon arc (because of its size it was relatively fixed in orientation), light sources could be rapidly positioned to shine on the comb from various directions. All sources accomodated various spectral filters which could be quickly changed. The transmission characteristics of the main filters used in these experiments are summarized in Table IV-1.

5. Data summary diagrams.

Experimental data are summarized in polar histograms of bin-width 5° (total of 72 bins for each diagram). Each symbol on the edge of the circle always corresponds to the direction of a single waggle run during a dance (i.e., all identical symbols correspond to the observed waggle runs during a complete dance). Tick marks specify 15° intervals. Angles are measured from 0° to 360° counterclockwise. Unless noted to the contrary, each different symbol refers to separate bees.

Information included in each summary is the date, time, (Eastern Daylight Time, EDT), the zenith distance and azimuth of the sun, general sky conditions, and physical parameters of the test light (e.g., color, E-vector orientation, and zenith distance). E-vector orientation is given according to previous conventions: "+" means clockwise from vertical while looking at the source. Unless specifically noted on these

TABLE IV-1

Optical Filters

Hoya UV 330	Broad UV transmission (90% at 330 nm.) Some Infrared transmission.
Hoya UV 360	Strong UV transmission (70% at 360 nm.)
Hoya R-70	Sharp cut at 700 nm.; 90% transmission for longer wavelengths.
Hoya L-42	Sharp cut at 470 nm.; 0% transmission less than 410 nm.
Corning Glass Works No. 3389	Sharp cut at 580 nm.; 0% transmission less than 530 nm.
Corning Glass Works No. 5900	Peak transmission at 400 nm.; slow decrease throughout rest of visible wavelengths
Corning Glass Works No. 3390	Black glass; virtually opaque between 200 nm. and 5 micrometers.
Polarizing Filter	Polacoat, Inc. 105UV; transmits down to 200 nm.
Kodak Wratten No. 35	Violet, maximum transmission (57% at 430 nm.) Long red wavelengths included.
Kodak Wratten No. 47	Blue, maximum transmission (50% at 440 nm.) no long wavelengths.
Kodak Wratten No. 58	Green; maximum transmission (54% at 530 nm.)

plots, the experimental light is assumed to be the quartz-halogen source.

When the stimulus was polarized, the E-vector orientation theoretically always corresponded to two points in the natural sky of that zenith distance, which were used to predict the waggle dance orientation. The sign of the azimuth indicates which side of the solar vertical the point in question is located: "+" means to the right.

The zero direction of the plots is specified by the "0" inside the circle, and its significance depends upon whether it is a "fixed" or "normalized" histogram. For fixed histograms, "0" is identical in each experiment and corresponds to the top of the field of view of the video camera which recorded all waggle dance directions. In this fixed configuration, true North is at 235° on the circle. In general, experimental light sources had bearings close to zero. The location of each source was constant for data obtained on a specific date and is listed in Table IV-2.

Two different expected directions are indicated in some fixed polar plots: each is symbolized by a radius. 1) The longer radius vector always indicates the expected waggle dance direction if the bee interpreted the experimental light as the sun (control direction). It is found by using spherical trigonometry to calculate the difference in bearing between the sun and the food source for that particular time. 2) The shorter radius vectors always indicate the expected waggle dance direction when bees interpret the experimental light as a part of the sky, on the basis of E-vector orientation alone. Thus, for these experiments the expected directions always occur in pairs. When the source E-

Table IV-2

Dates of Experiments Reported

Date	Solar[#] Dec.	Feeder[*] Location	Source[+] Bearing	Source ZD	Sky Conditions
15 Aug.	14.0°N.	B	335°	DC = 50° AC = 38°	Clear; Partly hazy
19 Aug.	12.7°N.	C	335°	DC = 51°	Partly cloudy
20 Aug.	12.3°N.	A	335°	DC = 51° AC = 34°	Day began cloudy; cleared by experiment; cool, few clouds
23 Aug.	11.3°N.	A	335°	DC = 54°	Clear but very hazy; unsaturated Blue
24 Aug.	11.0°N.	A	355°	DC = 48°	Heavy overcast; cool
25 Aug.	10.6°N.	A	350°	DC = 27° AC = 53°	Deep Blue sky; cool
26 Aug.	10.3°N.	A	5°	DC = 27°	Partly cloudy
31 Aug.	8.5°N.	A	5°	DC = 27°	Very overcast; a little rain
1 Sept.	8.2°N.	A	10°	DC = 27°	Day began overcast; at about 1000-1100 EDT solar disc became visible thrugh clouds; then patchy clouds; very hazy; unsaturated Blue
2 Sept.	7.8°N.	A	350°	DC = 26°	Blue skies; but very hazy; hot
17 Sept.	2.1°N.	B	350°	DC = 33° MI = 54°	Experiments started when very cloudy; clearing at about 1300-1400; then hazy patchy Blue
12 Oct.	7.2°S.	--	--	0°	clear

[+] with respect to the Data diagram system.

[*] Location on campus map and in locale section.

[#] Dec. = Declination.

Symbols: DC = Direct Current operated Quartz Halogen System.

AC = Alternating Current operated tungsten lamp.

MI = Direct Current operated tungsten lamp.

ZD = Zenith Distance

vector orientation was 90° (horizontal), only one expected direction is visible, since the other is always superimposed on the longer (solar orientation) radius vector. For cases in which the responses of bees to more than one stimulus type are plotted in the same diagram, each is appropriately noted.

A fixed histogram does not allow easy comparison of data with differing expected directions, since they would be dispersed around the histogram circle. To allow direct comparison, the (divergent) expected directions for some experiments were normalized (rotated) to the "0" direction, symbolized by a long radius vector. Then, any deviation from expected can be simply observed as a non-zero direction in these normalized histograms. In this manner, results of experiments with very different observed waggle dance directions can be easily compared.

6. Determination of Expected Directions.

As outlined above, the general procedure for these honey bee orientation experiments consisted of three parts: 1) presentation of a physically well-characterized stimulus which corresponded to some part of the sky; 2) measuring the angle(s) between the waggle dance directions and the stimulus; and 3) comparison of the waggle dance orientation with the predictions made on the basis of Rayleigh scattering theory. The first two steps have been discussed in some detail. Here I outline how the predicted directions were calculated.

6.1 Solar position.

First, the solar position appropriate for the time of the experiment was calculated. This value was used for predicting the waggle direction of bees interpreting the stimulus as the sun (control) and also in the subsequent calculations for polarization orientation. To solve for solar position, three variables must be known: 1) the latitude of the observer (L), 2) the local apparent sun time (T), and 3) the solar declination (D). Time is expressed as hours from local noon (H) and is converted into degrees by the following relationship:

$$T = (15^{\circ}/\text{hour})(H).$$

(Hours before noon are taken as negative.)[12] Solar declination is a variable of the "equatorial system" and depends upon the time of year. It can be found for any day by use of Table IV-3.

Knowing these variables, solar zenith distance (ZS) is found by:

$$\cos(ZS) = \sin(D)\sin(L) + \cos(D)\cos(L)\cos(T).$$

The true solar azimuth (A) is found by substituting the solar zenith distance into:

$$\sin(A) = \frac{\cos(D)\sin(T)}{\sin(ZS)}.$$

Azimuth angles are measured from 0° to 360°, clockwise from North.

Numerical example. Suppose that Latitude = 40°N, declination = $+23^{\circ}$, for an observer at two hours before local noon (1000). Then, T = 2

12. Of course, if clock time is used, corrections are necessary if the observer is not at the Longitude defining the time zone. Since this study was done on almost exactly 75°W, no corrections were necessary. The small corrections in rate of movement of the sun necessary for extreme precision were ignored. During these experiments, such differences amounted to a maximum of 12 minutes (in October).

Table IV-3

DECLINATIONS OF THE SUN

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1	−23°04′	−17°20′	−7°49′	4°18′	14°54′	21°58′	23°09′	18°10′	8°30′	−2°57′	−14°14′	−21°43′
2	−22 59	−17 03	−7 26	4 42	15 12	22 06	23 05	17 55	8 09	−3 20	−14 34	−21 52
3	−22 54	−16 46	−7 03	5 05	15 30	22 14	23 01	17 40	7 47	−3 44	−14 53	−22 01
4	−22 48	−16 28	−6 40	5 28	15 47	22 22	22 56	17 24	7 25	−4 07	−15 11	−22 10
5	−22 42	−16 10	−6 17	5 51	16 05	22 29	22 51	17 08	7 03	−4 30	−15 30	−22 18
6	−22 36	−15 52	−5 54	6 13	16 22	22 35	22 45	16 52	6 40	−4 53	−15 48	−22 25
7	−22 28	−15 34	−5 30	6 36	16 39	22 42	22 39	16 36	6 18	−5 16	−16 06	−22 32
8	−22 21	−15 15	−5 07	6 59	16 55	22 47	22 33	16 19	5 56	−5 39	−16 24	−22 39
9	−22 13	−14 56	−4 44	7 21	17 12	22 53	22 26	16 02	5 33	−6 02	−16 41	−22 46
10	−22 05	−14 37	−4 20	7 43	17 27	22 58	22 19	15 45	5 10	−6 25	−16 58	−22 52
11	−21 56	−14 18	−3 57	8 07	17 43	23 02	22 11	15 27	4 48	−6 48	−17 15	−22 57
12	−21 47	−13 58	−3 33	8 28	17 59	23 07	22 04	15 10	4 25	−7 10	−17 32	−23 02
13	−21 37	−13 38	−3 10	8 50	18 14	23 11	21 55	14 52	4 02	−7 32	−17 48	−23 07
14	−21 27	−13 18	−2 46	9 11	18 29	23 14	21 46	14 33	3 39	−7 55	−18 04	−23 11
15	−21 16	−12 58	−2 22	9 33	18 43	23 17	21 37	14 15	3 16	−8 18	−18 20	−23 14
16	−21 06	−12 37	−1 59	9 54	18 58	23 20	21 28	13 56	2 53	−8 40	−18 35	−23 17
17	−20 54	−12 16	−1 35	10 16	19 11	23 22	21 18	13 37	2 30	−9 02	−18 50	−23 20
18	−20 42	−11 55	−1 11	10 37	19 25	23 24	21 08	13 18	2 06	−9 24	−19 05	−23 22
19	−20 30	−11 34	−0 48	10 58	19 38	23 25	20 58	12 59	1 43	−9 45	−19 19	−23 24
20	−20 18	−11 13	−0 24	11 19	19 51	23 26	20 47	12 39	1 20	−10 07	−19 33	−23 25
21	−20 05	−10 52	0 00	11 39	20 04	23 26	20 36	12 19	0 57	−10 29	−19 47	−23 26
22	−19 52	−10 30	0 24	12 00	20 16	23 26	20 24	11 59	0 33	−10 50	−20 00	−23 26
23	−19 38	−10 08	0 47	12 20	20 28	23 26	20 12	11 39	0 10	−11 12	−20 13	−23 26
24	−19 24	−9 46	1 11	12 40	20 39	23 25	20 00	11 19	−0 14	−11 33	−20 26	−23 26
25	−19 10	−9 24	1 35	13 00	20 50	23 24	19 47	10 58	−0 37	−11 54	−20 38	−23 25
26	−18 55	−9 02	1 58	13 19	21 01	23 23	19 34	10 38	−1 00	−12 14	−20 50	−23 23
27	−18 40	−8 39	2 22	13 38	21 12	23 21	19 21	10 17	−1 24	−12 35	−21 01	−23 21
28	−18 25	−8 17	2 45	13 58	21 22	23 19	19 08	9 56	−1 47	−12 55	−21 12	−23 19
29	−18 09	−8 03	3 09	14 16	21 31	23 16	18 54	9 35	−2 10	−13 15	−21 23	−23 16
30	−17 53	xx xx	3 32	14 35	21 41	23 13	18 40	9 13	−2 34	−13 35	−21 33	−23 12
31	−17 37	xx xx	3 55	xx xx	21 50	xx xx	18 25	8 52	xx xx	−13 55	xx xx	−23 08

Solar declinations given in this table are the average for the 4 years of a leap-year cycle. Individual years may vary slightly from the figures given here, although at the solstices the errors are negligible, and at the equinoxes, when they are greatest, they do not exceed 8′ to 9′ of declination in leap years and in years next preceding leap years; and in the other years they never exceed about 3′ of declination even at the equinoxes.

(from Waugh , Sundials, Dover Publ., New York, 1973)

hours(15°/hour) = -30°. 1) The sun's zenith distance is found by:

$$\cos(ZS) = \sin(23)\sin(40) + \cos(23)\cos(40)\cos(-30)$$

and

$$\cos(ZS) = 0.862 \text{ and } ZS = 30.5^{o}.$$

2) Azimuth is found by using this value of ZS:

$$\frac{\cos(23)\sin(-30)}{\sin(30.5)}. = 0.908 = \sin(A)$$

Thus, the azimuth is 65.2^{o}.

6.2 Sky location of E-vectors.

As discussed in Chapter I, von Frisch showed clearly that bees can use the E-vector of polarized light for orientation and that the degree of polarization is important only in that it needs to be greater than a certain threshold value. Thus, the experiments described here initially assumed E-vector orientation as the important variable.

A given E-vector orientation at a specific elevation generally occurs at two different points on the skyvault, as explained in Chapter II. The relative bearing of these two locations from the sun (corresponding to the zenith distance and E-vector orientation of the experimental stimulus) can be derived by the four steps summarized below. A solution[13] requires knowledge of the zenith distances of the sun (ZS), and polarized source (ZP), and the E-vector orientation (X; angle measured from vertical).

Analytical method of determining the bearing of points on the natural sky (assuming Rayleigh scattering only) which correspond to an artificially

13. A more detailed geometrical consideration can be found in Chapter II and Appendix A.

polarized stimulus. Variables:

ZP = zenith distance of the artificial source

ZS = zenith distance of the sun

X = E-vector orientation (measured from vertical; + clockwise)

C = bearing of the skypoint from the sun

A,B = intermediate variables

(1) Determine angle A:

$$A = 90^{\circ} \pm X$$

(2a) Determine the four possible values for angle B by use of the equation:

$$\sin(B) = \frac{\sin(ZP)\sin(A)}{\sin(ZS)}.$$

(2b) Use the trigonometric fact that if ZS > ZP, then B < A to reduce the number of possible solutions to two. (3) Calculate the relative bearing C for each permitted value of A and B by use of the equation:

$$\cot\tfrac{1}{2}(C) = \frac{\tan\frac{1}{2}(A-B)\sin\frac{1}{2}(ZS+ZP)}{\sin\frac{1}{2}(ZS-ZP)}$$

(4) To determine in which half of the sky (divided by the solar vertical) each skypoint is located, the following rules are used: (A) If angle A < 90°, then the bearing of the skypoint has the same sign as the E-vector orientation. (B) If angle A > 90°, the sign of the azimuth is opposite to the orientation of the E-vector. Here positive refers to the right of the solar vertical; negative to the left.[14]

Numerical example. Suppose (ZP) = 40°, ZS = 60°, and X = $+25^{\circ}$ (E-vector

14. When ZS < ZP (sun at a greater elevation than the source) the azimuth angles of the two skypoints with equal E-vector orientation have the same sign, i.e., they are located in the same half of the sky. Similarly, if ZS > ZP (sun at smaller elevation than the source) then the two corresponding azimuth angles specify opposite halves of the skyvault.

25° to the right of vertical). Then by step (1) from above

$$A = 90^{\circ} \pm 25^{\circ} = 65^{\circ} \text{ and } 115^{\circ}.$$

Using step (2),

$$\sin(B) = \frac{\sin(40)\sin(65)}{\sin(60)}$$

and thus $B = 42.3^{\circ}$ and 137.7°. Since ZP < ZS, it follows that A > B and the allowed values of A and B are:

$$B = 42.3^{\circ};\ A = 65^{\circ}$$

$$B = 42.3^{\circ};\ A = 115^{\circ}.$$

Further, by rule (4), these values give skypoints on opposite sides of the solar vertical. Using step (3),

$$\cot(\tfrac{1}{2}(C)) = \frac{\tan\frac{1}{2}(65-42.3)\sin\frac{1}{2}(40+60)}{\sin\frac{1}{2}(60-40)}$$

and

$$\cot\tfrac{1}{2}(C) = \frac{\tan\frac{1}{2}(115-42.3)\sin\frac{1}{2}(40+60)}{\sin\frac{1}{2}(60-40)}.$$

Solving these two equations,

$$\text{azimuth angle (1)} = +97^{\circ} \text{ (since } A < 90^{\circ})$$

$$\text{azimuth angle (2)} = -34.2^{\circ} \text{ (since } A > 90^{\circ})$$

6.3 Consideration of other variables.

Although they are not summarized on the data diagrams, sky points corresponding to different variables (e.g., degree of polarization) can also be calculated by the methods outlined in Chapter II and Appendix A. How well a bee's orientation can be explained by use of these diverse variables is discussed when appropriate in Chapter V.

7. Variability of dance measurements.

7.1 Individual variations of dancing.

The direction of each waggle run during a dance is not identical. An extreme example is the "sickle" dance which occurs for Apis mellifera ligustica (Italian bees) during the transition from round to waggle dances as a function of distance of the goal (von Frisch, 1967; Fig. 56). The goal direction generally corresponds to the bisection of the angle between two alternating dance directions. This regular source of dance error can be greatly reduced by training bees to forage at greater distances, although substantial errors may still be observed for bees flying to even very large distances (e.g., 2 km, von Frisch, 1967; p. 142).

In addition, individual dance differences are often quite large for bees foraging from the same feeder: many may be quite precisely oriented while others dance in a much more variable manner. Such individual differences in dance precision could conceivably depend in large part upon foraging experience. Von Frisch felt that with increasing age of a bee, the dance accuracy improves (von Frisch, 1967; p. 149). I observed a number of individually identifiable bees over a large part of their foraging life, as long as two weeks, and some individuals exhibited much more precise orientation than others. It was also my impression that most new recruits were less well oriented than established foragers, especially under conditions of overcast sky. However, occasionally even efficient foragers which had visited the feeder many times exhibited very imprecise dances, while other bees were simultaneously quite well oriented. I could discern no underlying physical factors to explain

these observations.

In practice, I used the following rule to evaluate the quality of a specific waggle dance: if only a few bees were disoriented while the majority were not, the imprecision was assumed to arise from unknown, individual factors. Such bees were identified, but not generally included in the data summaries. This arbitrary exclusion undoubtedly eliminated many interesting individual aspects of the processes of orientation. Specific experiments to investigate these details will be both important and interesting.

7.2 Measurement Errors.

The two principle errors of measuring the dance orientation arose from drawing the dance direction on the television monitor and measuring it with a protractor. To determine what magnitude of error was introduced by these two factors, video records of individual dances were independently analyzed several times, and the divergences between individual waggle direction measurements were mostly less than 5° and virtually always less than 10°. Errors in measuring with protractor the drawn dance directions were limited to a maximum of about 1° and not significant at the level of analysis used here.

7.2.1 Parallax. The artificial light sources did not produce perfectly parallel rays. To minimize parallax errors, bees were continuously centered within a fixed, small spot of light from the source (by translocating the hive). While inside the spot of light, the maximum error in relative zenith distance and azimuth of the light was about $\pm 4^{\circ}$. If the source was interpreted as the sun, this parallax produced a maximum error

of about 8° in azimuth. When used as polarization cues, however, small changes in zenith distance sometimes lead to much larger changes in the relative azimuth of the corresponding sky spot, particularly for E-vector orientations close to vertical (these correspond to sky points quite close to the sun for the elevations used in these experiments). For parts of the sky where the E-vector orientation changes much more slowly as a function of position on the sky vault, the error can be considered as negligible in most cases. In each specific instance, the error could be found by substituting the appropriate maximum and minimum values for the source zenith distance into the trigonometric equations or by using the derivative of azimuth with respect to zenith distance.

Because of these characteristics of the artificial stimuli, and also because they did not reproduce all polarization parameters of the natural sky, errors of 10° to 20° from the calculated expected directions will in most cases be considered as insignificantly different from predicted. Judicious selection of stimuli allowed many experiments to have the various expected directions diverge by angles larger than 20° so that the results were usually relatively unambiguous.[15]

An important measure of the precision of dance orientation is the scatter of waggle dance directions for individual bees. Well-oriented dances cluster tightly around a mean direction, poorly-oriented ones do not. To determine whether individual scatter was greater for horizontal

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15. One frequent exception was for E-vector orientation close to the horizontal. Then, one of the expected directions was very close to the control, solar orientation. In these cases, other experiments were needed to distinguish whether the animal was using the polarization in the stimulus as an orientation cue.

hives (with the associated parallax) than for vertical hives, the orientation of bees dancing under both conditions was compared. Vertical dances were recorded by the methods already discussed except that a 25 watt deep-red light was used for illumination.[16]

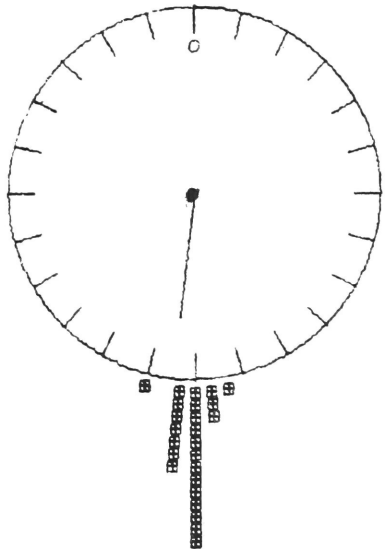

Figure IV-3. Vertical dance by a single bee. Long radius vector indicates expected direction calculated as the angle between the sun and food source.

The results of one typical series of experiments is summarized by Figure IV-3, which shows the waggle dance directions of a single bee on a vertical comb after visiting a feeder 700 m from the hive at azimuth 60°. In the polar histogram, "0" refers to straight up on the honeycomb; the expected direction vector is calculated from the difference in azimuth between the feeder and the sun at the time of the observations. These data illustrate the dance characteristics of well oriented bees: almost

16. As judged by its lack of effect on dance directions, the bees appeared insensitive to this red light. However, the bees still showed some simple phototactic responses, proving that they could perceive this light.

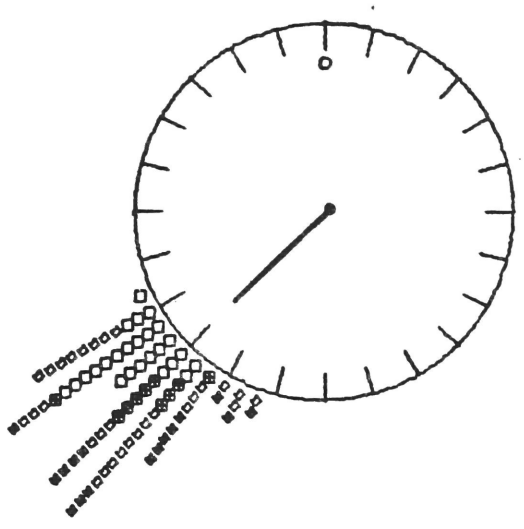

Figure IV-4. Vertical dances of a number of bees. Each symbol represents a separate bee. Long vector indicates expected dance direction (angle between the sun and food source).

all of the waggle dance directions occurred within 15° of each other. Figure IV-4 summarizes similar vertical dances of a number of bees except that the individual scatter increases the distribution considerably, so that now almost all dance directions fall within about 30° of each other. For comparison, Figure IV-5 shows the responses of bees dancing on a horizontal comb under a small, unpolarized white light which they use as the sun. Like the vertical dances, most of the scatter occurs within about 30°. Considering a series of these measurements, well oriented bees on both vertical and horizontal comb seem equally precise.[17]

17. Von Frisch (1967; Table 21, p. 133) and other well-trained observers (e.g., M. Lindauer) performed detailed observations for which they measured dance directions within 0.5°. They concluded that with a free view of the sun and the sky, horizontal dances generally fell within 0.2° of the expected direction, and compare very well with the observered accuracy of vertical dances.

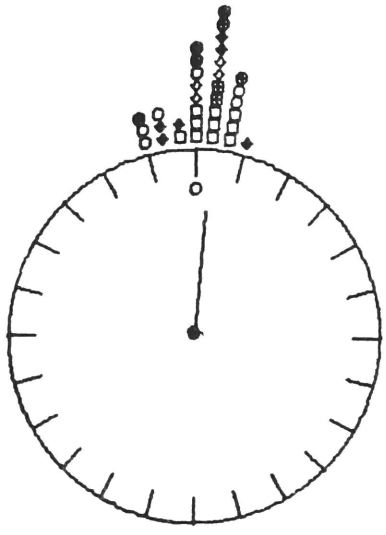

Figure IV-5 Dances on a horizontal hive to a white, unpolarized light source. Each symbol is a separate bee. Long vector indicates the expected dance direction if the bees interpret the light source as being the sun.

However, one major artifact was associated with my horizontal hives: several sections of the honeycomb were not level--e.g., cracks near the edges. If a bee danced in these areas, gravity influenced her orientation, as, for example, shown in Figure IV-6. Although such dances were affected by the E-vector orientation of the stimulus, the results were unpredictable and thus never included in analysis.[18]

18. Edrich, 1977, has studied the interaction of unpolarized light and gravity as cues for the waggle dance orientation.

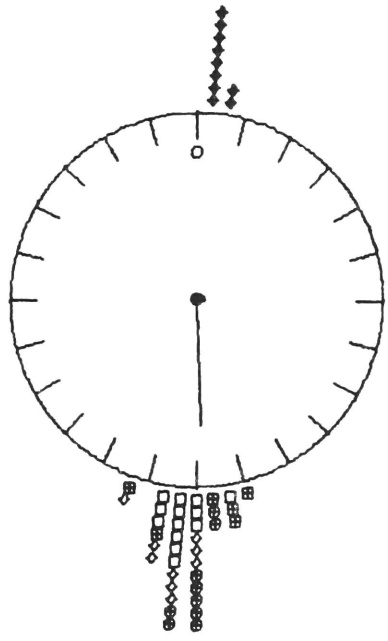

Figure IV-6. Bees dancing to white, unpolarized light in a horizontal hive. Filled triangles correspond to the dance directions of a single bee dancing in a crack at the edge of the honeycomb.

CHAPTER V.

BEHAVIORAL OBSERVATIONS.

This chapter summarizes the orientation of horizontally dancing bees to artificial light sources with diverse polarization and spectral characteristics. The representative samples given here have been selected from a much larger body of analyzed dances (about 2500) to illustrate the basic characteristics of the behavior discussed in the text. For almost all of these experiments, the results are especially significant because a single bee served as its own control--i.e., changes were made in the stimulus parameters and the resulting immediate changes in dance orientation (if any) were noted. In this way, the stimulus could be made to represent the sun or various parts of the blue sky in serial order during a single dance. This procedure often resulted in particularly clear results which could be easily compared to various analytical predictions (see Chapter II and Appendix A).

Each diagram presents the results of an experiment as a polar histogram of 5° bin-width with all the information necessary to appreciate the details of the point it illustrates. As described in Chapter IV, a long vector indicates the direction the waggle dances would point if the bees interpreted the experimental light source as the sun and shorter vectors correspond to the dance directions if the bees interpreted the light on the basis of its E-vector orientation as a part of the blue sky.

I found that the reactions of bees to the polarized stimuli depended in part on the sky conditions during the previous foraging flights. The

simple case of clear sky will be discussed in section 1, the properties of overcast will be discussed later in section 6. Table V-1 summarizes the experimental conditions described in this chapter.

1. Responses of Bees to Unpolarized White Light.

1.1 Sun directly visible during foraging flights.

When dancing bees could see only a white, unpolarized light on clear days, they oriented their waggle dances in a direction which indicated that they interpreted the test stimulus as the sun.

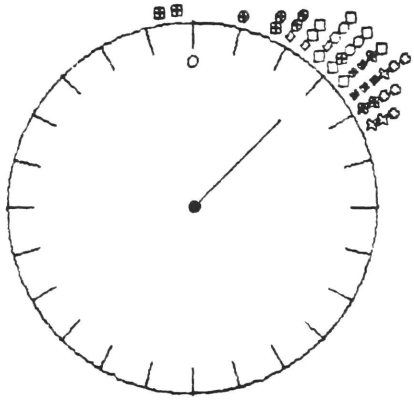

Figure V-1. Orientation of individual bees to a small, unpolarized, AC white light source at the asterisk with a ZD of 27°. 26 August, 1150 EDT, partly cloudy. Sun at ZD of 34°, AZ of 150°. Vector indicates the direction bees should dance if they use the source as the sun

Table V-1. Experimental conditions summarized in Chapter V.

I. Unpolarized white light

- A. sun visible
- B. sun hidden

II. Polarized light

- A. Some clear sky visible
  - 1. White polarized light
  - 2. non-white polarized light
    - a. blue polarized light
    - b. other visible wavelengths
    - c. UV polarized light
- B. Overcast conditions

Figure V-1 illustrates several points, for which the stimulus light was located at an azimuth of 225°. At the time of the experiment (1150 EDT) the sun had an azimuth of 150° and an elevation of 34° and could be seen (by me) despite a partly cloudy sky. The bees were foraging from a feeder at azimuth 60°, 700 m from the hive. On their outward foraging flights the bees saw the sun 90° to their right (i.e., the expected solar direction is the long vector in the diagram 90° to the left of the light source). The dances recorded in Figure V-1 show waggle directions of about 315°, (90° to the left of the stimulus), which matches the actual solar-feeder angle at that time very closely and indicates that the bees used the experimental white stimulus as if it were the sun.

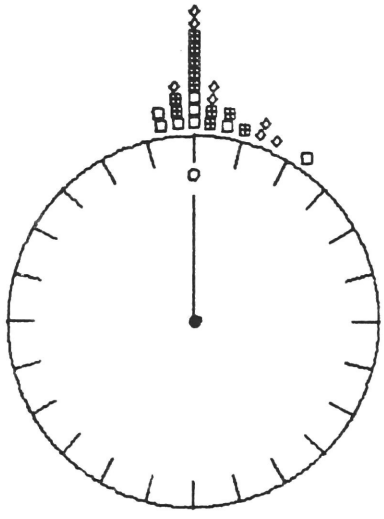

Figure V-2. Orientation of bees to a white, unpolarized light source at ZD of 57°. 17 September, completely overcast, 1145 EDT, sun at ZD of 42°, AZ of 152°.

There are a number of interesting aspects to consider about this solar orientation behavior. For example, bees always interpreted stimuli

as being the sun, irrespective of the actual zenith distance. In Figure V-2 for example, the solar orientation of the bees was quite precise even though the difference in zenith distance between the source and the sun as seen just previously by the bees outside the hive was 15°. The apparent unimportance of solar zenith distance for use of the sun as an orientation cue by animals is well known and was first reported by von Frisch (reviewed, 1967; p. 136) for honey bees. During the experiments summarized here, the artificial light sources at best only approximated the actual solar zenith distance at any time and the largest divergence was 30°. Over this rather limited range, there were no observed effects of solar zenith distance on the resultant waggle dance orientation. Presumably, the lack of importance of zenith distance is diagnostic of the mechanism of orientation.

While the bees were obviously insensitive to solar zenith distance, the opposite was true for the azimuth, since any change in the bearing of the source immediately produced deviations in the dance directions of the same magnitude and sign.

Another interesting aspect to consider was whether the light source needed to be constant in intensity (DC) to function as an effective cue. Although previous workers (e.g., van Praagh, 1975) have found that AC modulated lights induce aberrant flight behavior in honey bees, a series of simple tests comparing the orientation of bees to DC and AC powered light sources demonstrated no substantial differences for solar orientation under the conditions of my studies, as illustrated by Figures V-1 and V-2.

1.2 Sun hidden behind clouds during previous foraging flights.

When the sun was hidden behind cumulus clouds and patchy blue sky was visible, the waggle dance orientation to an unpolarized white light source did not differ in form or precision from those instances when the sun was directly visible. Even under complete overcast conditions during these experiments (uneven altostratus), the bees exhibited precise solar orientation. (On these reasonably warm overcast days with no rain the bees still foraged in large numbers.)

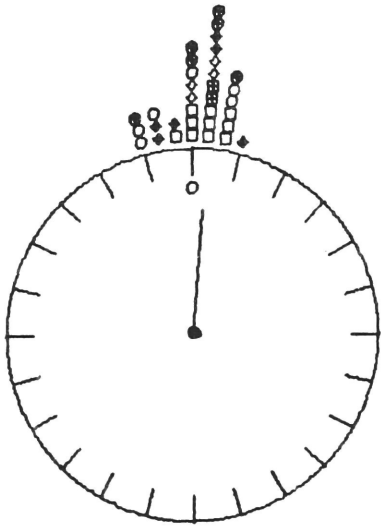

Figure V-3. Orientation of bees to a white, unpolarized light at ZD of 27° under complete, heavy overcast. 31 August, 1430 EDT, sun at ZD of 37°, AZ of 219°.

For example, the heaviest overcast (neither solar disc nor any blue sky visible) during an experiment occurred on 31 August 1977, when very dark, non-uniform altostratus clouds completely covered the sky. Figure V-3 summarizes the waggle dance orientation under these conditions and shows that in every respect they were as precise as dances when the sun could

be directly seen (by me). These results of good orientation on overcast days confirm the observations of von Frisch (1960, rev. 1967; pp. 366 ff.), in which he always found the bees well oriented to an artificial sun. The sky patterns which exist on overcast days are discussed in detail in Chapter III.

2. Responses of Bees to Polarized Light.

2.1 Some clear sky visible.

2.1.1 White polarized light.

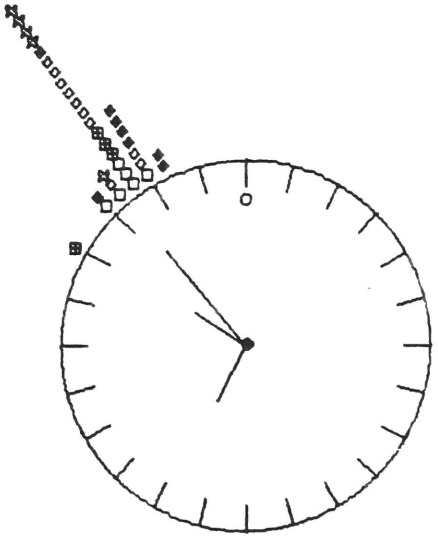

Figure V-4. Orientation of a single bee to polarized and unpolarized small white lights. 23 August, hazy blue sky, 1040 EDT, sun at ZD of 41°, AZ of 125°. Long vector indicates solar direction, short vectors are the two expected directions for the +50° E-vector.

When dancing bees were shown a small, white polarized light source, they almost always ignored its polarization and used it as if it was the sun.

Figure V-4, for example, illustrates that the waggle dance orientation to an unpolarized light source (with zenith distance 30°) was the same as that to a source polarized with an E-vector orientation of +50° (and zenith distance 54°). In this case, although it is clear that there are no dances in the direction corresponding to an interpretation of the stimulus as the part of the sky 113° to the right of the solar vertical, it is less certain that the bees are not interpreting the source as an area of the sky 14° to the right of the sun. However, since the distribution is peaked around the solar direction and is indistinguishable from the responses to an unpolarized light, it seems unlikely that the bees are using the polarization of the light source.

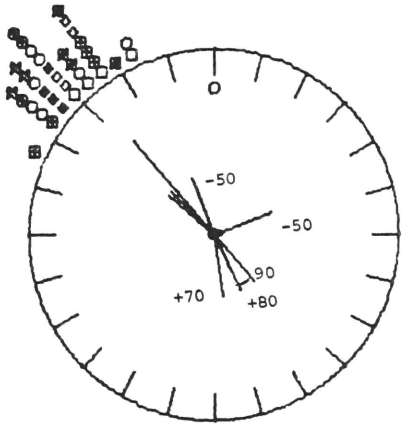

Figure V-5. Different bees dancing to a white, polarized light at ZD of 54°. 23 August, hazy blue sky, 1050 EDT, sun at ZD of 41°, AZ of 126°.

This is a principal methodological problem with this type of experiment: some E-vector orientations cannot be directly tested, since one of the

expected directions is so close to that predicted for solar orientation that it is impossible to distinguish between the two possibilities. Another example can be seen in Figure V-5 which summarizes the waggle dance directions of bees shown a light of a constant zenith distance (54°) but with varying E-vector orientation. Although it is obvious that none of the waggle dances are oriented in the direction appropriate for an interpretation of the source as a part of the sky relatively far from the sun, nothing definite can be concluded about whether the bees used the source as the sun or, on the basis of E-vector, part of the sky close to the sun.

At first thought, a simple solution to this ambiguous situation is to test the orientation of bees to an E-vector for which both corresponding points on the natural sky are relatively far from the sun. Considering the source zenith distances used here, in practice this meant that the E-vector orientation had to be close to vertical. Figures V-6 and V-7 for example, are the results of such a test and summarize waggle dance directions of bees viewing vertically polarized light. As shown in the first diagram, on the basis of the E-vector orientation of the source both predicted directions are located more than 50° in azimuth from the solar orientation prediction. Obviously, the bee danced in the solar direction and not in either of the directions predicted on the basis of the polarization. There is, however, one further possibility to control for: the bees may in fact be using the polarization but since there are two equally probable directions, they dance the <u>average</u> direction. This possibility can be tested by arranging for both predicted directions to fall on the same side of the sun. In no case I observed did the bees

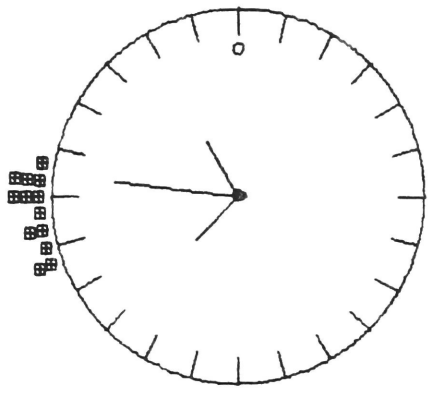

Figure V-6. Waggle directions of a bee to a vertically polarized, white light at ZD of 27°. 1 September, hazy blue sky, 1105 EDT, sun at ZD of 41°, AZ of 133°.

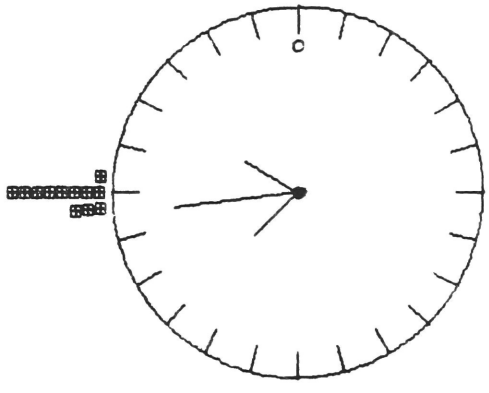

Figure V-7. Waggle dance directions of a bee to white, vertically polarized light at ZD of 27°. 26 August, partly cloudy, 1200 EDT, sun at ZD of 33°, AZ of 152°.

ever average the two possible directions derived on the basis of polarization.[1] Although E-vectors which are relatively close to vertical can be

1. Horizontally dancing bees in fact never averaged even two

directly tested, horizontal (or nearly horizontal) E-vectors must be tested by different methods since one of the predicted directions is the solar direction. There are a number of ways to do this and one is described below in section 2.3.2 which discusses the importance of source visual angle in honey bee orientation.

There is other evidence that honey bees do not respond to the polarization of small, white lights. For example, if the E-vector of the source is rotated into any position, a dancing bee never alters her dance orientation. Also, if bees are shown patterns which do not exist in the sky at a particular time, they nevertheless exhibit precise solar orientation. This is very different from when dancing bees do try to respond to "impossible" polarization patterns of a stimulus (discussed below). From the results of numerous tests, I conclude that bees either ignore the polarization of small, white lights or else they are incapable of detecting it.[2] Other examples supporting this conclusion are given in data of the following sections.

2.1.2 Non-white polarized light. The results just discussed show that when blue sky was visible during the foraging flights, bees interpreted a white, polarized source as the sun even if its E-vector orientation

---

different unpolarized sources visible to them. More extensive study of this phenomenon may give insights into the mechanism of how bees use visual cues while dancing.

2. It is interesting to note that these results agree with von Frisch's observations that dancing bees do not respond the E-vector orientation when they view the sun itself through a polarizing filter (von Frisch, 1967; p. 402). He found, for example, that rotation of the filter does not affect the dance orientation in any way. His bees, however, were sensitive to larger white polarized sources. These factors are discussed in detail below.

corresponded to a point in the natural sky. However, such a source may not have really been "natural" to the bees because although such a stimulus matched a part of the sky in E-vector orientation, in numerous other respects it did not. For example, obviously the clear sky is not white but blue (to us). Is color an important cue for the bees? To test this possibility, a series of experiments were carried out using different band-pass filters (Table IV-2) which were inserted perpendicularly into the stimulus beam. Each filter was individually tested to make certain that these experimental procedures did not change the polarization in the beam. The principle results are summarized below.

2.1.2.1 Blue polarized light. As discussed above, the basic experiments relied on using individual bees as their own controls: dancers oriented themselves to a series of different colored polarized lights. Two blue filters were used: (1) A Wratten #47 which is quite sharply peaked at 450 nm, and a Corning Glass Works #5900 which peaks at 400 nm, but has a broad transmission shoulder over most of the visible range. Results typical for such tests are shown in Figure V-8 (blue light produced by a #47 wratten filter). For this case, it is quite clear that the bees used such a polarized source as if it were the sun and there was no indication that its polarization was even detected. Analyzing a number of these cases, it was clear that the bees used both blue and white polarized stimuli only as if they were the sun.

2.1.2.2 Other visible wavelengths. In tests using other filters transmitting visible light listed in Table IV-2, the bees always interpreted a polarized source as the sun, regardless of the E-vector orientation, exactly the same as for white light. The only exception was for

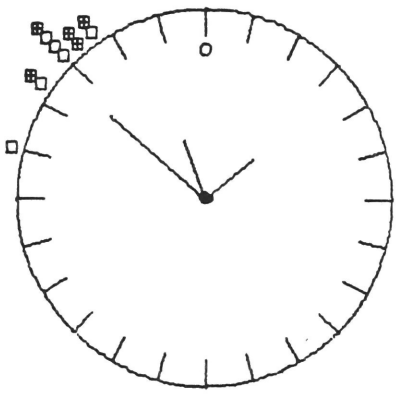

Figure V-8. Bee dancing to white (filled squares) and then a blue polarized light (open squares) at ZD of 54°. 23 August, hazy blue sky, 1115 EDT, sun at ZD of 37°, AZ of 134°.

the long wavelength red filter (Hoya R-70), to which the bees were always disoriented. This is understandable since the transmitted wavelengths (all greater than about 700 nm) fell outside of the visual range of bees (see, for example, von Frisch, 1967; pp. 471 ff.).

2.1.2.3 Ultraviolet. Unlike other spectral regions tested, when a source was made relatively rich in UV (either by absorbing the visible wavelengths of a white source, or using a rich UV source such as a mercury arc), the bees always interpreted it as if it were a part of the natural, polarized sky. Figure V-9, for example, illustrates the responses of an individual bee to successive changes from white to UV polarized light (zenith distance 27°) for two different E-vector orientations of 0° (vertical) and +60°. In this case, the bee began dancing to white, vertically polarized light. The crossed square symbols show that

the waggle dance orientation changes, pointing in one of the two directions predicted on the basis of the E-vector orientation of the light. Specifically, the bee interpreted the stimulus as if it was a point on the sky vault about 53° to the right of the sun. (As discussed above, since the dances take place under a fixed light source, the shift in horizontal dance direction is <u>opposite</u> to the relative bearing.) Then the filter was rotated 60° clockwise so that the E-vector orientation of the UV light was $+60^{\circ}$. The waggle dance directions immediately changed to one of the directions predicted on the basis of the $+60^{\circ}$ E-vector orientation, as illustrated by the filled diamond symbols. It is immediately puzzling that the responses to the polarization are not bimodal. This will be discussed in detail starting with section 2.2.1. Throughout these observations, a principal characteristic of the bees when they were using the polarization of the stimulus was that they always responded to changes in E-vector orientation by instantaneous shifts in their waggle dance direction.

It can be shown in a number of ways that the bees were really using the polarization of the stimulus to orient their waggle dances. As illustrated by the representative Figures V-10 and V-11, for example, the sign of the E-vector orientation determines which side of the plane of the solar vertical the corresponding point on the skyvault is located. Opposite E-vectors specify points of the sky with the same relative azimuth, but on opposite sides of the solar vertical. Thus, if the polarization is being used by the bees, the waggle dance direction should be reflected around the solar vertical by merely changing the sign of the E-vector orientation. Figures V-10 and V-11 (for the same bee) demon-

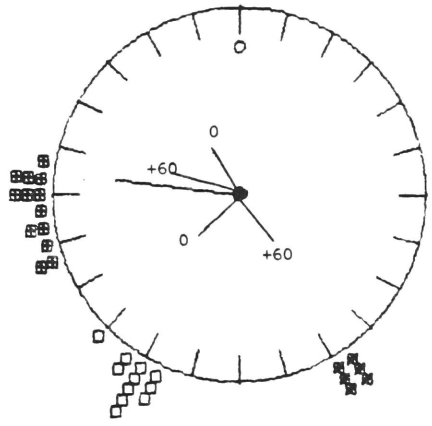

Figure V-9. Single bee dancing to white (filled squares) and then to UV polarized light.

strate this for a $\pm$ 50° E-vector orientation of a small UV light. Notice that at the same time $\pm$ 50° E-vector orientation of a white light elicits only solar orientation. This shows again the striking dependence of the interpretation of a white light as the sun and orientation on the basis of polarization on the wavelength distribution of the light source. Another example of the orientation of bees to E-vectors of equal magnitude but opposite sign is given in Figures V-12 and V-13 for a larger number of bees. Here, the change from +40° to -40° E-vector of an UV light resulted again, as predicted, in dance directions which are mirror images around the solar vertical. (The two waggle runs directly opposite to the principal directions in Figure V-13 will be discussed in detail in Chapter VI.) Figures V-14 to V-19 give additional examples of the orientation of bees to specific E-vector orientations. The bees assumed only one of the waggle directions predicted on the basis of the polarization only if the light was relatively rich in UV. If the stimulus was white,

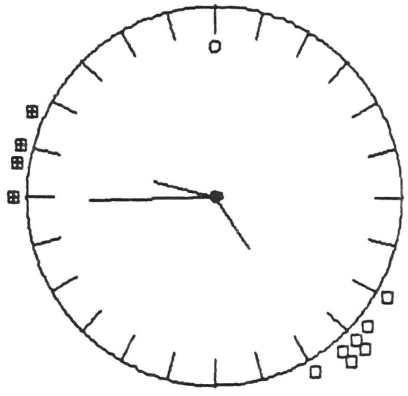

Figure V-10. Single bee orienting to a white and then a UV polarized light (open squares) at ZD of 27°. 1 September, hazy blue, 1110 EDT, sun at ZD of 40°, AZ of 135°.

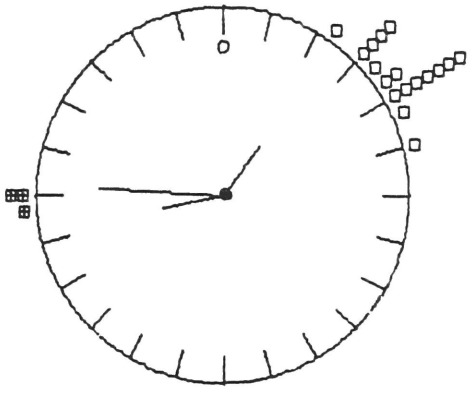

Figure V-11. Single bee (same as previous figure) orienting to a white (filled squares) and then UV polarized light.

(or another non-UV color) then it was interpreted by the bees as the sun.

There are several interesting aspects of the bees' orientation which will be considered here in some detail. 1) the importance of UV

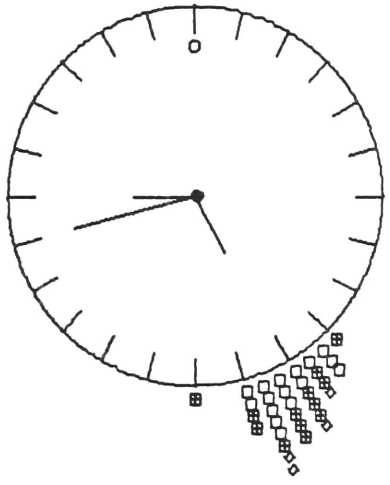

Figure V-12. Bees dancing to UV polarized light at ZD of 27° with E-vector at $+40^{o}$. 1 September, hazy blue, 1130 EDT, sun at ZD of 38°, AZ of 142°.

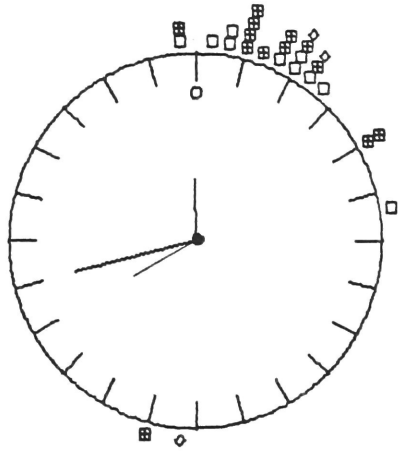

Figure V-13. Same bees as in Figure V-12 dancing to a -40° E-vector orientation.

wavelengths and 2) the influence of source size for honey bee orientation. The fact that bees orient by the polarization of an UV light is not of itself surprizing or new. As discussed in detail in Chapters I and III, von Frisch (1967; pp. 401 ff.) concluded that UV receptors alone

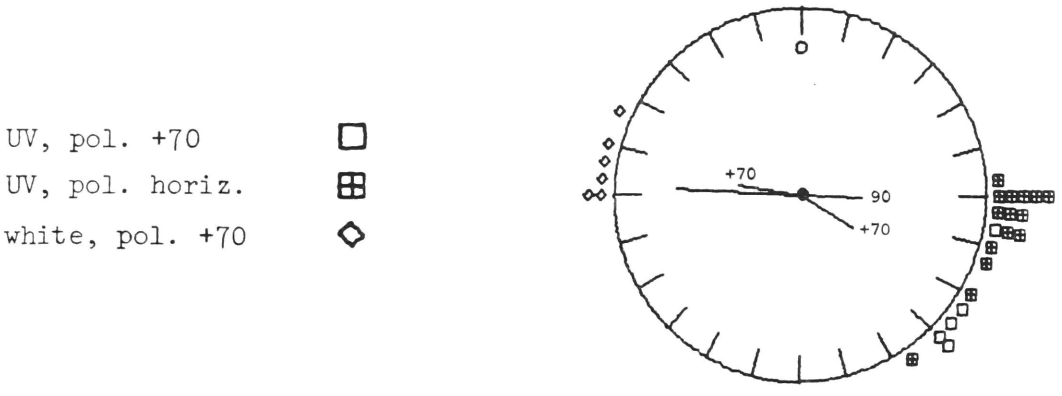

Figure V-14. Bee dancing to white and then UV polarized light. 1 September, clear sky, sun at ZD of 40°, AZ of 137°.

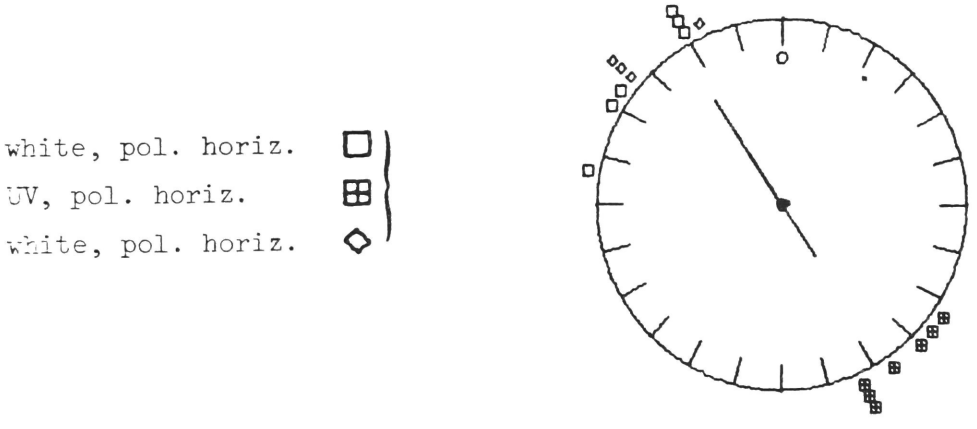

Figure V-15. Bee dancing to white and then UV polarized light at ZD of 33°. 17 September, patchy blue sky, 1340 EDT, sun at ZD of 39°, AZ of 196°.

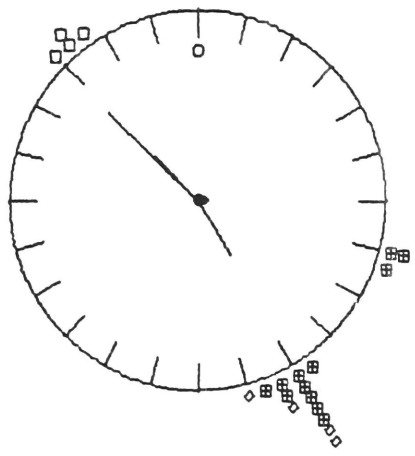

Figure V-16. Bee dancing to white (open squares) and then UV +80° polarized light at ZD of 51°. 20 August, 1110 EDT, sun at ZD of 37°, AZ of 131°.

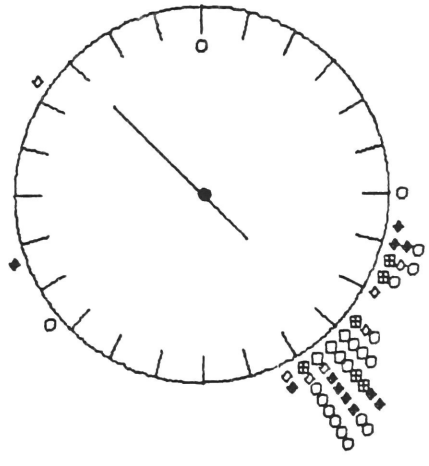

Figure V-17. Bees dancing to UV polarized light with horizontal E-vector at ZD of 54°. 23 August, 1045 EDT, clear blue sky, sun at ZD of 41°, AZ of 125°.

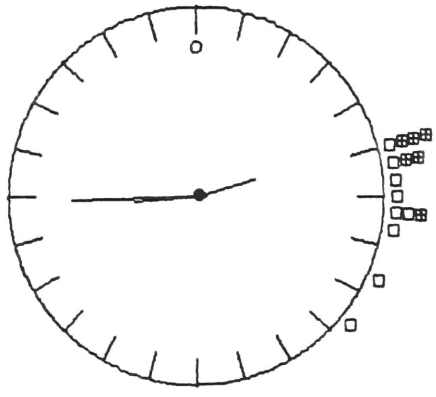

Figure V-18. Bee dancing to UV polarized light with -80° E-vector, ZD of 27°. 1 September, 1140 EDT, sun ZD of 37°, AZ of 145°.

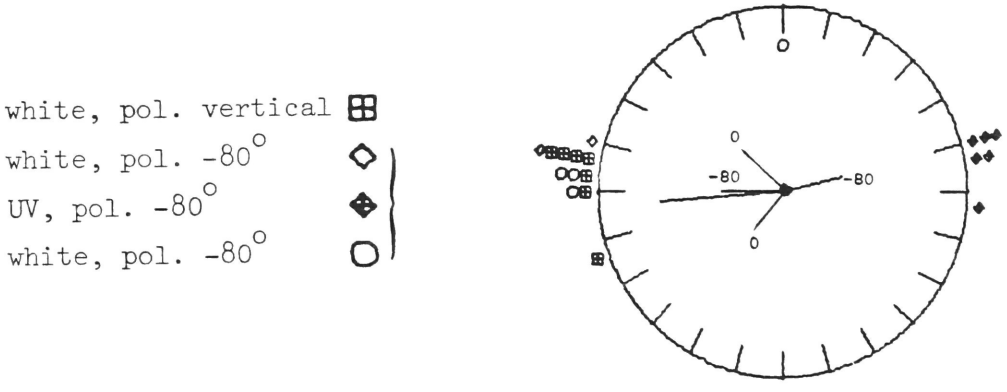

Figure V-19. Bees dancing to white and then UV polarized light at a ZD of 27°. 1 September, 1140 EDT, clear blue sky, sun at ZD of 37°, AZ of 145°.

are probably responsible for polarization sensitivity in honey bees and this has been confirmed by other behavioral (von Helversen and Edrich, 1974) and neurophysiological (Menzel and Snyder, 1974) studies which show that responses to the polarization of light depend on the UV receptors. What is novel about my results is that the bees responded to the polarization in a stimulus only if it was relatively rich in UV. This is puzzling because von Frisch found that honey bee polarization orientation was qualitatively the same whether bees viewed blue, UV, or even white (containing UV) polarized sources (von Frisch, 1967; p. 396). In contrast, under the experimental conditions reported here, honey bees did not orient to the polarization of a blue light, nor to a white, polarized light which contained more UV photons that when a UV transmiting filter was used alone.

Such differences could be explained by "masking" effects if, under certain conditions, longer wavelengths inhibit the polarization responses of the bees so that they use only solar orientation in their dances. This hypothesis was supported in an interesting way by testing bees with a Kodak #35 Wratten filter, which transmitted a large amount of UV, and also a fair amount of blue and long wavelength red. Considering the relatively large UV content, and also the longer wavelengths, I expected that some intermediate "masking" might be evident. Indeed, as Figure V-20 shows, the waggle deviation was much higher than with the other, "purer" UV filters and both solar and polarization orientation was assumed by individual bees. The orientation responses to polarized light transmitted through a Wratten #35 filter were always intermediate in form when compared to those for white or UV light derived by the use of other

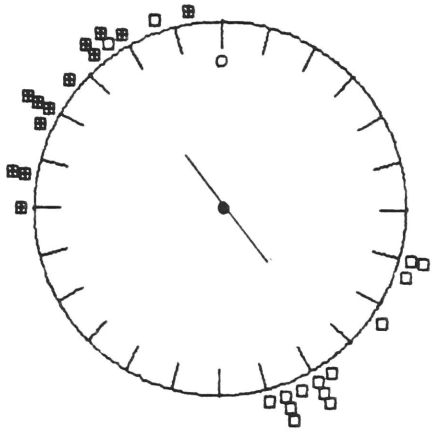

Figure V-20. Orientation of a individual bee to a horizontally polarized light seen through a Wratten #35 filter at ZD of 54°. 23 August, hazy blue sky, 1105 EDT, sun at ZD of 39°, AZ of 129°.

filters.

2.2 The unimodal dance orientation to polarized light.

The results of the previous experiments show that bees orient their waggle dances to small, polarized UV stimuli as if they were parts of the blue sky. One curious feature already noted is that in their dances the bees generally assume only one of the two directions predicted on the basis of the E-vector orientation of the stimulus light--somehow they eliminate the other possibility and dance unimodally. Does this mean that additional polarization variables besides the E-vector orientation are important in honey bee orientation? This possibility can be appreciated by considering again the fact that although a particular E-vector orientation (at a specific zenith distance) generally exists at two different spots in the natural sky, these points are not physically

equivalent. For example, they usually lie at different angular distances from the sun which means that they have unequal scattering angles and thus differ in color, degree of polarization, and intensity.

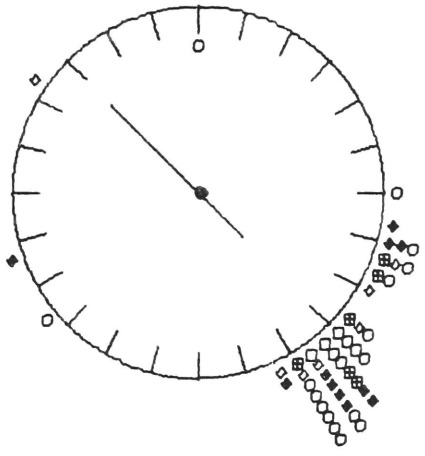

Figure V-21. Bees dancing to UV, horizontally polarized light at ZD of 54°. 23 August, hazy blue, 1045 EDT, sun at 41°, AZ of 125°.

As a specific example of unimodal orientation, Figure V-21 shows that bees viewing a horizontally polarized light danced mainly in one direction. On the basis of E-vector orientation alone, the stimulus corresponded to skypoints with zenith distances of 54° in the solar and antisolar vertical. Although these points have the same E-vector orientation, their scattering angles are very different: 13° and 96°. The large scattering angle for the second point means that the corresponding place on the sky vault had a high degree of polarization (close to the band of maximum polarization at about 90° from the sun), was a relatively saturated blue, and had relatively low radiance. This contrasts to the first point which corresponds to a low degree of polarization, unsa-

turated color, and a relatively high radiance since it is quite close to the sun. Considering these factors, the artificial polarization stimulus corresponded more closely to the second point since it was relatively rich in UV and highly polarized.[3] Did the bees use this (or some similar variable) to distinguish between the two possible directions based on E-vector alone?

2.2.1 Further tests for unimodal orientation. Fortunately, it is easy to arrange a straightforward test to show whether the bees are using associated optical cues to distinguish between the two possibilities. This test employs two skypoints which are physically identical in all respects except azimuth. Then, any asymmetry in the bees' responses must arise by biological factors alone. Such skypoints do exist naturally on the sky vault, and have vertical E-vector orientations ($X = 0^{\circ}$). All skypoints with vertical E-vector orientations are located symmetrically on the opposite sides of the solar vertical. Since these two points have the same scattering angle, they are theoretically identical in color, radiance, and degree of polarization. A bee shown such ambiguous stimuli should be unable to distinguish between them by using any optical cues.

For an experiment, well established foragers (from a feeder 700 m distant) danced on a horizontal hive under a vertically polarized light of wavelengths below 410 nm. The general experimental procedures were identical to those already described, except that the predicted directions were calculated in advance of the experiment to make certain that

3. Of course the radiance of the artificial stimulus was very different from the natural sky. But is is difficult to imagine how the bees could compare the absolute radiance inside the laboratory to that in the natural sky outside.

the zenith distance of the vertically polarized source was appropriate for artificial sky spots corresponding to a part of the natural sky polarized highly enough to be detected by the bees on their foraging flights outside. This was a practical necessity because for the zenith distances used in these experiments, vertical E-vector orientation tended to occur only relatively close to the sun. In practice, the zenith distance of the artificial source was selected so that the spot had a corresponding bearing greater than 40° from the sun. For the natural summer sky at Princeton, N.J., this area of the sky generally had greater than 15% polarization in the UV (see Chapter III).

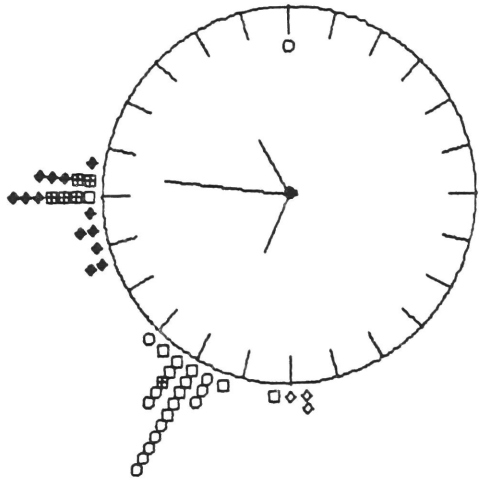

Figure V-22. Two bees dancing to a white (filled symbols) and then UV vertically polarized light at ZD of 27°, 1 September, hazy blue, 1105 EDT, sun at ZD of 41°, AZ of 133°.

A representative example of these experiments with vertical E-vectors is Figure V-22. When the bees were shown vertically polarized white light they interpreted the stimulus as if it was the sun (except for a single waggle run). But, when wavelengths greater than 410 nm were removed from

the beam, both bees selected only <u>one</u> of the two predicted directions.

In the series of vertical polarization tests, the bees <u>never</u> danced in directions appropriate for the two predicted polarization directions, although they did occasionally dance bimodally.[4]

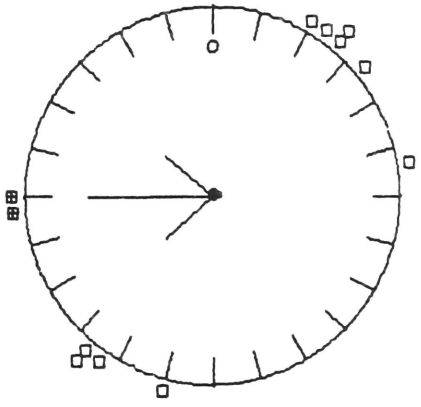

Figure V-23. Dance of single bee shown white, vertically polarized light (filled squares) and then UV, vertically polarized light at ZD of 27°. 26 August, patchy blue sky, 1145 EDT, sun at ZD of 34°, AZ of 146°.

But, as illustrated by Figure V-23, the two resulting dance directions did <u>not</u> correspond to those predicted on the basis of E-vector orientation. Rather, in addition to dancing in the same direction as the unimodally oriented bees, they also danced in the <u>opposite</u> direction. The implications of these oppositely directed bimodal dances will be discussed in Chapter VI.

4. When the E-vector orientation was close to vertical I observed a definite tendency for bees to dance to even a white, polarized source as if it was a skypoint. This is discussed below.

2.2.2 How do bees select only a single direction under these circumstances? One possible way bees might select a single direction from two physically equivalent possibilities is that during their flights outside the hive, the two different skypoints did not have the same "salience". This could possibly arise from many factors--e.g., interactions of the geometry of the celestial cues and the direction of the foraging flight, the effects of atmospheric disturbances, and so on. These factors are especially important in view of the observations of von Frisch (1967) and Lindauer (1961) that the actual flight path of bees is strongly influenced by optical features of the local terrestrial environment. For example, bees are easily "misled" by roads, hedgerows, stands of trees, and so on. By using displacement methods, Otto (1959; reviewed by von Frisch, 1967; pp. 169 ff.) investigated these phenomena extensively and showed that dances could be affected in similar ways. Specifically, he found that in general the position of the sun on the outward flight was the important optical cue for the dances, as long as the solar bearing was greater than 30° from the line of flight. If it was not, then the bees danced opposite to the predicted directions, and they indicated a flight direction which they never flew. Considering the vertical polarization experiments just discussed, was it possible that the bees selected only one of the two predicted directions because for some reason the patterns were of different optical "importance" to them? Stated in another way, did the bees eliminate the orientational ambiguities by weighting the optical cues unequally depending upon their relative orientation during flights to the goal? For example, the direction selected by a bee in one of these vertical E-vector experiments (Figure V-23) corresponds to the skypoint behind the bee on its outward flight. Do

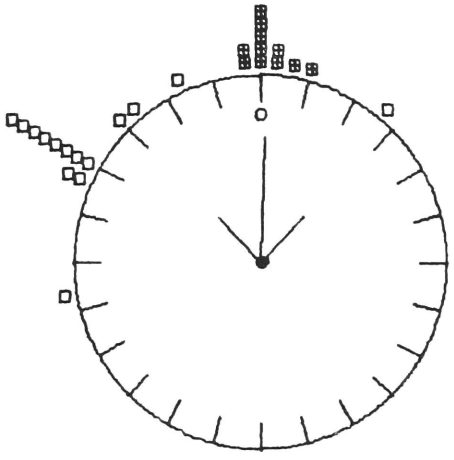

Figure V-24. Orientation of a single bee to a white unpolarized (filled squares) and then a UV vertically polarized light at ZD of 33°. 17 September, partly cloudy, 1145 EDT, sun at ZD of 42°, AZ of 157°.

bees always use for their dances the sky point which is farther behind them?

To test for possible effects of such salience, dancing bees were shown vertically polarized stimuli after they had flown directly towards the sun over a large, relatively featureless field to reach the goal. On their outward flights these bees could see two skypoints with identical polarization located symmetrically to their body axis. Assuming that the compound eyes are symmetrical, if the waggle directions were still unimodal under these conditions, it could not be easily explained by any "weighting" strategy.

Due to procedural difficulties, only one of these experiments was performed. Initially the sky was quite overcast but it had cleared to large areas of unsaturated blue by the time of the experiment. Bees were

trained to forage from a feeder (distance of 200 m) on the Princeton University campus over an athletic playing field. Two light sources located in the same vertical were used as stimuli back inside the hive. One was unpolarized and established the solar (control) dance direction. The other was a polarized quartz-halogen source with a UV transmitting filter (Hoya 330). When the sun was in the direction of the feeder, individually marked bees were shown vertically polarized UV light (E-vector selected to correspond to an azimuth greater than 40° from the solar vertical) when they returned to the hive. As illustrated by Figure V-24, the bee responded to the vertical polarization of the artificial stimulus by orienting most of her dances dances in only <u>one</u> of the two predicted directions. Even though the two points of the sky corresponding to the artificial source were made as similar as possible, the bees still selected only one of the pair. It is very interesting to note that in these vertical polarization experiments the bees always used a direction which corresponded to a skypoint on the <u>right</u> of the solar vertical. Although some bimodal dances did rarely occur, no waggle runs ever corresponded to the direction of points in the sky to the <u>left</u> of the solar vertical. Rather, these rare exceptions were exactly <u>opposite</u> to the skypoint on the right of the sun. This hypothesis should be tested under completely clear conditions. However, in view of the absence of any demonstrable physical differences between the two sky points at that time, the factor(s) allowing the bees to select between the two possibilities must exist in the nervous system of the bee. Perhaps they have evolved certain "rules" for eliminating all ambiguous situations. Considering the natural history of bees, this is especially important because the effectiveness of the dance language depends to a large extent

on how well the bees are able to specify unambiguously the precise location of a goal. This subject is discussed in detail in Chapter VI.

2.3 Importance of visual angle.

That bees use a small, white polarized stimulus as the sun, unlike UV-polarized sources, has already been described. Another interesting aspect of my experiments were observations of orientation to polarized UV stimuli much smaller (as small as 0.5^{o}) than the minimum von Frisch found for his bees. Are the unimodal dances somehow dependent on the size of the stimulus? For example, the stimuli might just have been incident on an area of the eye smaller than the minimum receptor configuration necessary to detect white polarized light. To test for this possibility, an experiment was carried out to determine whether larger sources of white polarized light, which stimulated the compound eye more extensively, might provide effective polarization stimuli.

There are several important considerations in the design of such an experiment. For example, changing the visual angle by moving a single extended source relative to the bees was not appropriate since a constant geometry should not be assured and the quick changes of stimulus configuration necessary to test a single bee were impossible. To circumvent this problem I utilized the fact that the light sources used in these experiments possessed slightly diverging beam cross sections. By inserting translucent screens perpendicularly into the beam at various distances from the source, the apparent source size as seen by the bee could be changed over relatively wide limits while still preserving by and large the geometrical configuration.

One important consideration in this study, of course, was that such a screen could not change the polarization form. By trial and error a frosted cellulose acetate was found (#300 matte "supersee", Morilla Company, New York City) which had high transmission (including the near UV), low depolarization, and very low birefrigence. Thus, polarized light passing through this sheet was quite similar to the incident light, except that to the bees, it appeared to come from a larger, dimmer source. In this way, the visual angle could be continuously varied from about 5° (0.006 ster) to about 32° (0.25 ster).

In preliminary experiments, individually marked bees were trained to forage from a feeder (700 m distant at azimuth 60°), and when they returned to the horizontal hive they were presented with the adjustable diameter polarization source as an orientation cue. The results of these tests showed that when the visual angle subtended at the dancing bees was large enough, the bees <u>did</u> interpret a white polarized source as a part of the sky and oriented their waggle dances on the basis of its E-vector. For example, small rotations of the polarizer produced immediate changes in waggle dance direction. Since the other variables were virtually constant under these conditions, this could only happen if the bees were using the <u>orientation of the E-vector</u> in the stimulus light as an orientation cue. The behavior was quantified by recording actual dance directions, such as in the examples illustrated by Figures V-25 to V-28 which summarize the responses of bees to horizontally polarized light. First, these bees were allowed to make several waggle runs under a small, white, polarized source (control) before the diffusing screen was inserted into the beam to produce a larger visual angle (about 18° in this figure).

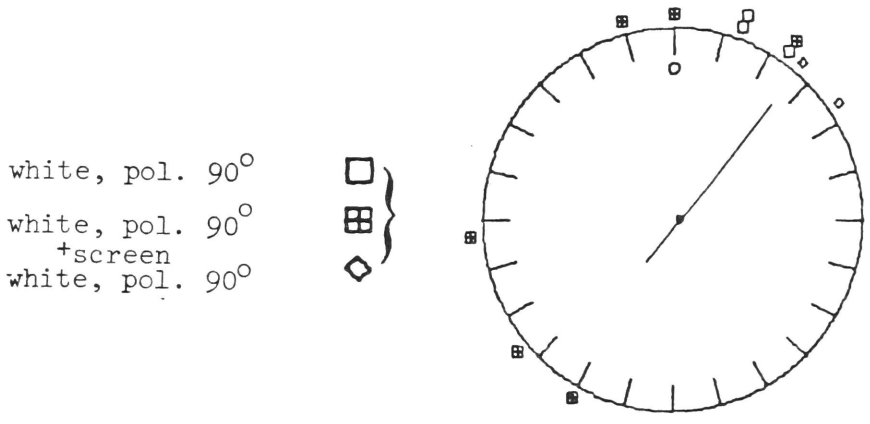

Figure V-25. Bee dancing under a diffusing screen. 15 August, 1100 EDT, clear blue sky, sun at ZD of 38°, AZ of 128°.

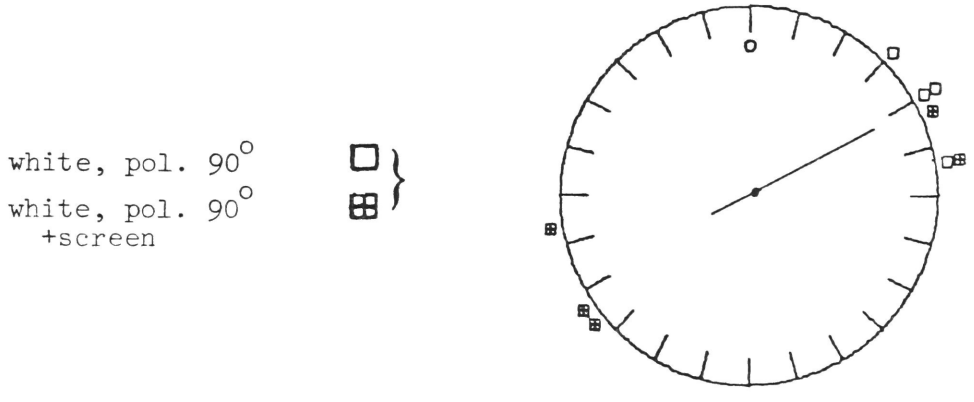

Figure V-26. Bee dancing under a diffusing screen to a horizontal E-vector at ZD of 50°. Spot szie about 18°. 15 August, 1115 EDT, sun at ZD of 35°, AZ of 132°.

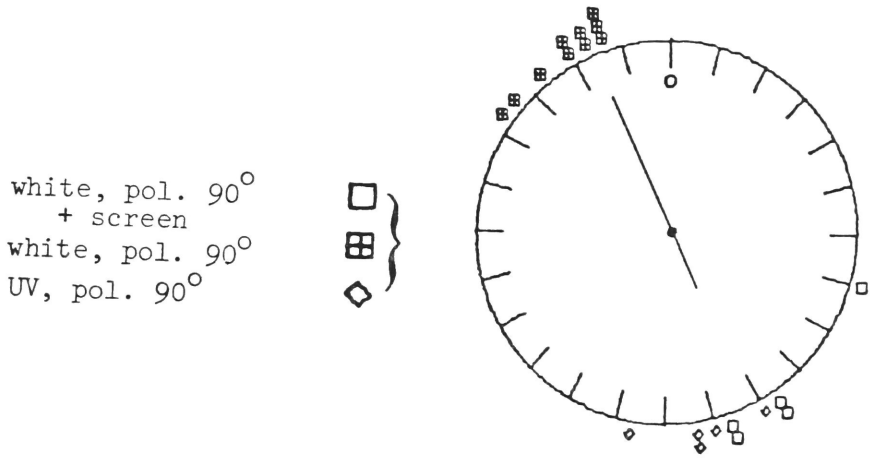

Figure V-27. Bee dancing under a diffusing screen to horizontally polarized white light and then a UV light. 15 August, 1115 EDT.

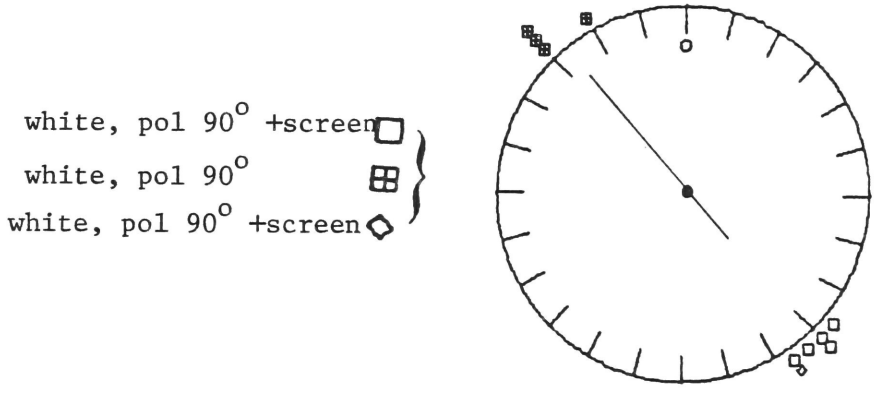

Figure V-28. Bee dancing under diffusing screen to horizontally polarized white light. 15 August, 1105 EDT.

Assuming that bees use the E-vector orientation, the expected waggle directions (in this case horizontal E-vector) are in the control direction (no screen) and 180° (opposite to it). Results of these experiments showed clearly that the bees selected only the 180° direction[5] and are identical to the results previously reported for small, UV sources which were horizontally polarized (for example, by Figure V-17).[6]

3. The importance of visual angle, spectral distribution, and degree of polarization.

The results of the preliminary experiments suggest that the spectral distribution and the visual angle subtended by a polarized light source were important factors in determining whether a source was interpreted by the bees as a part of the sky or as the sun. Since it is of interest to know specifically how these variables interact, a detailed experiment[7] was carried out which tested the variables of spectral distribution, and visual angle, along with per cent polarization, another possibly important variable. As summarized in Table V-2, sixty-six combinations of these three variables were shown to bees dancing under a xenon arc lamp. Horizontal E-vector orientation was used throughout so that the predicted

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5. It was my impression that dance directions were more scattered than for non-horizontal E-vector orientation. This factor should be investigated more thoroughly.

6. It is important to point out that the dance directions elicited by a visual stimulus subtending about 18° of visual angle are qualitatively the same as those for small, UV polarized lights with the same E-vector orientation. This shows the dance direction is not necessarily selected on the basis of either spectral distribution or size of the visual stimulus.

7. Done in collaboration with James L. Gould.

Table V-2. The 118 stimuli combinations used to generate Figure V-29. An "x" indicates waggle dance data were collected for that Stimulus configuration.

visual angle	zero				twenty				forty-one				sixty-five				one hundred (% UV)				
	0	18	56	94	0	18	56	94	0	18	56	94	0	18	56	94	0	18	56	94	(% polarization)
30	x	x	x	x	x	x	x	x	x	x	x	x					x		x	x	
25	x		x	x	x		x	x	x		x	x					x	x	x	x	
20	x	x	x	x	x	x	x	x	x	x	x	x					x		x	x	
15	x	x	x	x	x	x	x	x	x	x	x	x					x		x	x	
10	x	x	x	x	x		x	x	x	x	x	x		x			x	x	x	x	
7.5	x		x	x	x		x	x	x		x	x			x	x	x		x	x	
5	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
2.5	x		x	x	x		x	x	x		x	x			x	x	x		x	x	

Table V-3. Results of tests of 118 different stimulus configurations of per cent polarization, visual angle, and per cent UV (with respect to the bees' visual sensitivity function). The number of dances observed (of at least five waggle runs) are given in parentheses. Numbers after "/" indcate dances which had relatively large deviations. S = interpretation of the source as the sun; P = interpretation of the source as a part of the sky (on the basis of its E-vector orientation); D = disoriented dances. Thus, s(45/8) indcates that 45 dances showing a solar interpretation were observed with an additional 8 exhibiting increased deviation, although still predominently in the solar direction.

	VISUAL ANGLE	0	20	41	65	100 % UV
0 % POLARIZATION	30	s(10)	s(10)	D(10)		D(10)
	25	s(5)	s(10)	D(10)		D(10)
	20	s(45)	s(35)	D(25)		D(15)
	15	s(40)	s(15)	D(15)		D(10)
	10	s(30)	s(15)	D(15)		D(10)
	7.5	s(39)	s(25/2)	D(15)		D(11)
	5	s(157)	s(50/5)	D(10)		D(18)
	2.5	s(45)	s(25/2)	D(12)		D(5)
18 % POLARIZATION	30	D(10)	P(9/1)			
	25					P(10/1)
	20	D(12)	P(10)			
	15	s(9/3) D(4)	s(5/2) P(8/1)			
	10	s(10)		P(10)	P(10/1)	P(10)
	7.5					
	5	s(10)	s(8/2) D(2) P(4/1)	P(6/4)	P(12/1)	P(10)
	2.5					
56 % POLARIZATION	30	D(7)	P(8)	D(5) P(25/3)		D(6) P(13/2)
	25	D(5)	P(8)	s(1) D(2) P(12)		s(1) P(23)
	20	s(17/2) D(18)	s(14) D(9) P(18)	s(3) D(3) P(18)		s(1) P(21)
	15	s(24/5) D(2)	s(13) D(2) P(10)	P(13)		P(10)
	10	s(36/2)	s(5) D(2) P(16)	P(19)		P(10)
	7.5	s(19)	s(8) D(1) P(8)	P(12)	P(5)	P(10)
	5	s(35/1)	s(13/10) P(3)	s(4) D(2) P(4)	P(10)	P(15)
	2.5	s(40)	s(4/12)	s(9) P(11)	P(10)	P(10)
94 % POLARIZATION	30	D(10)	P(5)	P(10)		P(10)
	25	D(10)	s(1) D(2) P(6)	P(10)		P(10)
	20	s(12/1)	s(9) D(9) P(31)	P(20)		P(25)
	15	s(28/7)	s(10) D(4) P(6)	P(10)		P(15)
	10	s(10)	s(8) D(5) P(4)	P(10)		P(15)
	7.5	s(45/8) D(3)	s(21/8) D(4) P(14/2)	s(3) D(3) P(20/3)	P(10)	s(2) D(1) P(27/1)
	5	s(10/12)	s(71/6) D(7) P(6)	s(6/2) D(8) P(35/7)	P(10)	P(35/7)
	2.5	s(45/2)	s(10/10)	s(10) D(8) P(10/2)	P(10)	P(5)

solar direction differed maximally from the dances cued by the polarization. Under these conditions, bees were easily categorized into 5 classes: 1) solar orientation; 2) sky orientation; 3) oriented in some other direction; 4) disoriented; or 5) orientation including both sun and sky components was observed. Only dances of greater than 5 cycles each were used, and a total of about 2500 complete dances were analyzed. The results are summarized in Table V-3 and shown graphically in the three dimensional plot of Figure V-29.

3.1 Demonstration of the importance of source size using a single source. The effects of visual source size on honey bee orientation can be demonstrated with a single lamp. I used an ordinary 75 watt desk lamp with a white reflector of 20 cm diameter, located about 55 cm from the dance floor which subtended a visual angle of about 20° (0.1 ster). If a large piece of HN-32 neutral polarizing film (Polaroid Corp.) was placed over the entire lamp/reflector, the bees interpreted this source as if it was a part of the blue sky, and used its E-vector orientation. If, however, a sheet of translucent, white paper (which virtually depolarized the transmitted light) with a 5 cm diameter hole was placed over this polarized source (visual angle of the polarized spot was then about 5°), the bees danced as if the polarized light was the sun. In this manner, the waggle directions could be made to assume either solar or skylight orientation at the experimenter's choice, merely by making the source subtend a larger or smaller visual angle.

3.2 Can bees ever use the polarization in a small white source?

Several previous investigations of the importance of polarization source

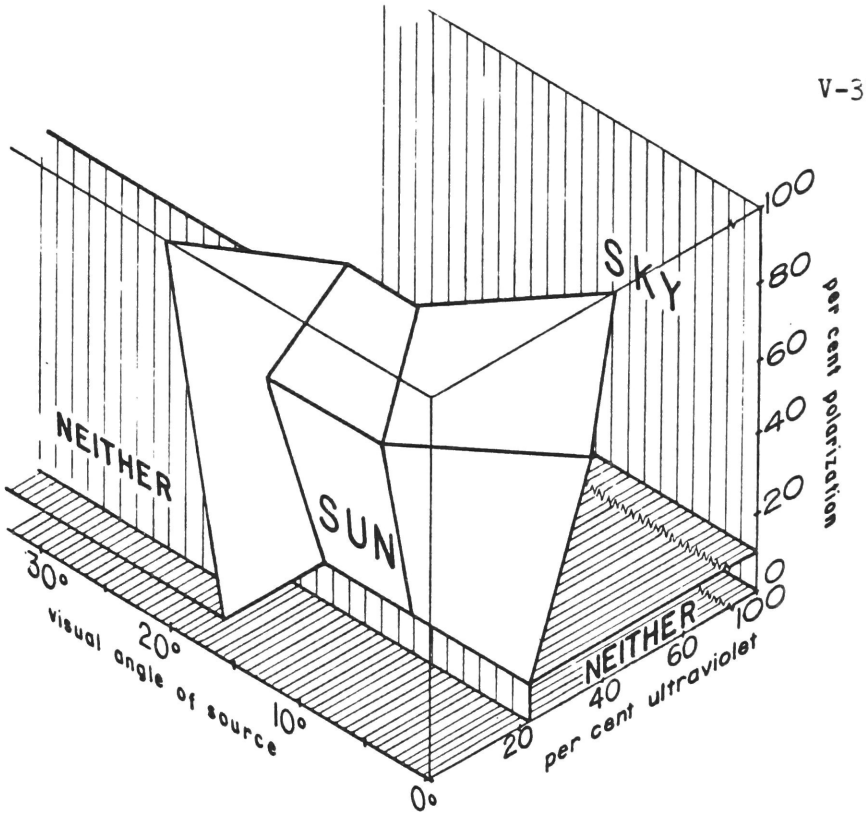

Figure V-29. Optical properties that determine whether a light is interpreted by honey bees as sun or sky.

Bees dancing on a horizontal surface were presented with stimulus diameters of 2.5, 5, 10, 20, and 30° (near boundaries also 7.5, 15, and 25°), polarization of 0, 18, 56, and 94%, and spectral distributions of 0, 20, 41, 65, and 100% UV. Approximately 2500 dance cycles were recorded: at least five cycles from each of at least five dances. The bees interpreted these stimuli in three ways: As the sun, as blue sky, or neither. Near the boundary surface between "sun" and "sky", a bee may exhibit both types of orientation in different dance cycles. The threshold of approximately 10% polarization confirms the data of von Frisch. Absolute intensity is unimportant unless the light is so dim that the bees are disoriented. Conditions resulting in disorientation ("neither") do not exist in the clear natural sky. Only the relative proportion of UV seems important in spectral composition. Elevation of the stimulus pattern was usually 33°; but except in the zenith, this factor also seems unimportant to bees for distinguishing between "sun" and "sky".

size and bee orientation (von Frisch, 1948; 1949; 1967; p. 380; and Zolotov and Frantsevich, 1973) concluded that the lower spatial threshold for polarization orientation is about 10° - 15° of visual angle. This contrasts greatly with my results just described which show clearly that

bees dancing on a horizontal surface use a small, white, polarized source as if it was the sun. They also differ from those of Edrich and von Helversen (1976), who used small fields of polarized light from a xenon arc lamp and also 1) white, 2) broad band UV (derived by a Schott UG-1 filter), or 3) narrow band UV (by a 355 nm interference filter). They found that dancing bees were quite well oriented for white light stimuli down to 1° visual angle.[8] What are the sources of these major differences?

One main methodological difference between my experiments and those of Edrich and von Helversen is that they presented their stimuli only from the zenith (to make certain that about the same group of ommatidia were always stimulated regardless of the circling movements during the dance). Choice of the zenith direction may have been unfortunate since it is a singular point on the sky vault and lacks an azimuth. Thus, due to this factor alone, honey bees (with their orientation system based on relative azimuth), cannot be expected to interpret a source in the zenith as the sun and might be "forced" to use polarization cues instead. That the sun in the zenith cannot provide a direction for the bees is supported by the work of Lindauer (1957), New (1961), and New and New (1962) who have shown by behavioral experiments performed in the tropics that when the sun passes through the zenith, bees can no longer reference directions with respect to the sun and are disoriented. In contrast to an ambiguous zenith sun, azimuth <u>can</u>, of course, be specified for a linearly polarized zenith light, since polarization has the added

8. Their observations that the visual fields required for good orientation to UV light were larger probably result from the general decrease in beam intensity produced by the ultraviolet filters.

geometrical dimensionality of E-vector orientation. This means that the zenith can be used at least as a skymark. However, the consequences of primary scattering impart additional information since the sun is always located along a great (vertical) circle passing through the zenith and is perpendicular to the E-vector of the polarized light there. Thus, with no other optical cues, it would be expected that solar azimuth determined from zenith point polarization characteristics should be bimodal: i.e., 180° apart. Such bimodality was always observed by Edrich and von Helversen (1976) during their investigations and also by von Frisch (1967; p. 397) in his zenith polarization experiments. It thus seems probable that the observations of Edrich and von Helversen are actually a special case--polarization orientation to small, white sources for zenith stimuli may exist because they cannot be used as the sun.

To test this idea, dancing bees were shown polarization patterns in the zenith. For all observations, when the bees viewed a small, white polarized stimulus their waggle dance orientation showed precise, bimodal dances in the directions expected on the basis of the E-vector orientation. For example, Figures V-30 to V-35 show this feature for the dance directions of single bees. Figures V-30 and V-31 summarize the waggle direction of a single, long-dancing bee to a specific orientation of the E-vector (Figure V-30) and then a 45° rotation of it (Figure V-31). Clearly, the waggle directions changed by the predicted 45°.

It can be very easily demonstrated that short wavelengths are essential for this orientation by using filters which absorb UV. For example, Figure V-36 records the disoriented dances which occurred when UV was removed from a white light source by using a filter which absorbed UV

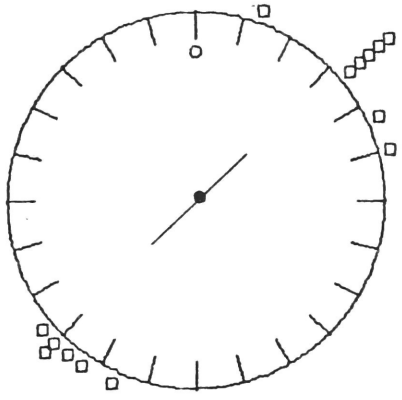

Figure V-30. Single bee, dancing for a white polarized light in zenith. 12 October, clear sky, 1520 EDT, sun at ZD 45°, AZ of 233°.

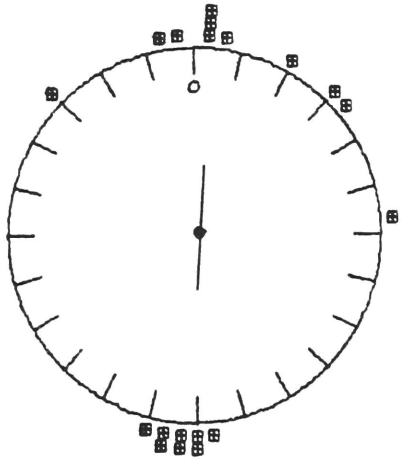

Figure V-31. Same bee as Figure V-30 dancing to a 45° shift in the E-vector orientation.

less than 420 nm (Hoya L-42 filter). Even flickering (60 hz AC) lights did not drastically affect the dance orientation underneath zenith lights, as Figure V-37 shows. The dependence of the orientation on UV wavelengths was shown in another way by using a tungsten filament with

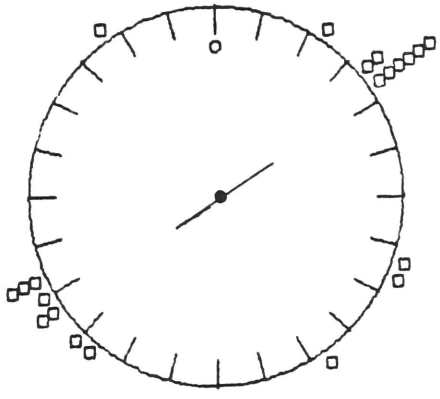

Figure V-32. Bee dancing under a white polarized light in the zenith. 12 October, clear sky, 1835 EDT, sun at ZD of 90°, AZ of 260°.

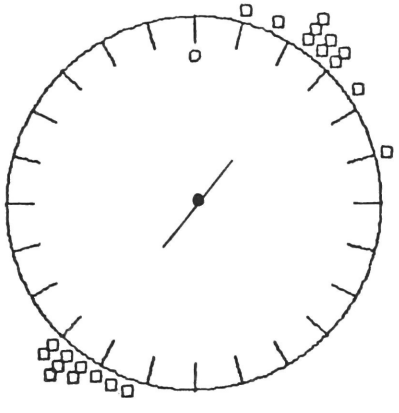

Figure V-33. Different bee dancing under a zenith polarized source, under the same conditions as Figure V-32.

little UV. All dances to such a source, as summarized by the example of Figure V-37, showed much greater variance.

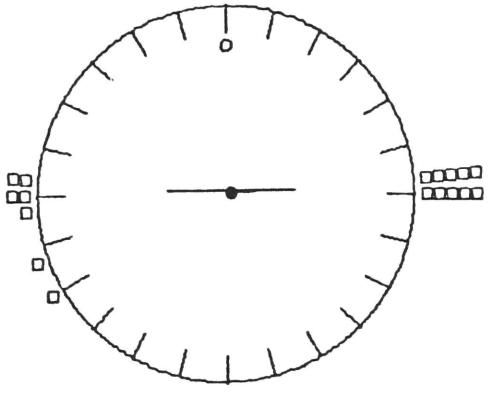

Figure V-34. Different bee dancing to a shift of the plane of polarization under the same conditions as Figure V-32.

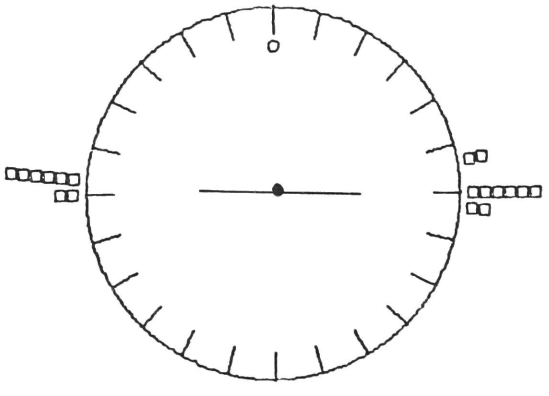

Figure V-35. Different bee dancing to the same conditions of Figure V-34.

Although no systematic tests were performed to determine at what zenith distance honey bees begin to interpret a small, polarized white source as the sun, a few rough measurements indicated that the transition occurred at least by a zenith distance of 8°. I expect that a detailed study will

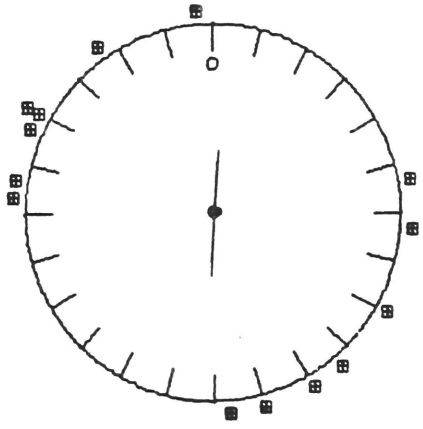

Figure V-36. Waggle directions of a bee dancing under a zenith polarized light with UV wavelengths removed. Same conditions as Figure V-32.

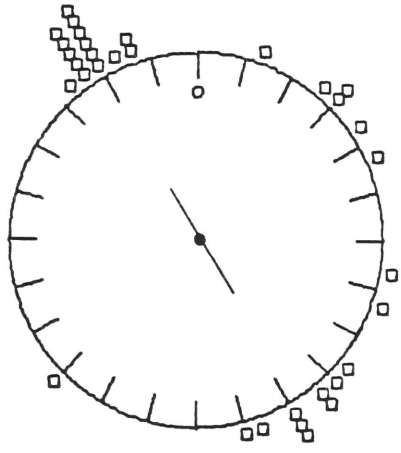

Figure V-37. Waggle directions of a bee to an AC white polarized light in the zenith. 23 August, clear sky, 1150 EDT, sun at ZD of 33°, AZ of 147°.

show that the transition point corresponds to the maximum solar zenith distance which can still be successfully used for solar orientation,

which has been worked out by Lindauer (1957). Specifically, as the sun passed overhead through the zenith, he observed dances on a horizontal comb and found that when the solar zenith distances was less the 2° - 3°, the bees stopped their foraging and refused to dance. The few individuals that tried to continue dancing were disoriented.[9]

3.3 Importance of source intensity.

The results of the previous sections show clearly that although bees do not respond to the polarization of a small, white light source, they generally do so if it is made relatively rich in ultraviolet photons. Is this a function of UV wavelengths or does it depend in some way on how the stimuli are generated? For example, in these experiments sources were made rich in UV by using band-pass filters which absorbed in the visible regions and transmited near UV and some IR, such as the frequently used Hoya 330 which has a broad transmission band from 220 to 380 nm (90% transmission at 330 nm) and a much smaller transmission band at deep red and near infrared wavelengths (transmission about 40% for 750 nm). Controls for long red wavelength polarized sources (e.g., derived by Hoya R-70 which absorbed all wavelengths below 700 nm) showed that the bees could not use these sources even as the sun and were disoriented.[10]

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9. Von Frisch (1967; p. 162) points out the very interesting fact that the minimum zenith distance at which bees can use the sun as an orientation cue (about 3°) corresponds remarkably well to the interommatidial measurements of the most dorsal part of the honey bee worker's eye, which del Portillo (1936) and Baumgartner (1928) have measured to be about 2° to 3°. More recent measurements by both optical and electrophysiological methods have shown the half-width of the sensitivity curve of a single dorsal ommatidium is about 2.6° (Laughlin and Horridge, 1971; Eheim and Wehner, 1972).

10. Detailed spectral sensitivity experiments by Heran (1952) and reviewed by von Frisch (1967; pp. 471 ff.) have shown that

Did the dancing bees use a UV polarized source simply because of the great decrease in total flux?

To test whether intensity was an important factor in the bees' orientation, the source intensity needed to be changed over a wide range during their dances. One straightforward experimental approach would have been to use neutral density filters to attenuate the source flux. However, many commercially available filters work only for visible wavelengths and with respect to the UV are either (1) not neutral or (2) highly absorbing. Special UV neutral density filters were not available to use for these experiments. Although the source radiance could be easily changed by decreasing the current flow through the lamp filament, such a manipulation was not acceptable due to the large spectral changes produced as the source became redder (cooler) while the current diminished. Obviously, any changes in spectral distribution could confound interpretation of the results of the proposed experiment.

Two properties of the commonly available, dichroic ("polaroid") polarizing filters can be employed to make a variable intensity polarized source which is constant in relative spectral energy distribution. (1) These polarizers are acceptably neutral and produce only relatively small changes in the spectral distribution of the transmitted flux. (2) Linearly polarized light is transmitted in proportion to the square of the angle (θ) between the E-vector direction and the transmission axis of the polarizer. This property is known as "Malus's law" and is mathematically expressed as:

$$I_{tr} = A[I_{in}\cos^2\theta],$$

---

bees are blind to long red and near infrared wavelengths.

where I_{tr} is the transmitted intensity, I_{in} is the incident intensity, and A is a constant.

With two serial polarizers, the transmitted intensity is continuously variable from a maximum (transmission axes of the two polarizers parallel) to almost zero (axes perpendicular: "crossed"), while at the same time the spectral composition remains quite constant.[11] While it may seem that such a pair of polarizers would possess a variable E-vector orientation, this is not necessarily true because the E-vector is determined only by the orientation of the final polarizer in the beam--if it remains constant, E-vector orientation does not change.

To test the bees, two polaroids were arranged in the beam of the quartz-halogen light source. The one closer to the dancing bees was fixed in its orientation, while the polarizer nearer the source could be rotated to change the flux intensity incident on the bees. Spectral filters, of course, could also be used to limit the test to various wavelength intervals. Unfortunately, absolute measurements of the intensity were not obtained, so a series of simple relative standards was devised, based on measuring the beam with a sensitive photographic meter. Four very different levels were selected: (1) polarizers parallel (maximum transmission) 64 footcandles (FC); (2) 16 FC; (3) 8 FC; and (4) polarizers crossed, minimum intensity (less than 1 FC).

---

11. Commercially available polarizers, however, actually deviate from these theoretical conditions by a "blue defect". This descriptive term indicates that their polarizing capability decreases somewhat for smaller wavelengths. Such unpolarized light leaks through even two perpendicular polaroids, and imparts a distinct violet hue to the transmitted light.

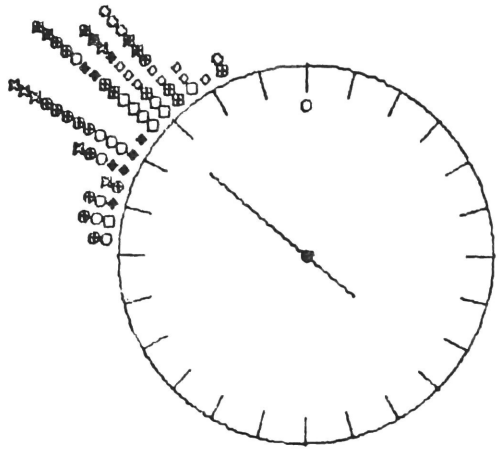

Figure V-38. Dances of a bee to two polarizers with transmission axes parallel. White light, 64 FC.

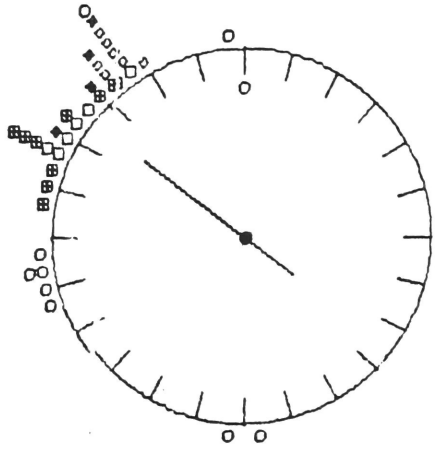

Figure V-39. Dances of a bee to two polarizers, white light, 16 FC.

A number of bees were tested under these conditions, and the results are summarized by the examples shown in Figures V-38 and V-39 which show the waggle runs of a number of individual bees as a function of source intensity. The orientation of the second polaroid, which determined the

E-vector orientation seen by the bees, was always 90° (horizontal). As before, the long vector indicates the dance direction expected if the bees interpreted the source as the sun, while the short vectors (one is superimposed on the solar prediction) correspond to the directions bees would dance if they used the source as a part of the blue sky. The control (Figure V-38) corresponds to two polarizers which are parallel (maximum intensity of about 64 FC), and shows that the bees interpreted the source as if it were the sun. This white source is equal to about 90% of the light transmitted through a single polarizer. In all cases, the observed distribution of waggle dance directions compared well with other examples of solar orientation.

When the angle between the transmission axes of the two polarizers was adjusted so that the light incident on the dance floor was about 16 FC, Figure V-39 shows that except for a single bee, the waggle dance directions have the same distribution as the control (light at full intensity). The bees, however, had obvious difficulties in orienting to such stimuli. They would frequently circle back and forth "searching" without striking out in a particular waggle direction, and, as a result, the total number of dances observed in equivalent time intervals decreased compared to controls. (This can be seen by the smaller number of waggle dances actually recorded.)

When stimulus intensity was reduced to only 8 FC (Figure V-40) the bees virtually stopped dancing. The few dances which did occur, however, exhibited the same solar orientation as the controls. Thus, even at these very low light intensities, when the bees used a white polarized source, they used it as if it were the sun. Figure V-41 shows how the

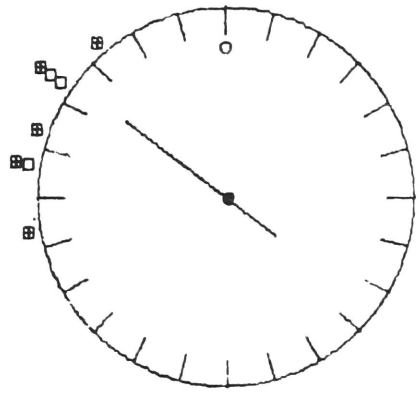

Figure V-40. Two polarizers; 8 FC; white, horizontal E-vector orientation.

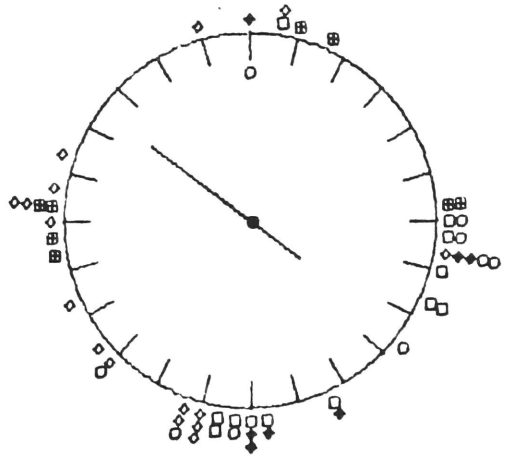

Figure V-41. Two polarizers; crossed; 1 FC.

bees treated an occluded beam produced by inserting an opaque metal sheet or by crossing the polarizers: they no longer treated the source as a celestial cue. However, the distribution of dance directions did not appear to be random, and were quadrimodally distributed. This interesting response is briefly described in Appendix A and seems to depend on

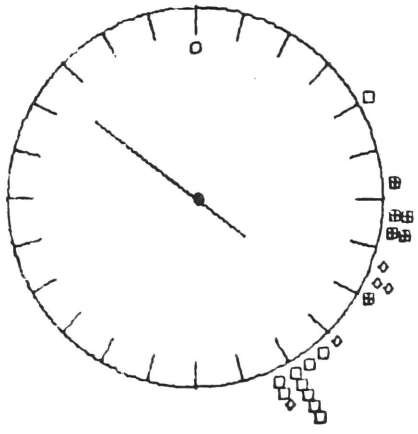

Figure V-42. Two polarizers parallel, 64 FC, UV horizontal E-vector.

the local direction of the earth's magnetic field at the dancing bee.

To control for any unknown factors introduced by the serial polarizers, bees were also tested to determine if they could orient on the basis of E-vector orientation by inserting a UV filter into the beam of parallel polarizers (maximum intensity). As Figure V-42 shows, the waggle dance orientation clustered in only one of the directions predicted on the basis of its polarization, and the responses appear identical to those of bees dancing to a single polarizer with the UV filter (e.g., Figure V-17).

A number of widely separated E-vector orientations were tested to make certain that these results did not depend in some way on horizontal E-vectors. These tests always produced the same results. For example, Figure V-43 summarizes the responses of a group of bees for a -50° E-vector orientation. As before, in these histograms "0" corresponds to

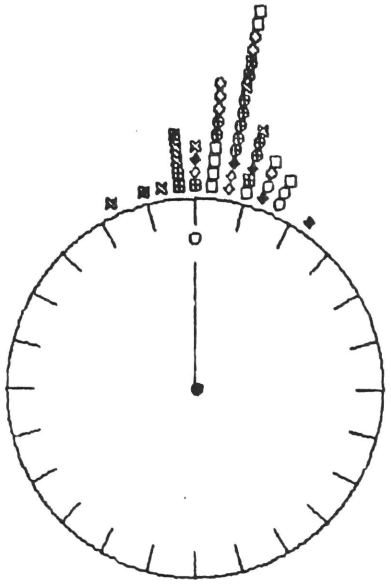

Figure V-43. Two polarizers parallel; 64 FC; white, -50° E-vector orientation. Long vector indicates predicted solar direction. 2 September 1977. Hazy blue sky.

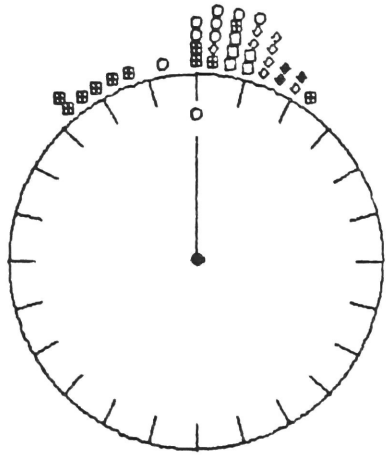

Figure V-44. Two polarizers, 8 FC; white, -50° E-vector orientation.

the direction bees would point their dances if they use the stimulus as the sun. In Figure V-43, the bees are well oriented in the solar direction for a high intensity (64 FC) white, polarized source. (If the bees used the E-vector orientation, their dances should have deviated from the

solar direction by about 118° and 10°.) A very similar distribution was observed for a low intensity (8 FC) polarized white light (Figure V-44).[12] Again, it is important to note that bees dancing under very low source intensities exhibited much more hesitant behavior, which resulted in recording far fewer dances, which exhibited higher deviations.

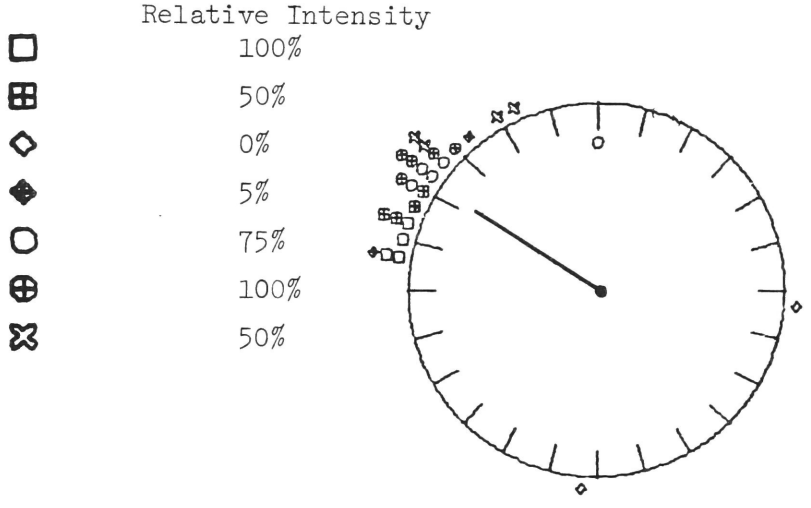

Figure V -45. Single bee dancing to a variety of polarized source radiances.

The principal results of these source intensity experiments are summarized by Figure V-45 which shows the responses of a bee under a variety of source radiances. Except under crossed polaroids (virtually no light visible to the bees), the waggle dance directions corresponded to solar orientation and were not affected by the E-vector orientation. The results of these experiments clearly show that the bees do not use the E-vector orientation in a small, polarized UV source simply because it is

12. The apparent clockwise rotation of the dance orientation with respect to the expected solar direction cannot correspond to the 10° shift predicted by the polarization of the source, since it is present under both the high intensity and the low intensity stimulus situations.

much reduced in total intensity. The waggle dances remained oriented as if the test light were the sun over very wide range of intensities, until the bees became disoriented with crossed polarizers. There was never any indication that the polarization was perceived by the bees.[13]

4. Deviations of waggle dance orientation.

The results of experiments described thus far confirm previous findings that: (1) a small, white light is used as if it were the sun whether it is polarized or not; (2) a colored, polarized source is interpreted on the basis of its E-vector orientation only if it is relatively rich in ultraviolet wavelengths (less than about 410 nm). I also found that honey bees are able to distinguish between the two directions predicted on the basis of the E-vector orientation, even when the corresponding points in the natural sky are optically equivalent. But these statements describe only a major part of the basic story, since there are also deviations of the waggle orientation from expected directions which occur under specific conditions. These deviations are quite variable--sometimes bees are oriented, but not in a predicted direction ("anomalous orientation"), while other times they seem completely disoriented. Several types of the observed deviations had quite a clear association with specific experimental conditions and the results are discussed in

13. That the absolute intensity of the source was not a factor in whether the bees used the polarization or not was easily shown in another way. A sunlamp (Sylvania Inc.; 100 watt low pressure mercury arc in series with a 150 watt incandescent lamp) was powered by DC and projected through a large area, UV transmitting, visible absorbing filter (Wratten 18a) and a UV transmitting polarizer. This polarized source was brighter than even the xenon arc lamp--yet the bees always used it on the basis of its polarization and never as the sun.

this section. Specifically, the influence of (1) overcast sky and (2) E-vector orientation on dance deviation is considered.

4.1 Overcast conditions.

In this section, "overcast" means that throughout the experiment no blue sky was visible during the previous foraging flight (determined by frequent direct observation of the sky), but the overcast category includes times when the solar disc was visible through complete cloud cover (stated in the figure legends). A necessary condition for all experiments under overcast sky considered here was that the bees continued to forage vigorously from an artificial feeder.

One of the most striking observations under overcast conditions was that even well established foragers (i.e., those who had visited the feeder under clear sky) when shown small, white, polarized sources danced in a much less predictable manner than when tested under clear conditions. For example, sometimes bees used a polarized artificial source as if it were the sun, other times as if it were part of the sky, or even both, with the waggle directions changing between the predicted directions based on solar and polarization orientation. In addition, some dances were occasionally anomalously oriented or even disoriented.

Under cloudy conditions, when the dance orientation was based upon a solar interpretation of the polarized stimulus, the distributions of waggle directions were generally very similar to responses under a clear sky. The precision of the dances seemed directly related to the density of the cloud cover: the lighter the overcast, the greater the bees' precision. Under extremely dark, overcast conditions, such as those

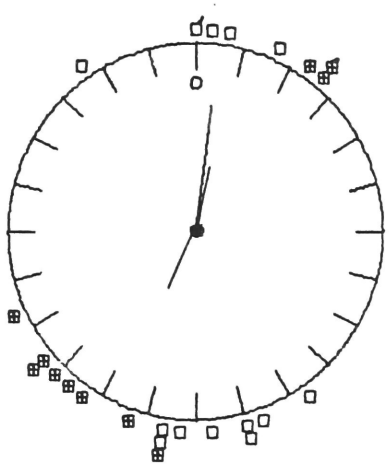

Figure V-46. Dance directions of a single bee to a white polarized light at ZD of 27° polarized at +80°. 31 August, overcast sky, 1418 EDT, sun at ZD of 36°, AZ of 215°.

corresponding to Figure V-46 the deviations of dances from the solar direction were much higher than for less dense cover. As shown in this example, a striking observation was that the deviant dances were often oriented in a direction predicted by the E-vector orientation of the stimulus. This, of course, differed greatly from the characteristics of orientation to white, polarized sources under clear skies. At the same time, it is important to know that these dancing bees appeared very disturbed and circled hesitantly for long periods of time without dancing. Even when a waggle run direction was finally selected, those bees often changed their course <u>during</u> a single waggle run. Thus, compared to the form of dances when the sky was clear, the chances that a small white light will be interpreted as sky or sun varies with the sky conditions the bee saw outside the hive a few minutes previously.

Figures V-47 and V-48 illustrate these characteristic differences for white, vertically polarized light. Figure V-47 summarizes data for a quite clear day with large areas of the blue sky visible, and displays the typical, precise solar orientation of the waggle dances for a number of bees. This contrasts greatly to the the data of Figure V-48, taken when no blue sky was visible (the solar disc could be observed by me through altostratus clouds). When shown unpolarized white light, typical solar orientation of the waggle dances was evident. But when the light was made vertically polarized (during the same dance) the bee assumed one of the directions predicted on the basis of the E-vector orientation of the source.[14]

Sometimes the bees danced bidirectionally in one of the polarization directions and in the solar direction. They did not seem to <u>average</u> the two possibilities. An example is shown in Figure V-49 which records the waggle runs of a single bee. She began her dance under an unpolarized white light and the open squares of her waggle directions show that she interpreted this source as if it were the sun. Then the light was made vertically polarized and she continued to dance, but in different dance cycles along <u>both</u> the solar and polarization predicted directions. The relative frequency of these bimodal effects seemed characteristic of individual bees, since many times they exhibited qualitatively the same

14. Again, the typical <u>unimodal</u> dance orientation to polarized light can be seen. But in this case, the light was white and not rich in UV as is characteristic of clear sky conditions. This observation is additional evidence that the selection of a single direction by a bee viewing polarized UV light does not necessarily depend upon its wavelength composition, and also shows that bees are capable under some conditions of using the E-vector orientation of a small (5°), white source not in the zenith.

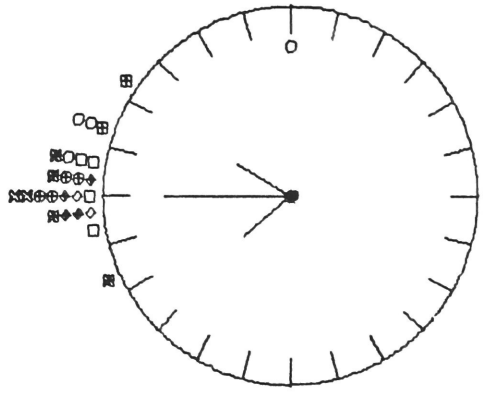

Figure V-47. Waggle directions of bees dancing to a white, vertically polarized light at ZD of 27° when blue sky was visible during the foraging flights. 26 August, 1140 EDT, sun at ZD of 34°, AZ of 146°.

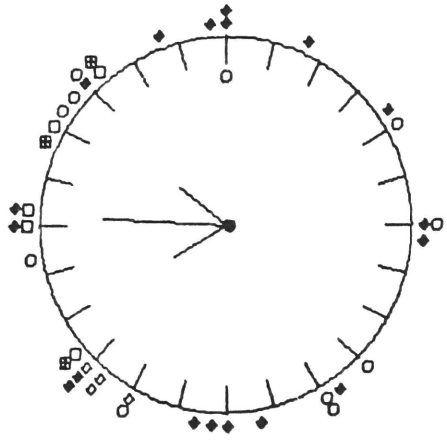

Figure V-48. Waggle directions of bees for the same stimulus as for Figure V-47 of white vertically polarized light, except the sky was completely overcast. 31 August, 1240 EDT, sun at ZD of 32°, AZ of 171°.

behavior under similar experimental conditions.

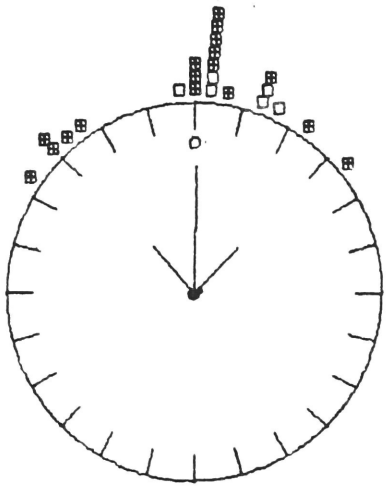

Figure V-49. Waggle directions of a bee to white unpolarized light (open squares) and then white, vertically polarized light. sky overcast but the sun's disc was visible. 17 September, 1140 EDT, sun at ZD of 42°, AZ of 150°.

Another feature of overcast conditions was that not every dance under white, polarized light was oriented in one of the polarization directions: often the bees were anomalously oriented or even disoriented. This observation can be readily appreciated by comparing the differences between dances under both clear and cloudy skies by use of normalized polar histograms. As described in Chapter IV, in the normalized histogram all of the diverse, predicted directions (corresponding to data collected at different times) are adjusted to coincide in the zero direction so that they can be directly compared. In Figures V-50 and V-51 the long vector in the normalized histogram indicates the predicted solar orientation. Under clear skies (Figure V-50), the bees oriented themselves very well and exhibited little dance deviation by using a white, vertically polarized source as if it were the sun. This contrasts greatly to Figure

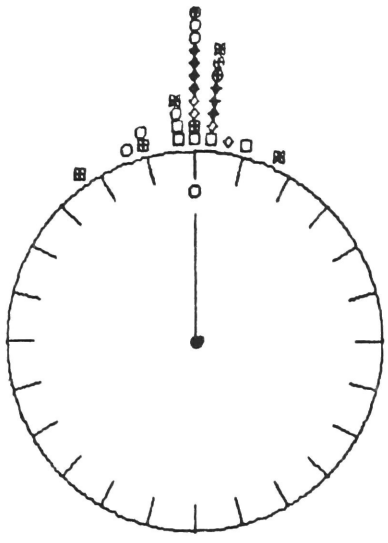

Figure V-50. Dances of separate bees to white, vertically polarized light on 26 August 1977 when the sky was relatively clear. Long vector predicts solar orientation.

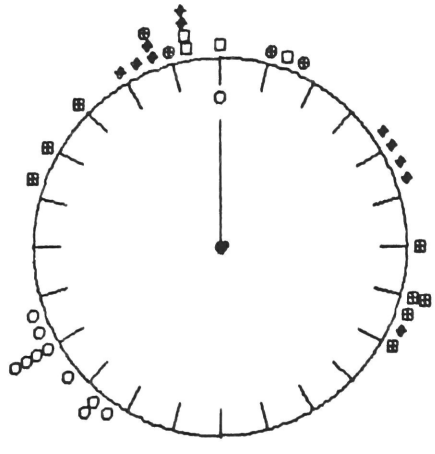

Figure V-51. Dances of separate bees to white, vertically polarized light on 17 September 1977 when the sky was overcast.

V-51 where under overcast skies, bees obviously danced with much inferior orientation.

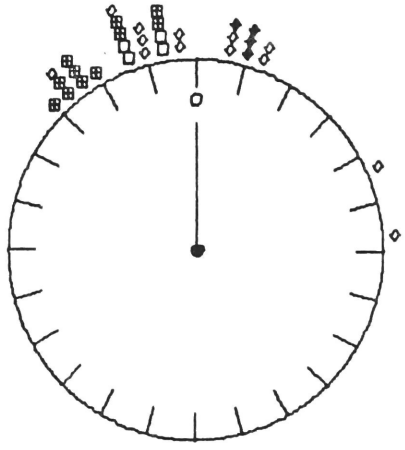

Figure V-52. Dances of individual bees to a white, horizontally polarized light on 23 August 1977 when the sky was clear but hazy.

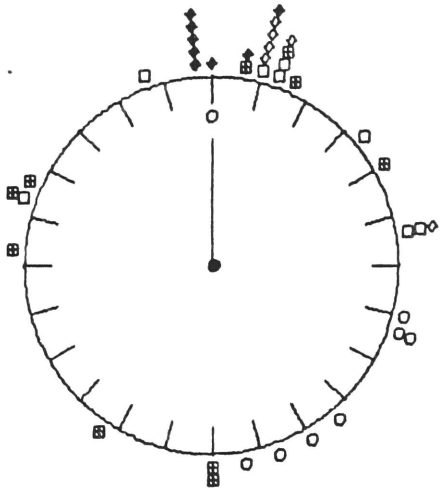

Figure V-53. Dances of bees to a white, horizontally polarized light on 31 August 1977 when the sky was overcast.

To illustrate that these observations do not depend upon a vertical E-vector orientation, Figure V-52 and Figure V-53 compare orientation under clear and cloudy skies for horizontally polarized white light. For the clear day (Figure V-52) the bees danced for solar orientation, butt

under heavy overcast (Figure V-53) for which the dance deviations were much larger, although some solar orientation was observered.

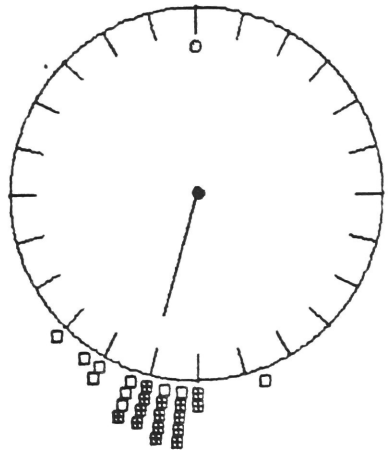

Figure V-54. Dances of a bees to a white (filled squares) and then UV horizontally polarized light.

From the results of a series of these observations, the chief characteristic of honey bee dance orientation under overcast conditions is variability. As a final illustration of this unpredictability, Figure V-54 shows that when a bee was shown a polarized, UV source (which ordinarily is always interpreted as a part of the blue sky) the bee ignored the polarization information, and danced as if the stimulus were the sun (the same as white light). Although such results were relatively rare, it was striking that they were always observed under cloudy conditions.

Thus, in general, when bees viewed UV, polarized light under overcast conditions, the observed waggle dance directions possessed much higher deviations than those under white, polarized light with the same E-vector orientation. In fact, for many specific instances the bees

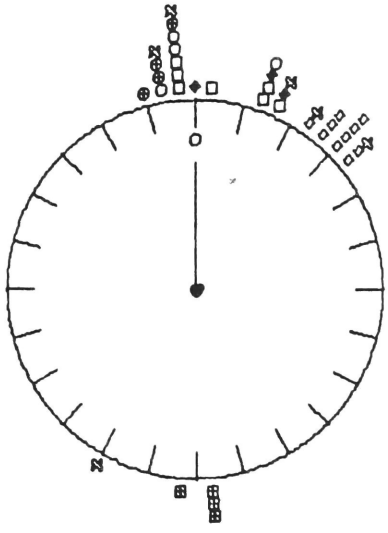

Figure V-55. Dances of individual bees to a UV horizontally polarized light on 17 September 1977 under overcast skies (sun visible through clouds). Long vector is the principle polarization predicted direction.

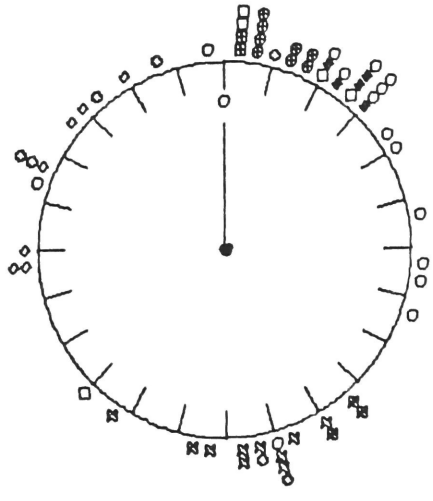

Figure V -56. Dances of individual bees to a UV horizontally polarized light on 31 August 1977 under complete overcast.

actually appeared to be disoriented. Further, the amount of dance deviation appeared to be directly proportional to the extent of the cloud cover. (However, the total number of different days available for

analysis was not large.) Another set of typical examples are given in Figures V-17, V-55, and V-56. These correspond to horizontal E-vector orientation on a clear (Figure V-17), moderate overcast (Figure V-55), and heavy overcast (Figure V-56) sky. As seen in Figure V-17 (clear), the waggle orientation of all of the bees clustered around the predicted polarization direction farthest from the sun (i.e.,the one the bees always choose under clear conditions). Figure V-55 (medium overcast) and Figure V-56 (heavy overcast) are polar histograms normalized for the predicted polarization direction of the skypoint farther from the sun and are quite different because of the larger dance deviations. These increases in deviation are shown well in Figure V-56 (heavy overcast), where it is clear that some bees are even <u>disoriented</u> to a UV, polarized light source.

In summary, overcast skies generally were correlated with increased dance deviations. Also, under these conditions bees often interpreted white, polarized light as a part of the sky, although sometimes they were anomalously oriented or disoriented. Finally for UV, polarized stimuli, under overcast conditions the dance deviations were much greater, and often the bees displayed little evidence that they interpreted such sources as a part of the blue sky.

The observations that the precision of the bees' dances depends on the sky conditions should be verified and extended. It would be especially interesting to compare the quality of orientation of new recruits and foragers already familiar with the feeder under clear sky to determine how important experience is a factor in the observed behavior. At least under some experimental circumstances von Frisch (1967; p. 396)

felt that under cloudy skies new recruits danced to a polarized stimulus with an inferior orientation than established foragers. The results of these observations and experiments will be very important because they provide data to evaluate whether bees are able to use the patterns of skylight polarization without having actually seen them on previous foraging flights. That is, whether the relationship of the polarization patterns and solar position per se are known by the bees. This topic will be discussed in Chapter VI.

4.2 E-vector orientation.

Observation of the orientation of bees to artificial light stimuli under overcast conditions revealed that the direction of polarization appears to directly influence the deviation of waggle dance direction. Specifically, E-vector orientations close to vertical tended to increase 1) the probability that a white, polarized source was interpreted as a skypoint, and 2) the waggle run deviations.

The first effect has already been mentioned in the results of earlier experiments for white, unpolarized light, since occasionally single waggle runs occurred in one of the predicted polarization directions. For example, Figure V-22 shows that for vertically polarized, white light, one bee pointed a single waggle run in the direction indicated by other bees under UV polarized light, as shown by the single filled square among the other open symbols. Thus, on that dance circuit, the bee interpreted the stimulus as if it was a part of the blue sky. This is quite unlike horizontal polarization patterns to which bees are usually well oriented in the predicted directions; they never interpret a white

polarized source as being part of the sky (except, as just discussed, under overcast conditions).

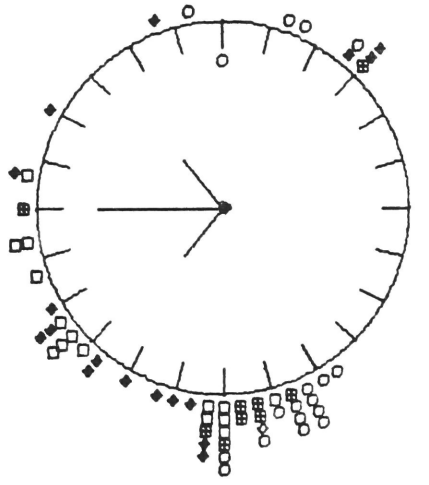

Figure V-57. Dances of bees to UV vertical polarization at ZD of 27°. 1 September, patchy blue sky, 1130 EDT, sun at ZD of 39°, AZ of 140°.

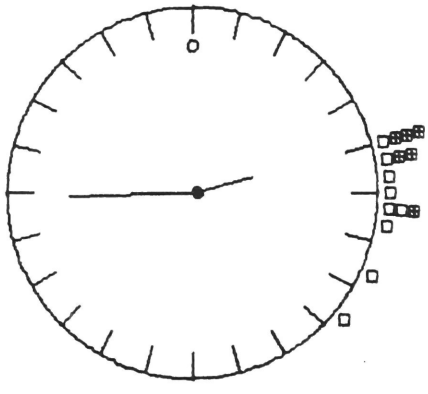

Figure V-58. Dances of a bee to UV polarized light of E-vector orientation -83° under the same conditions as Figure V-57.

These E-vector orientation effects do not seem to depend upon whether the

light source is white or contains only UV. For example, Figure V-57 shows that a vertically polarized UV light shown to bees exposed to a patchy blue sky produced large deviations of the waggle dance with very few in the predicted directions. At the same time, the responses of bees to UV light (Figure V-58) with E-vector close to horizontal (-83°) was much more precise and in the expected directions.

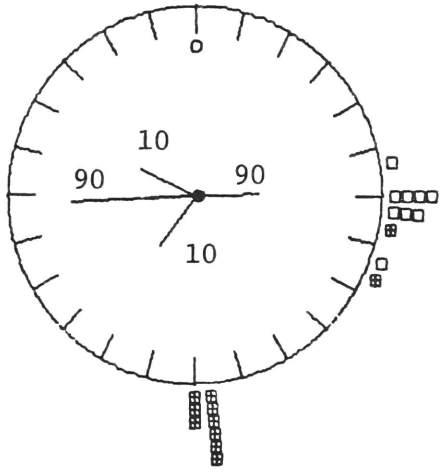

Figure V-59. Dances of a bee to a UV horizontally polarized light and then a $+10^{o}$ source at ZD of 27°. 26 August, sky fairly clear, 1150 EDT, sun at ZD of 33°, AZ of 149°.

A prime characteristic of these effects was that they were extremely variable. For example, Figure V-59 corresponds to a $+10^{o}$ UV light which was shown to several bees at approximately the same time as Figures V-57 and V-58. Yet the bees were quite well oriented along one of the predicted polarization directions for the $+10^{o}$ light, unlike the vertical stimulus. Finally, Figure V-60 also illustrates that the same E-vector effects can even be observed for a fairly clear day. In this experiment a bee was well oriented to the horizontally polarized UV stimulus (open

squares), in contrast to the anomalous orientation evident for the almost vertical (+10°) stimulus (filled squares). Again, when deviant orientation was observed it was frequently associated with more nearly vertically polarized sources.

Several experiments just discussed (e.g., Figure V-59) illustrate that sometimes bees were relatively well oriented to an artificial sky spot, but their dance orientation did not correspond to any theoretically predicted directions (i.e., anomalous orientation). Again, the E-vector orientation seemed related in a general way to this behavior, since anomalous orientation was much more likely to occur for stimuli with E-vectors close to vertical. In fact, for the 2500 dances analyzed, there were literally no observations of anomalous orientation for E-vector orientations greater than 70° from vertical, while they were very commonly observed for vertically polarized light, even under the clearest sky conditions.

In summary, waggle dances show scattered or anomalous orientation under overcast conditions and when the E-vector orientation is more nearly vertical. These appear to be additive in effect, so that the worst dance orientation observed usually corresponded to a vertically polarized light on a completely overcast day.

5. Sky color and dance orientation.

It has been mentioned above that under clear skies bees always responded to small, unpolarized light sources containing wavelengths longer than about 410 nm as if they were the sun. Although similar solar orientation

was observed for UV, unpolarized stimuli, another response was often observed. Specifically, many times when a stimulus was made relatively rich in UV wavelengths (by absorbing visible wavelengths) the bees pointed their waggle runs in a mirror image of the solar orientation: they oriented themselves as if the source they saw was a point on the skyvault in the antisolar vertical.

These "antisolar" dances were not limited only to unpolarized UV light because relatively rarely, dancing bees responded similarly to a polarized UV light, <u>regardless</u> of the E-vector orientation.

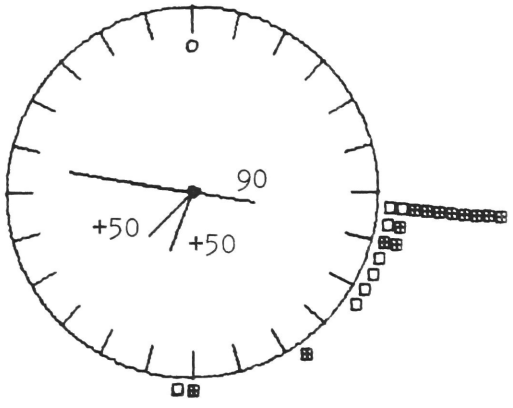

Figure V-60. Waggle directions of a bee to a UV light polarized at +50° (open squares) and then UV horizontally polarized. Source ZD was 51°. 20 August, clear sky, 1130 EDT, sun at ZD of 34°, AZ of 140°.

For example, Figure V-60 shows that for an E-vector orientation of +50° and 90° the waggle orientation is about equal and opposite to the solar direction.[15]

One of the most interesting aspects of these observations was that the UV induced antisolar dance behavior seemed to occur only when the sky is relatively cloud-free. Under completely overcast conditions, antisolar dances were practically never observed. Patchy cloud cover had an interesting influence on this behavior, as illustrated by Figures V-61 to V-63 which show the orientation under heavy cloud cover to patchy blue sky. Figure V-61 corresponds to heavy clouds through which only the solar disc was visible. Obviously, making the stimulus rich in UV wavelengths did not affect the dance orientation. Figure V-62 corresponds to a short time later when some patches of blue sky appeared and a difference between the white and UV stimuli was not obvious. The relative bearing of the blue patches seemed to correspond in a general way to the foraging geometry. When the cloud cover closed again (Figure V-63), the differences between the UV and white light source disappeared. Unfortunately, because of more pressing experiments and the inability to make accurate observations of the sky correlated with the dance behavior, I do not have more extensive data pertaining to this phenomenon. It appears, though, that bees can recognize different points of the sky vault on the basis of sky color.[16] Further, it seems possible that these identified sky spots are used as orientation cues only if they have just been observed by the bee on her previous foraging flights. These ideas

15. It should be noted that the relatively few observations of this type occurred when a new feeder location was established. This may be an important factor to consider.

16. After these observations of antisolar dance orientation to UV, unpolarized light were made, I became aware that Edrich (per. comm.) has independently observed that bees exhibit reverse dance orientation to an ultraviolet light. However, he reports this behavior exists at all times, mentioning no effects of cloud cover. Perhaps his data were gathered only on clear days.

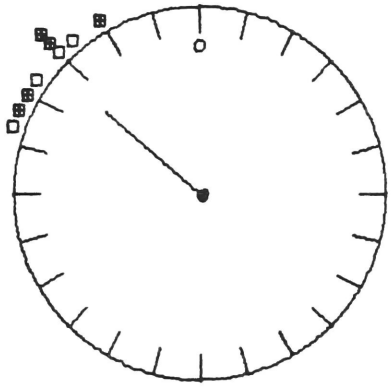

Figure V-61. Waggle directions of a bee to white, unpolarized light (open squares) and then UV unpolarized light (ZD of 33°) for an overcast sky. 17 September, 1420 EDT, sun at ZD of 43°, AZ of 212°.

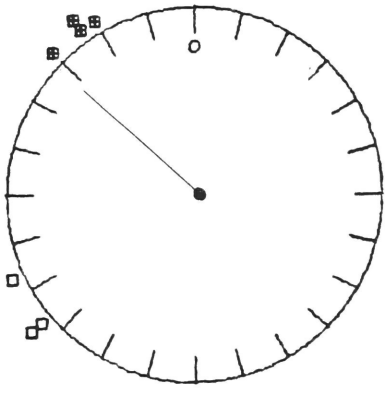

Figure V-62. Waggle directions of a bee to white unpolarized light (filled squares) and then UV unpolarized light. 17 September, 1430, sun at ZD of 43°, AZ of 212°.

are discussed in some detail in Chapter VI.

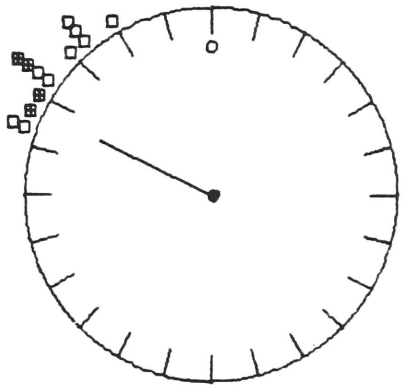

Figure V-63. Waggle directions of a bee to white unpolarized light (filled squares) and then UV unpolarized light under complete overcast. 17 September, 1510 EDT, sun at ZD of 49°, and AZ of 227°.

CHAPTER VI

DISCUSSION.

1. Significance of the behavioral results.

The behavioral observations summarized in Chapter V have shown that after flying under a clear sky, bees almost always orient horizontal waggle dances in only one of the two directions predicted on the basis of the E-vector orientation of a polarized light. They were able to do this even when the area of the stimulus was so small that it provided only a minimum amount of information about the sky pattern. That is, these stimuli corresponded to single points for which only a single E-vector orientation was discernable rather than the whole pattern available in the natural sky. Since a specific E-vector orientation generally exists at two places on the sky vault, it is obvious that the bees used some other means for resolving the ambiguity. In this section, the results of the geometrical analysis described in Chapter II are applied to this problem.

The basic geometrical consideration of skylight radiation is the scattering triangle formed by the skypoint, sun, and zenith point (Figure II-5, reproduced again here). We assume that the sun itself is not visible to an animal, but that optical features in the blue sky are used in its place. As discussed in Chapter II, there are six important variables: 1) the zenith distance of the sun (ZS); 2) the zenith distance of the skypoint (ZP); 3) the relative azimuth (C); 4) the sun angle (B); 5)

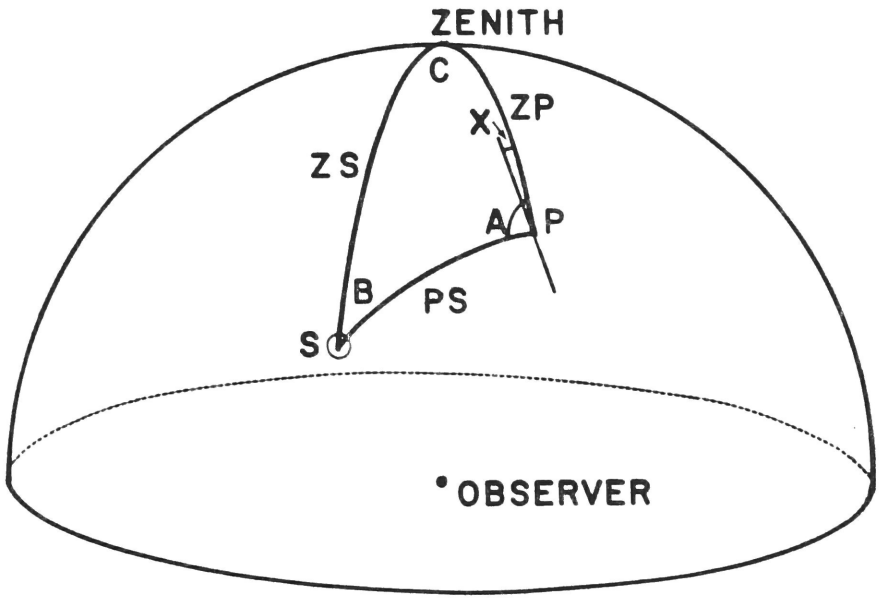

Figure II-5 The scattering triangle.

the skypoint angle (A); and 6) the scattering angle (equal to arc PS). X, as before, is the E-vector orientation.

By observing a patch of skylight, an observer fixes its zenith distance. Thus two or more components of the scattering triangle are required to find the sun's position. These possibilities can be separated into two different groups: those for which (1) the other parameters are determined from the skypoint itself and 2) solar variables are used (e.g., zenith distance of the sun). Table VI-1 lists the possible combinations of the variables, with comments about each solution. Each case (assuming Rayleigh scattering) is considered in analytical detail in Appendix A, with somewhat more extensive comments about expected orientation behavior.

TABLE VI-1

Scattering Triangle Analysis by Information from only a Single Skypoint

Because the skypoint is directly observed, ZP is assumed to be known.

	KNOWN VARIABLES OF THE SCATTERING TRIANGLE	PHYSICAL SIGNIFICANCE OF KNOWN VARIABLES	COMMENTS
A. Variables from skypoint radiation alone.			
i.	X	E-vector orientation with respect to vertical	not enough information to determine relative azimuth; gives only a great circle along which the sun lies.
ii.	PS	scattering angle (related to polarization, color, brightness); defines scattering plane	same as in i.
iii.	X, PS		in general; solution for azimuth is ambiguous; there are two possibilities.
B. Solar zenith distance known.			
iv.	ZS	solar zenith distance	not enough information to determine relative azimuth
v.	X, ZS		ambiguous azimuth determination
vi.	PS, ZS		unique solution of solar position and relative azimuth
vii.	X, PS, ZS		unique solution of solar position and relative azimuth

To apply the results of analysis of the scattering triangle to animal orientation, and perhaps deduce how polarization information is used as a cue, the correspondence between the scattering triangle variables and the physical characteristics of the artificial polarization sources used in these experiments must be determined. In addition, the behavioral observations of Chapter V indicate that it may be important to know how individual characteristics compare with the actual sky conditions just prior to the behavioral observations.

In considering this problem, it is easy to appreciate that the zenith distance of the artificial source and E-vector orientation (X) determine the scattering triangle parameters ZP and A (since $A = 90^{\circ} \pm X$) respectively. In Chapter II I described how the scattering angle (PS) theoretically determines the degree of polarization, color, and brightness of light coming along a specific line of sight of the sky. As discussed in detail in Chapter III, for the natural sky all three of these variables are quite different from theoretical predictions, just as they are, of course, for almost any artificial source. Thus, if the magnitude of these variables are used directly in scattering triangle analysis, they would provide incorrect values, and presumably would result in characteristic deviations of orientation behavior. For example, my artificial polarized sources usually possessed a very high degree of polarization (virtually 100%). On the basis of Rayleigh scattering, such high levels of polarization correspond to a scattering angle of 90°, and are, of course, not dependent on the E-vector orientation. Some of the analytical possibilities using these large values of degree of polarization are discussed in Appendix A. None of these possibilities can

account for the observed dance orientation of honey bees described in Chapter V. The same is also true for source brightness and color which are much different from the natural sky, and from predictions based on Rayleigh scattering and also are not a function of E-vector orientation. Thus it seems clear that as long as the magnitude of these parameters is above threshold, they are unimportant, at least in the context of these experiments.[1]

The apparent unimportance of the degree of polarization in waggle dance orientation to polarization cues has already been discussed in general in Chapter I. Von Helversen and Edrich (per. comm., 1978) have recently provided more detailed information about the importance of degree of polarization in the waggle dance orientation. In an experiment designed to determine whether honey bees detect polarization parameters instantaneously, they varied the degree of polarization of a small (3°) zenith stimulus sinusoidally (at 0.1 to 50 Hz) between 0 and 100% polarization while holding the total intensity and E-vector constant. Although the variance of the horizontal dances they observed was somewhat higher than for similar ones under constant, white, polarized light, the bees remained well oriented over almost the entire range of degree of polarization. Unfortunately, detailed information about this experiment is not yet available for critical examination. This is especially important because rapid changes of per cent polarization alone are technically difficult to achieve without other changes, and many artifacts are possible. But their results which indicate that the degree of polarization is irrelevant as a cue for orientation agree very well with other

1. Since only small spots were used in my experiments, rate of change and other similar variables were eliminated.

observations already discussed. It therefore seems appropriate to exclude on physical and behavioral grounds the scattering angle as a variable that animals might use to solve the scattering triangle.

Besides the zenith distance of the observed point and the E-vector orientation, the only remaining variable which can be determined by direct observation is solar zenith distance (see Appendix A). However, in the experiments described in Chapter V the bees could not observe the sun itself as they danced. Therefore if zenith distance of the sun was used in their orientation, it must have been remembered from the last foraging flights.[2] Referring to Table VI-1, it can be appreciated that if ZP, ZS, and X are the known variables of the scattering triangle, in general <u>two</u> azimuth angles can be specified. (This means, of course, that the E-vector orientation X appears at the same zenith distance at two different locations on the skyvault.[3])

1.1 <u>Do such ambiguities exist for bees?</u>

In the section on the rationale of these orientation experiments, I explained how the degree of polarization (or related cues) may not be used as a specific numerical value in scattering triangle analysis, but still enable an animal to decide between two possible orientations. For example, if a highly polarized stimulus appears to an animal on the basis

2. Of course it is possible that bees can, with the aide of their internal clocks, "calculate" the sun's zenith distance.

3. Kirschfeld <u>et al</u>. (1975) have also pointed out that given a specific E-vector orientation there are two possible values of solar position. Their analysis, however, was strictly geometrical, from which actual values could not be calculated and thus was of limited use for behavioral experiments. In addition, their considerations did not include other possible variables of the scattering triangle.

of its E-vector orientation to be either a point on the sky vault quite close to the sun (small degree of polarization) or another point farther away from the sun (large degree of polarization) then the animal might interpret it as the point farther from the sun simply because the test source was highly polarized. As discussed in Chapter V, vertical polarization patterns were used in order to eliminate this possibility. Because of their symmetry with respect to the sun, the two points with the same E-vector are optically indistinguishable. As the results clearly show, the bees tested with this stimulus were always oriented in one of the predicted polarization directions, which corresponded to the point in the sky which is farthest from the sun, or in the case of vertical E-vectors, to the point on the right of the sun. Usually, only this direction was danced, but occasionally dances were also oriented at 180° to this preferred direction. Thus, the behavioral results did not indicate that for the bees a geometrical ambiguity existed.

The results of these experiments differ from von Frisch's statements about honey bee orientation to identical E-vectors which exist at two different places on the sky vault. He concluded that under these conditions, bees danced in both of the appropriate directions (von Frisch, 1950; reviewed 1967; pp. 391 ff.). Unfortunately, he did not usually include sufficiently detailed data to allow adequate reexamination of his interpretation of the bees' responses. The only experiment which can be analyzed in some detail took place 7 September 1949 at about 1715. Von Frisch states that at this time a particular pattern occurred both at 340° and 196° true azimuth. The photograph he includes (1967; Figure 341) shows that this pattern was vertical, and thus corresponds to the

vertical polarization experiments described above; therefore both skypoints should be optically identical. Assuming that the solar declination was $16^{\circ}18'$, at a latitude of 47°N and longitude of 15°E, (approximate values for Austria on September 7) the solar horizontal coordinates were azimuth = 267°; zenith distance = 79°. The methods of Chapter IV give about 72° as the azimuth between the sun and the skypoints. Therefore, if the bees danced in both appropriate directions the angle between the two waggle directions should be $2 \times 72^{\circ} = 144^{\circ}$.

Although von Frisch stated that the bees danced in both of the appropriate directions, he actually wrote that these were oppositely directed dances: one waggle direction in a polarization predicted direction, and the other 180° from it. these results are obviously quite different from the predicted 144°. Von Frisch's methods of measuring dance direction were more than accurate enough to detect an angular difference of about 36° between mirror image dances and the prediction on the basis of E-vector orientation, yet he did not.

As already discussed, these results are very similar to many I recorded for bees using vertically polarized light as an orientation cue. In his 1967 review, von Frisch states that out of a total of 83 experiments, when two identical patterns could be seen (by him) in the sky, the bees always danced bidirectionally (total of five observations). He clarifies this statement, however, in his original paper (von Frisch, 1950) in which he states that during these 83 experiments, 5 times the bees indicated two directions and in four of these instances they were 180° to each other. Apparently, only after observing bidirectional dances, he searched the sky and found that the E-vector pattern existed

at two separate points on the sky vault. If the procedure of correlating dances with the existence of sky patterns always occurred in this sequence, then it is very possible that many dances which appeared unimodal, actually occurred when two patterns were visible in the sky at that time.

On the whole, what can be definitely interpreted from von Frisch's data agrees well with the results reported in Chapter V. The main conclusion is: rather than dancing in the two directions predicted on the basis of the polarization of a small stimulus, the bees danced to only one of them. If bimodal dances occurred, the incorrect ones were generally exactly opposite to this direction. It is interesting to note that like my observations, in the case described above von Frisch's bee interpreted a vertically polarized stimulus as being a point in the sky to the right of the sun.

1.2 Use of conventions to resolve ambiguities.

The observation of unimodal dance orientation to ambiguous sky cues suggests that bees may not analyze the pattern of skylight polarization geometrically to determine the solar bearing. It is not conclusive, however, because it is possible that an animal calculates the two possible solar locations and eliminates one by use of arbitrary "rules".[4] Obviously, any ambiguity in an orientation system can constitute a severe problem. But for honey bees, is even worse because the orientation cues are also used for the dance communication.

4. Data of this section were collected in collaboration with James L. Gould.

When a foraging honey bee discovers a food source, she can compute her distance and direction from the hive regardless of how circuitous her flight out may have been (von Frisch, 1948; 1951; 1967; pp. 173 ff.). On her return, she encodes this directional information into a dance which specifies the location of the food. Normally dances are performed on a vertical comb of the dark hive; the dance angle with respect to vertical ("up") is the same as the horizontal angle between the sun and the food (the relative azimuth). The arbitrary convention of defining "up" as the direction towards the sun permits recruits to decode and use the information. Since the communication system employs arbitrary conventions common to the members of a social group, von Frisch and others refer to it as a dance language.

Dancing in the dark is a consequence of living in insulating cavities--a behavioral adaptation which permitted Apis mellifera to penetrate into temperate latitudes (Wilson, 1971; p. 266). The tropical honey bee from which they evolved perform their dances on open clusters with a restricted view of the sky (Lindauer, 1961; pp. 59 ff.). They seem to lack the up-is-the-sun convention. Even today, on the surface of swarms (Lindauer, 1955), and at the hive entrance (von Frisch, 1946), our temperate zone honey bees often dance on a horizontal surface where the up-is-the-sun rule is useless. Since they are outdoors, the dancers, like their tropical relatives, must fall back on the evolutionarily more ancient form of the dance language and orient directly by cues they see in the sky: the sun and extensive patterns of polarized skylight (von Frisch, 1949; 1967; pp. 401 ff.). As long as dancers and dance attenders use the same reference system, the language works. However, bees fre-

quently must dance under marginal conditions--on completely or partly overcast days or in locations with a view of the sky restricted. In these situations it may not always be easy for them to agree among themselves whether what they can see is the sun or sky, and if it is part of the sky, which section. Nevertheless dancers seem to resolve possible ambiguities, and successfully recruit other bees. How do they manage this?

To work, language requires the use of arbitrary conventions or rules which are common to all members of a culture. For horizontal dances, bees use at least three "linguistic" conventions to eliminate inter-bee ambiguity. The arbitrary nature of the rules is most strikingly illustrated by the fact that although the rules frequently fail to identify physically the source of available visual cues correctly, they still work perfectly well because the dancers and attenders are consistent in their "mistaken" interpretations.

The first rule is used to determine whether the observed cue is the sun or part of the sky, and therefore which of two very different dance directions to take up. As described in Chapter V, bees make this distinction mainly by the size of the visual stimulus, its relative content of ultraviolet light, and to some extent its per cent polarization. Figure V-29 illustrates the interaction of these three variables, which is generated by these rules. Oddly enough, in distinguishing between sun or sky, the elevation is important only when the source is at or near the zenith: bees try to use any stimulus directly above them as if it were a part of the sky, regardless of its physical characteristics. This is not unexpected since a zenith sun has no azimuth and thus cannot be used

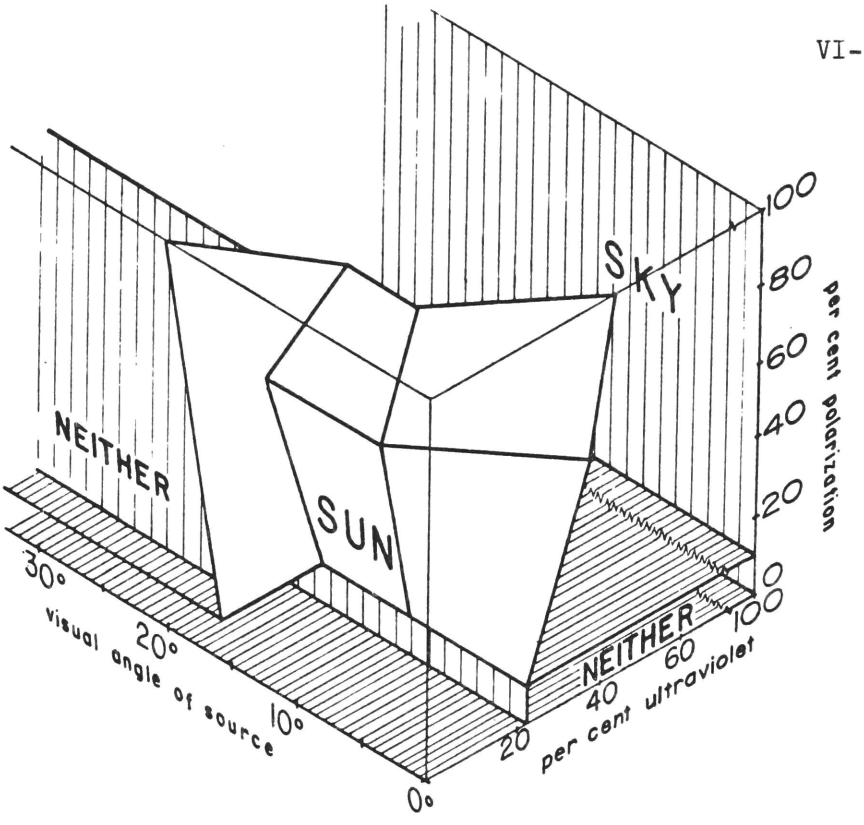

Figure V-29 Optical properties that determine whether a light is interpreted by honeybees as sun or sky. Bees dancing on a horizontal surface were presented with stimulus diameters of 2.5, 5, 10, 20, and 30° (near boundaries 7.5, 15, and 25°), polarization of 0, 18, 56, and 94%, and spectral distributions of 0, 20, 41, 65, and 100% UV. Approximately 2500 dance cycles were recorded--at least five cycles from each of at least five dances. The bees interpreted these stimuli in three ways: As the sun, as the blue sky, or neither. Near the boundary surface between "sun" and "sky", a bee may exhibit both types of orientation in different dance cycles. The threshold of approximately 10% polarization confirms the data of von Frisch. Absolute intensity is unimportant unless the light is so dim that the bees are disoriented. Conditions resulting in disorientation ("neither") do not exist in the clear natural sky. Only the relative proportion of UV seems important in spectral composition. Elevation of the stimulus pattern was usually 33°; but, except for the zenith, this factor also seem unimportant to bees for distinguishing between "sun" and "sky".

unambiguously in orientation. Again, it is important that all bees use the stimulus in the same way so that no misunderstanding ensues.

The effect of zenith source elevation explains the apparent conflict between von Frisch's report (1967; p. 402; confirmed in Chapter V above) that bees treat small sources of white, polarized light as the sun and the experiments of Edrich and von Helversen (1976) in which bees used similarly sized white, polarized stimuli as part of the sky. The latter investigators used only zenith patterns which, necessarily, resulted only in interpretations as sky. In addition, the differences between von Frisch's finding that bees need a minimum of about a 10°-15° patch of blue sky in order to orient to polarized light (which has been confirmed by Zolotov and Frantsevich, 1973) and those of Edrich and von Helversen in which bees oriented well to far smaller spots are explained. Radiation from the natural sky used by von Frisch falls behind the 15° sky/sun boundary in Figure V-29. Edrich and von Helversen's source was always in the zenith and thus was used only as the sky. However, their source probably fell to to the right of the 20-30% UV boundary and thus would have elicited a "sky" interpretation regardless of the stimulus size. The bidirectional dances reported by others (e.g., Rossel et al., 1978) probably result from using stimuli near the sun/sky boundary (except for the zenith patterns).

Edrich and von Helversen interpreted their results as an intensity effect: the eye as a whole needs a certain number of polarized UV photons for orientation, so that a small bright light works as well as a large dim one, or a part of the sky. However, except for a certain minimum threshold there are no important effects of intensity and these results may support a color-opponent process in which the ratio of UV to longer wavelengths is a crucial factor.[5]

The sky/sun rule corresponds roughly to physical reality, although this is not necessary for such a rule to serve as an effective arbitrary convention. On a photon basis[6] direct sunlight contains only about 8% UV while skylight ranges from 20 to 35% UV. Hence, the plane in Figure V-29 dividing sun from sky according to its UV content is sensible. Sunlight is unpolarized and, depending on the wavelength considered and the prevailing atmospheric conditions, the sky within 15° of the sun generally has less than 5% polarization (theoretically about 3.5%), while most of the rest of a clear sky ranges from 10%-65% polarization in the UV (see Chapter III). Hence, the second plane dividing "sun" from "sky" on the basis of per cent polarization is also sensible. That this boundary based on polarization does not extend into the area of small spots with low amounts of UV is an arbitrary feature which, while leading to improper identification of the source of the stimulus, probably results in better dance orientation and recruitment. The two regions of the graph for which the rules fail ("neither" in Figure V-29) correspond to conditions which do not occur in the natural blue sky.

The two other previously unknown rules are used when the patch is judged to be a part of the blue sky. In these cases, bees use the characteristics of the polarized light to identify which part of the sky they see, and then use the patch to orient their dances toward the goal.

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5. It is interesting to note in this regard that color-opponent visual neurons have been discovered in the honey bee by Kien and Menzel (1977). In addition, Kirschfeld (1973) has found that moving polarization patterns induce optomotor responses in bees only when the patterns are relatively rich in short wavelengths.

6. Derived from the energy data of Hess (1939) and corrected to relative photon flux, with respect to the visual spectral sensitivity of the honey bee.

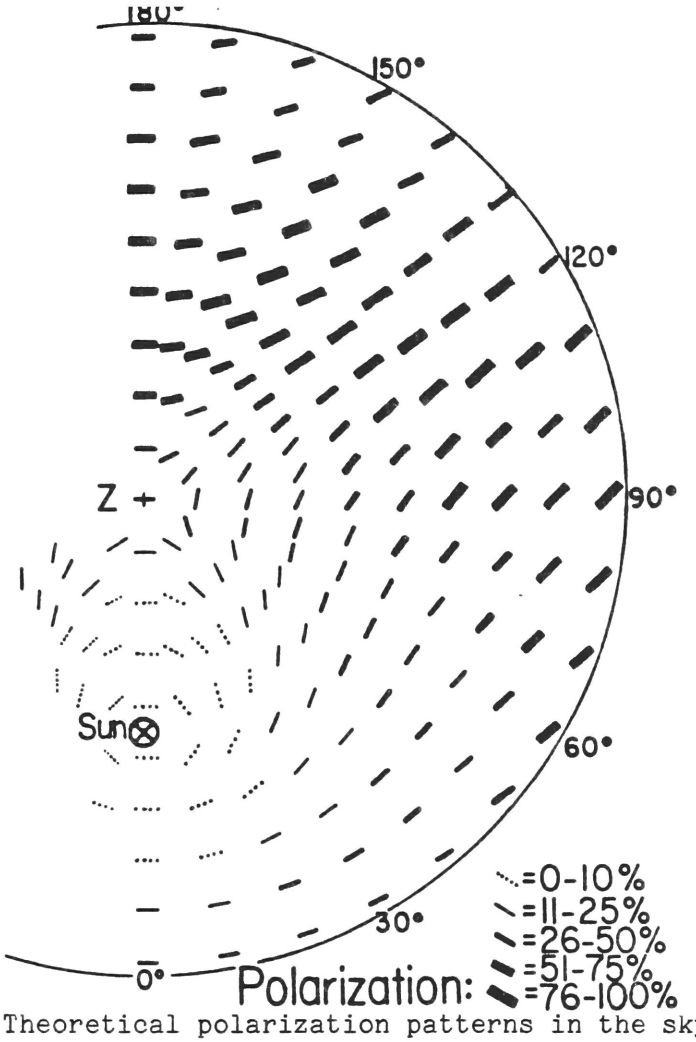

Figure VI-1. Theoretical polarization patterns in the sky with respect to the horizon.
The sun's elevation is 45°, and the degree of polarization is represented by the thickness of the lines, and dotted lines indicate polarization below the perceptual threshold of honey bees. "Z" is the zenith. Only half of the sky is shown, since the other half is a mirror image. Allowing for the distortion which is inevitable in depicting a hemisphere in a plane, the relationship between the E-vector orientation at any point and the sun's position is clear: the E-vector orientation is perpendicular to the plane passing through the sun, point in the sky, and the observer.

However, considering only the E-vector orientation, a given polarization pattern at a particular elevation generally exists in <u>two</u> places in the sky, as illustrated by Figures VI-1 and VI-2. How do bees decide which of these points they are actually seeing?

One possibility would be to measure the <u>degree</u> of polarization in the patch, since theoretical Rayleigh scattering predicts that this will correlate with the distance of the patch from the sun (see Chapter II).

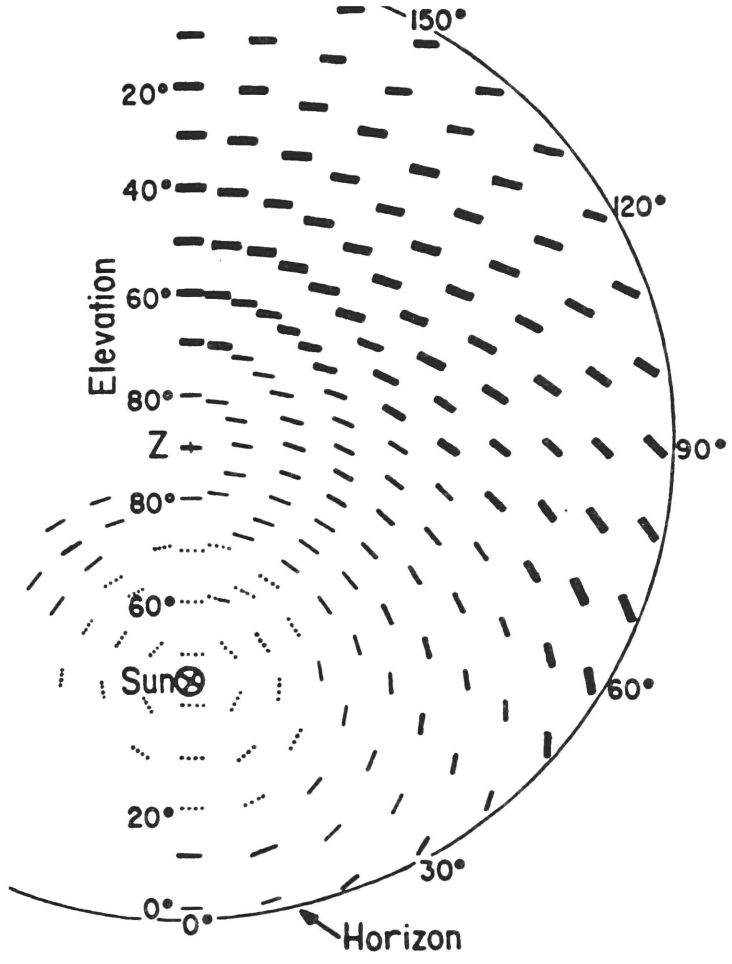

Figure VI-2. E-vector orientation plotted with respect to the page.

In this figure, the E-vector orientation of points with different azimuths may be directly compared. By this convention, for example, all vertical E-vectors in the sky are vertical in the figure, regardless of their azimuth. The circled points near the horizon correspond to one of many pairs at any particular elevation which have the same E-vector orientation, but which lie at different angular distances from the sun. The points in squares are one of several pairs which exist at the same elevation and at equal distances from the sun. Note that below the sun's elevation, no vertical or nearly vertical E-vector orientation occurs. At 20° elevation, for example, an E-vector orientation within $\pm 40^{\circ}$ is impossible since the great circle generated by such a pattern would not intersect the sun's elevation circle.

My direct measurements of UV skylight polarization, however, while demonstrating that actual E-vector orientations correspond quite well with theory, show that the theoretical degree-of-polarization relationship is highly distorted at best in the natural sky, and behavioral experiments clearly show that bees ignore it. In fact, as shown in Chapter V, bees

consistently interpret a stimulus as being the <u>further</u> of the the two possibilities from the sun, regardless of the direction of the food source. Although this second rule results in a stimulus being inappropriately identified half of the time, since the directions are referenced to the sun, these mistakes are automatically eliminated during the outward flight of potential recruits.

A third rule is used when bees see one of two physically identical patterns which are located the same distance from the sun (Figure VI-2). Although the "further-from-the-sun" rule fails, the bees are not confused. Regardless of the direction of the food source, the stimulus is always taken to be a part of the sky on the <u>right</u> of the sun.[7] This right hand rule, though technically wrong half of the time, eliminates another potential ambiguity. Again, since the errors are systematic, no mistakes occur during the flight out.

There exists, however, one point in the sky for which neither of these rules will suffice: the zenith. Here, the two possible locations of the sun are the same distance away, and neither left or right (Figure VI-2). As a result, both rules must fail. In fact, as discussed in Chapter VI, bees have no rule for this singular spot, and dance to both possible interpretations.[8]

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7. The behavioral observations of other workers also appear to show this rule. Von Frisch's vertical E-vector data discussed above also correspond to the point to the right of the sun (1967; pp. 391 ff.). The data of Rossel <u>et al</u>. (1978) which can be analyzed do not disagree with an interpretation of the point as being on the right of the sun.

8. These bimodal dances have been recorded also by von Frisch (1967), and Edrich and von Helversen (1976).

Bees also appear to use a fourth rule. When shown an E-vector orientation which does not exist at the chosen elevation, they still perform consistently oriented dances. It is not yet clear how this rule works since the dance orientation does not seem to be predicted by any geometrical theory of polarization orientation in bees, (e.g., those of Appendix A; Kirschfeld et al., 1975). Indeed, this ability on the part of bees suggests that they may not use the Rayleigh scattering relationships at all. Rossel et al. (1978) have also found that bees are oriented to impossible patterns which can be approximated fairly well by a specific trigonometric equation derived by curve fitting of their data.

These new rules join three previously known dance-language conventions--using the sun as the reference point, agreeing on vertical as the direction towards the sun,[9] and defining how far each additional waggle (or sound burst) in the dance specifies (von Frisch, 1946). The distance convention even differs between "cultures" so that each race of honey bees has its own private dialect (Boch, 1957). Each of these seemingly arbitrary rules is essential for the social communication of bees. They prevent misunderstanding by ensuring that both sender and receiver are using the same reference system. They are not, however, necessary or even desirable for any of the vast number of social and non-social animals which perform the same feats of navigation, but lack the symbolic communication system. As such, they are so far unique to the honey bees, and how they could have arisen in the course of evolution is an unanswered question.

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9. The use of "up" as toward the sun may have developed from the strong positive phototaxis observed for bees departing the hive (e.g., Jacob-Jessen, 1959).

Of course it is easy to develop a fascinating scenario of orientational capacities and reduction of ambiguities, and the many interesting facets of this problem must be experimentally tested. A start could be made by observing the foraging characteristics of potential recruits after they have viewed vertical polarization patterns during the dances on a horizontal surface. That is, even though she may follow a unimodal dance, the stimulus itself exists outside at two different spots in the sky, and a recruit must determine the location of the goal from this ambiguous information as she leaves the hive. It would be significant if in these situations new recruits fly to a feeder location using an interpretation of the vertically polarized light seen in the hive during the dance as being the point in the sky to the right of the sun.

2. How do bees use skylight polarization cues?

The behavioral experiments reported in Chapters I and V confirm that honey bees are able to use the linear polarization of a small patch of skylight as a compass cue. Some aspects of communication have just been discussed. It is of great interest to ask what mechanisms underly orientation behavior. How are animals able to use skylight polarization information for their orientation?

We know that a bee which can observe the sun and returns to a normal hive performs vertical dances which communicate the direction to the goal in terms of solar position. To what do the bees reference their dances when only polarization patterns are visible? By allowing bees to forage in the shadow of a mountain, so that during their flights they could see only blue sky, Von Frisch showed clearly that such dances

specify the angle between the sun and the goal (von Frisch, 1967; pp. 392 ff.). Somehow the bees are able to determine the relative bearing of the skypoint from the sun. This capacity could be based on at least three principal mechanisms. 1) Bees are able to "solve" the geometry of atmospheric scattering and "calculate" solar position directly. 2) The bees can "remember" the relative position of the sky patterns and the sun at all times during the day. Then, by observing a particular skypoint, their internal clock enables them to determine solar position even if the sun itself is not visible. 3) It is possible that bees do not "analyze" patterns of skylight polarization, but some hard-wired feature of their sensory nervous system enables them to directly determine solar position. For example, specific detectors for each polarization form might exist which, when lined-up with the sky pattern, automatically indicate the direction of the sun. These possibilities will now be discussed in some detail.

2.1 Orientation by calculation.

Unfortunately, none of the experiments discussed above, would be likely to provide data useful for evaluating whether bees determine solar position by a "calculation", using the variables of skylight polarization. One possible experiment which might accomplish this would be to find small sections of the natural patterns of polarization in the sky to which the bees cannot orient. If such patterns could be found, there are two possible interpretations, depending upon the form of the polarization. If the pattern is one predicted by Rayleigh scattering, then the disorientation of the bees would suggest that they do not calculate the solar bearing. If the pattern is a non-Rayleigh one, then the

disorientation of the bees would be evidence that they do calculate the solar position, since although they have observed the pattern on their foraging flights, they do not use it.

Von Frisch (1950; 1967; pp. 387 ff.) has reported part of such an experiment, although he did not discuss the implications of the results. In a total of 83 experiments in which he showed bees highly polarized, artificial patterns, he observed 10 for which the bees' were disoriented. These occurred when he used a pattern of polarization which he could just barely detect in the natural sky when he searched with his star analyzer. Because he did not show the bees parts of the sky close to the sun, these polarization forms almost certainly involved E-vector orientations predicted by Rayleigh scattering (see Chapter III), and thus the polarization was geometrically related to the solar position. In this case, apparently the patterns were not used by the bees as orientational cues only because the patterns outside were <u>below</u> the perceptual threshold. If this is generally true, it is an extremely important finding because it implies that what the bees cannot <u>see</u> in the sky, cannot be used as an orientation cue back in the hive.[10] Again, such observations eliminate the possibility that bees calculate the solar position from the polarization parameters because the bees were shown highly polarized artificial patterns (which they could perceive) which corresponded to points on the sky vault of very low polarization. Obviously, they should have been able to calculate a solar position as easily as for E-vector orientation which corresponded to a point on the sky vault with a high degree of

10. In fact, von Frisch commented "The evident relation between clarity in the pattern of the sky and in the indication of direction was particularly impressive." (von Frisch, 1967; p. 390).

polarization.

Another observation[11] which seriously challenges the idea that bees calculate the position of the sun from the polarization information is that they are oriented to impossible polarization patterns--ones that cannot exist in the sky at that time, given only primary Rayleigh scattering. Obviously, other mechanisms must be invoked to explain these observations. It is interesting to note, however, that these bees dance "hesitantly" while viewing impossible polarization patterns.

The results of the sky measurements reported in Chapter III provide yet a third kind of evidence which strongly implies that polarization orientation does not occur by calculation. There it was reported that the E-vector orientation is the skylight parameter which most closely approximates the predictions of simple Rayleigh theory, and even under the best conditions, it often diverges substantially from theoretical expectations. These divergences are generally greatest in the UV--precisely those wavelengths used by honey bees in their orientation to polarized light. Chapter III also points out that corrections for divergences that occur in the natural patterns are generally not easily or accurately made.

On the whole, the factors discussed so far strongly indicate that bees do not calculate the solar position in an analytical sense from the parameters of skylight polarization. This leaves two alternative mechanisms: 1) The bees have a "memory" of all sky positions of the polarization patterns and their relationship to the sun as a function of time or

11. Confirmed by Rossel et al. (1978).

2) bees can approximately determine the solar bearing corresponding to a specific pattern of polarization by use of some "automatic" detector system.

2.2 Orientation by remembering the form of the sky patterns.

The idea that bees can remember the patterns of skylight polarization and their diurnal motions across the skyvault was favored by von Frisch (1950; 1967; pp. 395 ff.), because he observed that under overcast conditions, his bees could still orient to artificial patterns of polarization. For example, he showed dancing bees a direct view of the cloudy sky. Their waggle dances were disoriented. He then interposed a polarizer, and for many orientations of the filter, the dances pointed in specific directions. Noting the relationship between the waggle directions and the orientation of the polarizer, he compared the patterns produced by the polarizer to what could be seen on a clear day at the same time. He found that the bees' responses were appropriate for the polarization being used as an orientation cue.

Unfortunately, to standardize the stimuli of his experiments von Frisch used an artificial polarization source placed in the zenith. We have already seen that zenith polarization patterns may be special; because, for one thing, the stimulus cannot be used for solar orientation. Von Frisch found that under these conditions the bees were well oriented to this artificial source with bimodal (180°) dances appropriate for orientation on the basis of the E-vector orientation of the light.

Obviously, these results seem to constitute negative evidence for the hypothesis that bees must see the polarization patterns in the sky

before they can use them as an orientation cue. But there also is the evidence, mentioned above, that bees cannot use patterns which exist weakly in the sky. How can these two very different observations be reconciled?

One possibility is that learning may play an important role in honey bee polarization orientation. That is, bees might learn the relationship of the polarization patterns to solar position, just as they learn how to use the sun for orientation (see Lindauer, 1961, for a review of what is known about the ontogeny of honey bee sun-compass orientation). For those patterns which appeared weakly in the sky and which von Frisch found were ineffective for orientation, perhaps the patterns were never above the threshold of the bees. That is, the bees could not learn to use something they had never detected. This possibility, however, seems very unlikely. For example, consider the data for 6 September 1949 (at 1330) which von Frisch includes (1967; p. 389). In this particular case, he states that the weak pattern he showed the bees was at azimuth 300°. Assuming the latitude was 47°N and the solar declination was 6°40'N, the sun would be at azimuth 213° and zenith distance 45°; the relative bearing of the pattern from the sun was about 90°. Since the sky patch was centered at about 40° in elevation, by the methods described in Chapter II and Appendix A, the scattering angle can be computed to have been about 60°. For a Rayleigh atmosphere this would correspond to about 60% polarization. The small degree of polarization observed during the experiment probably depended upon atmospheric turbidity or some other transient factor, and one would expect that on many days this pattern would actually be well above the perceptual threshold of the bees. Thus

they could have learned about its form and relative position as well as that of other points on the skyvault. (It is also possible that the bees von Frisch tested were very young foragers not yet experienced with the sky patterns.)

In addition to these puzzling differences of orientational ability, the results of the experiments reported in the last sections of Chapter V show that the waggle dance orientation to polarization patterns is unpredictable under complete overcast. For example, Figures V-54 to V-58 showed that dance orientation was much more precise on clear than on cloudy days. One of the most interesting aspects of this behavior is that a small, white polarized stimulus was frequently analyzed on the basis of its polarization (even though the orientation may not have been precise), whereas on clear days it would have been interpreted as the sun. This can be seen, for example, by the dance deviations of Figure V-56. Such behavior could depend upon several different factors. It could result from purely physiological effects. For example, the color receptors in each ommatidium are stimulated in different ratios outside the hive on clear versus cloudy days--the overcast sky is relatively richer in longer wavelengths that the clear blue sky. Perhaps a wavelength-dependent sensory adaptation occurs in the nervous system which could explain this behavior.

Or the observed differences might depend upon other characteristics of the visual system. For example, when the degree of polarization in the sky decreases, the sensitivity of the detector system might increase, to take advantage of any small amounts of polarization which sometimes exist under marginal overcast conditions (Chapter III). In this way, an

animal viewing a white, polarized light under clear conditions would possess a relatively low polarization sensitivity and would not respond to the E-vector orientation. But under cloudy skies, the polarization might be detected by an increase in the sensitivity of the detectors. These effects may also arise behaviorally; perhaps the responses to smaller, white polarized stimuli on cloudy days occur because the animal confines its attention to take advantage of any small patches of polarization visible between dense clouds. Another possible factor is that the overcast sky is approximately white. Perhaps the bee's responses to white, polarized lights inside the hive match what they saw outside in the sky on their last foraging flight. Obviously, if any of these behavioral suggestions are true, they imply that orientation on the basis of skylight polarization cues does not occur only in a stereotyped way, but is quite flexible.

One variant hypothesis of orientation has been proposed by Rossel *et al.* (1978). As discussed briefly in Chapter I, these workers have carried out experiments in which the orientation of bees to small (generally 10°) areas of the sky was observed. They assume that the sky patterns are too complex for an insect's brain to compute or remember and that bees use a "simplified" version of these cues. They further hypothesize that the bees know the rate of change in E-vector orientation as a function of azimuth along a circle of constant elevation.[12] This seems a rather strange *a priori* assumption since there are many other possibilities. Rossel *et al.* interpret their data to indicate that the bees use only a *single* relationship,[13] and that this scheme works best for

12. This, of course, is really not different from many other ways of calculating sun-sky geometrical relationships.

skypatterns nearest the zenith. The equation (derived by a least squares fit) which describes their data is:

$$X = c - 90^{\circ} + 9\sin(2c)$$

where c is the relative azimuth. We know, of course, that often the zenith area of the sky is obscured and still the bees remain well oriented. Thus they would have to apply this to other parts of the sky as well.

It is interesting to consider actual predictions of this relationship empirically derived by Rossel et al. For example, for vertical E-vectors, they would predict that the dance are always oriented 90° from the sun. Obviously the data for vertical E-vectors reported in Chapter V do support this interpretation; my bees were quite precisely oriented in the expected direction to the right of the sun (e.g., Figure V-24). Numerous other examples are presented in Chapter V which show that the bees are much more precisely oriented than the hypothesis of Rossel et al. would predict. In other respects, however, such as the bees using the pattern farthest from the sun, both sets of data agree qualitatively.

It seems strange that bees would use a generalized but incorrect representation of the sky patterns in their orientation. Why should their experiments which used natural stimuli provide less precise results than those of the artificial stimuli which I used? One possibility is that the relative UV content for the days Rossel et al. studied fell close to the threshold for sky orientation to spots of 10° (see Figure VI-2). Also, these restrictions seem unnecessary logically, because at

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13. The exact relationship for any constant elevation can be easily derived by calculating the derivative of the equations developed by analysis of the spherical trigonometric relationships in Chapter II and Appendix A.

least large areas of the sky patterns have a general form which should unambiguously indicate the solar position and thus imply a different mechanism than the one Rossel *et al*. conclude would have to be used. In fact, for single spots, under a wide variety of sky conditions a much better strategy would be calculations based on E-vector orientation as described in Appendix A. Then, only several variables need to be known, and could be applied in a simple, straightforward way.

Finally, while it is possible that the differences between the two sets of data exist because of the sensory capacities of the race of bees used, some artifacts might explain these differences, such as polarized reflections from the inside of the black plexiglas dome Rossel *et al*. used. Systematic investigation will be necessary to determine the importance of these differences.

2.3 *Orientation by use of an automatic detector system.*

The results of behavioral observations discussed so far seem quite paradoxical. On the one hand, von Frisch has shown that bees are disoriented if they view a pattern which existed only weakly in the sky when they were foraging a short time earlier. Yet on the other hand, both von Frisch and I have shown that bees can still orient by polarization cues even on cloudy days when *no* polarization had been visible in the sky outside the hive. In addition, bees can orient to polarization patterns not possible considering simple Rayleigh scattering.

One possible way to partially reconcile these very different observations of orientation is to postulate that the sensory system may function automatically to determine the bearing between the patterns of

polarization and the solar position, and that this mechanism can be "fooled" occasionally.[14] This idea is based on the fact that the pattern of skylight polarization depends only on the solar position and therefore the pattern is always the same with respect to the sun.[15] It appears different to an earthbound observer only because of the changing solar position.

Suppose an animal's visual system was designed to detect this constant, fixed form of the polarization pattern.[16] The animal could then find the pattern in the sky at any particular time by only making an adjustment in the elevation of the axis of the detector system, which, of course, would pass pass through the sun, the important variable in orientation. One could imagine, in a simple minded way, that the animal might turn back and forth until it visual receptors were stimulated in a specific manner by the skylight polarization patterns, which would then indicate that its head was pointed toward the sun. Such an automatic system would avoid many problems, since the bees would only need to know the movement of the sun, and from this make the appropriate adjustments in the orientation of the detector system. We already know from the experiments of Lindauer (reviewed, 1961) that bees do learn the solar

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14. Considering the spectral sensitivity of polarization detection in bees and the results of Chapter III, it seems likely that the experimental situation of highly polarized UV stimuli is extremely artificial and that under natural conditions bees have never seen such "impossible" patterns.

15. Actually, the thickness of the atmosphere greatly affects all the polarization parameters, except the E-vector, and hence modifies this statement. See Chapter III.

16. Since such a system would also be subject to errors due to the divergence of the sky patterns from theory, perhaps some "average" orientation system developed to use these patterns successfully.

movement quite precisely, and somehow know its position at any time of day.

One possible form of such an automatic system might take would be a set of E-vector sensitivities of different ommatidia corresponding to the E-vectors of sky points toward which these ommatidia are directed when the bee's head points toward the food source. If all these ommatidia were covered, the blue sky should no longer be adequate for orientation. Von Frisch (reviewed 1967; p. 411) performed an experiment which may directly apply to this idea when he painted over various parts of the compound eyes to determine their importance for orientation when dancing on horizontal surfaces. With this technique, he showed that the polarization sensitive detectors are located in the dorsal parts of the eye, in contrast to the ventral portions, which are insensitive to polarization patterns. Thus he was able to completely cover over the lower parts of the eyes without interfering with the orientation by celestial cues. But when he covered the part of the eye which viewed the source of polarization during the waggle run, the bee merely circled back and forth in a very hesitating manner, unable to initiate a waggle run.[17]

In pilot experiments where I also covered small sections of bees' eyes, I found that horizontal dancers could no longer orient to light sources, although they <u>were</u> able to perform normal vertical dances easily.

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17. This fact may also imply that use of polarization patterns as an orientation cue is not by calculation, because one expects that almost any part of the eye would be as useful for calculation as any other.

Van der Glas (1978) has formulated an interesting hypothesis about one automatic polarization detection system which might permit orientation on the basis of E-vectors. His idea is based on two facts: 1) the anatomical work of Menzel and Snyder (1974) has shown that with respect to the saggital plane of bees, and other insects which have been studied, the microvilli in opposite eyes are mirror images of each other; and 2) The E-vectors in each half of the natural, clear sky, (defined by the solar vertical) are mirror images of each other (see Chapter III). Thus an insect possessing these eyes should be equally stimulated when the body axis is in the plane of the solar vertical (i.e., towards or away from the sun). In all other orientations, stimulation would be asymmetric. Obviously, such a system would enable an animal to orient on the basis of the E-vector without analyzing the information--it would only have to turn about until the stimulation of both eyes was equal, which would result in heading toward or away from the sun. The angle between this direction and the direction toward the goal obviously is the relative azimuth which is the important variable in the dance communication.

Such an hypothesis is attractive because it could explain many observations. For example, the orientation would have a 180° ambiguity, because such a method determines only the solar vertical: an animal would not know whether it was pointing toward the sun or away from it. Ordinarily, the asymmetry of the E-vector patterns in these directions probably would allow an animal to distinguish between the two possibilities. (For example, in the antisolar vertical, the E-vector changes are much smaller than for equivalent cues around the sun.) This could explain why bimodal dances are not observed in <u>vertical</u> dances, since the bee could

use large parts of the natural sky visible during her foraging flights. However, in the horizontal hive experiments, the bees see only small spots of polarized light and even though they have determined the appropriate relative azimuth while outside, they probably are not able to do this with the tiny stimuli inside. Perhaps this is the basis of the occasional mirror image dances which I have observed.

In summary, the available data are insufficient to evaluate the possibility that bees can analyze the polarization patterns in the sky by an automatic detector system. Of the many possible tests, one is particularly simple to carry out and has already been suggested by van der Glas (1978). If bees do possess special feature detectors for the characteristic circles of polarization around the sun which enable them to determine when they are aligned with the pattern in the sky which gives solar position, it would be necessary for them to adjust continuously the reference axis of the detectors to be along the line of sight towards the sun. Since the eyes are rigidly fixed, elevation of the head during the dance under various experimental conditions would be a very important variable to observe.

2.4 Differences of orientation to vertical and horizontal E-vectors.

As described in Chapter V, bees frequently were much more precisely oriented to horizontal E-vector orientations, in contrast to nearly vertical patterns. What could be the source(s) of this divergence? Some interesting differences between vertically and horizontally polarized skylight can be appreciated by examining the theoretical E-vector orientation across the skyvault. A typical example is shown in Figure VI-3

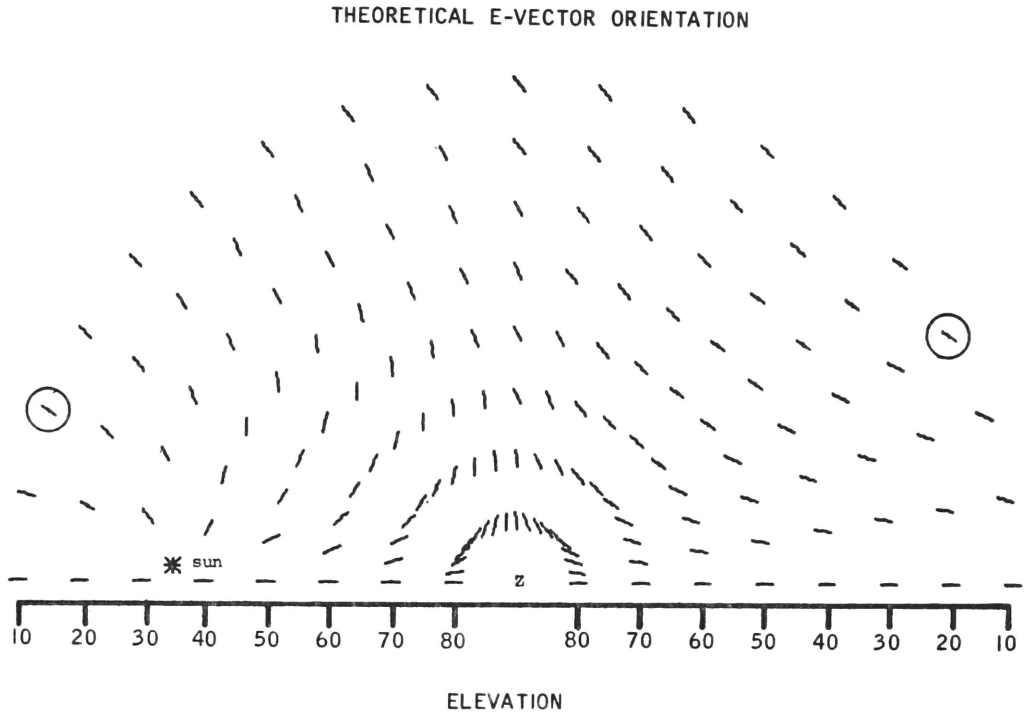

Figure VI-3. Theoretical values of E-vector orientation plotted relative to the horizon: horizontal line segments are horizontal E-vectors in the sky.

which corresponds to a solar zenith distance of 55°. Here, the values of the E-vector orientation which would be seen at each point in the sky are plotted relative to the horizon. Thus, if an E-vector appears vertical in the figure, it is also vertical in the sky. In this way E-vectors can be directly compared to one another. From this diagram, two characteristics of the E-vector outside are quite clear: 1) for a large area of the sky, the E-vector orientation changes only slowly as a function of position on the sky vault. In addition, 2) nearly vertical polarization occurs only relatively close to the sun, in the solar half of the sky.[18] The first observation means it is very important for bees to be able to

18. The greater the solar elevation, the closer the vertical patterns are to the sun. The largest relative azimuth (90°) that a vertical E-vector can have occurs at the horizon for sunrise and sunset.

distinguish between small differences in E-vector orientation close to horizontal. This is because, due to the slowly varying characteristics of the E-vector orientation, small errors in its determination can produce very large errors in determining the azimuth angle. The second observation emphasizes that patterns which are closer to vertical generally possess a smaller degree of polarization, since they are relatively close to the sun; they have smaller scattering angles. In addition, it is entirely possible that when vertical patterns are visible in the sky, the solar position can be determined by other means, such as by the radiance distribution. These differences between vertical and horizontal E-vector orientations may constitute selective advantages for a system which analyzes nearly horizontal patterns with much higher precision than nearly vertical ones. The existence of such a specialized sensory system could possibly explain other observed differences in the orientation of bees to vertical and horizontal patterns. For example, it was noted at the end of Chapter V that anomalous orientation was never observed to occur for E-vector orientations close to horizontal. Yet it frequently occurred for those close to vertical. This could mean that anomalous E-vector analysis arises because detector structure is adapted to analyze more nearly horizontal patterns at the expense of vertical ones. But this cannot be the entire story, because it has been shown clearly in the results of Chapter V that bees <u>can</u> be precisely oriented to vertical patterns.

If the above suggestions are correct, they may help to explain the observed differences between orientation on cloudy days, when bees oriented themselves to patterns they did not actually see in the sky, and

relatively clear days when bees could not orient to patterns which were weakly visible in the sky. The weak patterns would generally tend to have E-vector orientations closer to vertical since their low degree of polarization generally means that they were closer to the sun.

Another factor which could conceivably explain why bees are more precisely oriented to nearly horizontal patterns is learning. Just as in other orientation behavior, polarization orientation probably has some components which are improved by an animal's previous experience. For bees flying with a view of the clear sky, E-vector orientations close to horizontal are probably a very obvious feature, because skylight along the entire vertical circle containing the sun is horizontally polarized, and large sections of it are typically highly polarized. Perhaps, like other optical cues used in orientation, the bees pay more attention to those which are striking to them. Of course, to test these ideas appropriate experiments will have to be performed. One good one would be to use a horizontal E-vector orientation and change its zenith distance while observing the waggle-dance orientation of bees. Such an experiment would essentially move the point on the skyvault which corresponded to the artificial source, closer to or farther from the sun and would test whether the dance deviation changes dramatically as the sun is approached and the degree of polarization of the corresponding spot on the skyvault decreases while the E-vector of the experimental stimulus remains constant throughout. If the dances do become more variable, this may mean that the bees need to see the patterns in the sky outside while foraging.[19] A conclusive experiment might be one in which the skylight

19. Different receptors of the eye might possess different capacities for analyzing polarization, and this would

parameters are carefully monitored during the foraging flights of individual bees and compared to the observed dance orientation back in the hive.

To summarize this section, bees may have specially developed sensory systems which analyze horizontal E-vectors better than vertical ones to enable precise orientation to small parts of the sky. As a result, they may orient with less precision to patterns which are vertically oriented and typically of lower degree of polarization. Learning may play an important role in this and so much individual variation may be ascribed to the differing effects of experience. There is no positive evidence which indicates that honey bees calculate the solar position from the variables of the scattering triangle.

3. Color, visual receptors, and orientation.

So far this discussion has emphasized the geometrical aspects of orientation behavior. The experiments reported in Chapter V also have important implications about the properties of the receptors involved in polarization detection, especially their wavelength-dependent responses. They also provide some additional information about what kind of process polarization detection is for honey bees--whether it is a rigid, automatic behavior, or whether there is some flexibility in detecting and using skylight polarization cues.

In the past, properties of the compound eye, especially of the photoreceptor structures, have been the basis of many hypotheses about

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complicate the situation.

polarization analysis by animals. Therefore, a brief review of its anatomy is helpful in understanding the implications of the experimental results discussed here.

3.1 Honey bee compound eye.

The compound eyes of worker honey bees are composed of about 5500 ommatidia in the form of a convex ellipse with a field of view of about 190° by 145°. Each ommatidium is about 4 micrometers in diameter, and 300 micrometers (or more) in length (Menzel and Snyder, 1974), and consists of a retinula composed of rhabdomeres from parts of the nine individual visual cells. Over 99% of the eye is composed of units which in cross-section show only eight cells: the ninth cell is located proximately to the other sensory cells. But in about 60 ommatidia in the first four to five horizontal dorsal-most rows, the ninth cell is very long and extends through the retinula so that nine cells are seen in cross-section (Schinz, 1975). This area has been of great interest since von Frisch (1967; pp. 410 ff.) has shown that the dorsal part of the eye is the principal area mediating polarization sensitivity.[20] The rhabdomeres contain the pigments mediating the visual process, which are arranged on microvillar structures. This makes the photoreceptors sensitive to the polarization of the incident light, since light is absorbed in different amounts depending upon whether it vibrates parallel or perpendicular to the microvillar axis.

The eight cells usually seen in cross-section were originally hypothesized to mediate E-vector detection in a manner analogous to von

20. Weiler and Huber (1972) and Duelli (1975) have reported similar results for ants.

Frisch's star analyzer.[21] For bees, however, Goldsmith (1962) later found (by electron microscopy) that only two orthogonal directions were present in most of the ommatidia of the compound eye. Exceptions have been recently found for the very dorsal-most ommatidia mentioned above (Schinz, 1975). Here, the ninth cell is very long and extends over the entire length of the ommatidium, while the microvillar arrangement assumes three (or even more) orientations. To complicate the picture, except for the small, dorsal part of the eye just noted, the microvillae twist at a rate of about 1° per micrometer (Wehner et al., 1975). Cells appear to twist clockwise or counterclockwise randomly, since equal numbers of both types are found everywhere in the eye.

The honey bee possess true trichromatic vision with the sensitivity maxima of the color receptors at green (550 nm), blue (450 nm), and ultraviolet (350 nm) wavelengths (Menzel and Blakers, 1976). Specific receptor types can be found over the entire eye (Menzel, 1977; Autrum and von Zwehl, 1964). Each retinula consists of two pairs of green receptors, one pair of blue receptors, and one pair of UV receptors (Wehner, 1976). The ninth receptor cell is always a UV receptor (Menzel and Snyder, 1974).

3.2 Polarization sensitivity of receptor types.

Beginning with von Frisch's original observations (reviewed by von Frisch, 1967; pp. 401 ff.) that waggle dance orientation to polarized

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21. In review, this device consisted of eight polarizers cut in the form of isosceles triangles, and arranged radially to form an octagon. When linearly polarized light was viewed through it, the intensity distribution indicated the polarization form (von Frisch, 1967; pp. 385 ff., and pp. 423 ff.)

skylight was limited only to short wavelengths (almost completely to the ultraviolet), a number of workers have collected evidence which seemed to indicate that only UV receptors are responsible for polarization detection. For example, Menzel and Snyder (1974) accomplished the first intracellular recordings from worker bee retinular cells. They found little or no polarization sensitivity of the normal groupings of trichromatic cells. They confirmed, however, the theoretical predictions of Snyder (1973) and Gribakin (1973) that the ninth retinular cell should be an ultraviolet detector and is highly sensitive to E-vector orientation. In addition, they showed directly that green receptors are insensitive to polarization, while blue cells are only weakly sensitive. These physiological findings compliment the results of von Frisch's behavioral experiments very well.

In contrast to the widespread belief that ultraviolet receptors alone are responsible for polarization cued orientation behavior, van der Glas (1978; p. 15) hypothesized that polarization analysis might be mediated by the ninth cell, along with the action of other receptors. He proposed that due to the differential sensitivities of each receptor type, polarization patterns might actually be perceived as color patterns induced in the eye. In this way, polarization information would be color coded and processed through already existing channels in the nervous system. This presumably would reduce drastically the complex processing requirements of the central nervous system for polarization orientation.

3.2.1 Is polarization sensitivity mediated by UV receptors alone? In support of van der Glas' hypothesis, the results of wavelength sensitivity experiments reported in Chapter V provide evidence that the UV

polarization detectors do not, in fact, have a separate, unique line into the central nervous system. Specifically, it has been shown clearly that when the sky is clear, bees interpret a small, polarized UV light on the basis of its polarization only if it lacks longer wavelengths. It was found that these longer wavelengths mask the polarization of the beam and inhibit the polarization orientation behavior. This effect is strong evidence that other receptors interact in the central nervous system with the output of the ultraviolet photoreceptors which are more strongly stimulated by the white polarized light than the UV.[22]

As pointed out above, a similar observation by von Frisch (1967; p. 399) confirms the masking effect. When his honey bees viewed the sun itself through a polarizing filter, the E-vector orientation was not important to the bees; they completely ignored the direction of polarization of the artificially polarized sun. An additional interesting experiment was reported by Kirschfeld (1973). He was able to elicit optomotor responses in honey bees by rotating a set of narrow polarization filters alternating at $\pm 45^{\circ}$ so that to the bees the E-vector appeared to alternate back and forth. The bees responsed only when the illuminating light was restricted to short (i.e., UV) wavelengths. If the stimulus was also composed of longer wavelengths, the moving polarization pattern was

22. A possible selective advantage of masking becomes apparent when the wavelength distribution of polarization useful as orientation cues is considered. In the normal visual environment of bees, the only source of such cues is the blue sky, which, of course, emits predominantly short wavelengths. There are no white polarization sources in nature known to be useful for celestial orientation. In fact, appreciable amounts of long wavelength polarization are produced only by reflection from underlying substrates (see for example, Coulson, 1968; and Chapter III). Therefore, masking may be an adaptation to reject polarization "noise", so that only appropriate orientation cues will be used.

ineffective as an optomotor stimulus. With these striking observations of the interacting effects of longer wavelengths, van der Glas's induced color patterns take on additional interest and should be analyzed in greater detail.

3.3 Further details of honey bee orientation to colored lights.

Edrich (per. comm., 1978) conducted experiments which tested the influence of different colored lights on the orientation of bees dancing on a slightly inclined (20°) or horizontal hive. He found that when the hive was slightly tilted, the smallest amount of light needed to influence the (gravity cued) waggle dances had two minima: 450 nm (blue) and 550 nm (green). Effects of UV were conspicuously absent unless the UV source was polarized. Even though the bees did not respond to any unpolarized UV light while dancing, they were strongly phototactically attracted to it after they finished. Edrich interpreted this to mean that UV receptors were not involved in solar orientation, but only in polarization orientation.[23] These observations underscore the realization that each visual receptor can have quite different functions when stimulated by the same light source.

In his study of horizontal dances, Edrich reported that the bees interpreted a test light as the sun for all wavelengths greater than about 410 nm. With unpolarized UV lights, the bees danced opposite to the solar direction. Since it is well known that for clear blue sky the "bluest" (and darkest) point on the skyvault is located in the antisolar

23. This differs from the conclusions of von Frisch, et al., 1960, who reported that bees could perceive the sun through heavy overcast only at ultraviolet wavelengths.

vertical, he hypothesized that the bees exhibited "reverse dances" because they interpreted the source on the basis of its radiation as being this "antisun".

Independent, similar results were reported at the end of Chapter V, where under some conditions the bees were observed to reverse their solar orientation (i.e., treat the source as if it was an antisun) when a bee-white light (containing all wavelengths to which the bee is sensitive) was changed to UV wavelengths alone[24]. There was a major difference, however, in the results. My observations show that such antisolar orientation seemed to occur only when blue sky had been visible while the bees were outside the hive. Under completely overcast conditions, bees interpreted an unpolarized, UV light as if it was the sun. In addition, many of the dances recorded for small, UV polarized sources shown in Figure VI-2 as "neither" were opposite to the solar direction.[25]

While it is possible (as suggested by van der Glas, 1978) that the absence of antisolar dancing behavior on overcast days arises because the bees see the solar disc in the UV through light cloud cover (see von Frisch, 1967; pp. 366 ff.; von Frisch, et al. (1960), my measurements reported in Chapter III show that such a differential UV transmission of sunlight through overcast is probably a rare occurrence at best. It was interesting, though, that I observed that when large patches of blue sky

24. This is another example of masking by longer wavelengths, in this case, unpolarized ones, and suggests that masking may not be unique to polarized light.

25. However, many disoriented dances also occurred. This variability possibly depends on a number of factors, such as the fact that the mylar screen diffused the source extensively. These aspects need to be investigated in detail.

opened in an otherwise cloud-covered sky, the bees oriented their dances in directions which were generally appropriate for the spot of blue sky and the direction of the food source. However, as pointed out above, more extensive experiments which associate sky observations with the dance orientation are needed to clarify this question.

The variable effects of sky conditions and stimulus color on the orientation of horizontal waggle dances can be better appreciated by the much more extensive data for dances to small, white, polarized sources. On clear days, the bees rarely assumed any of the directions predicted on the basis of the E-vector orientation of the stimulus (especially for X close to 90°, that is, horizontal). Yet on completely overcast days, there was a widespread tendency to do this (e.g., Figure V-5).[26] All of this evidence indicates that orientation on the basis of polarization cues is less stereotyped than previously thought.

At this point, one additional experiment will be briefly described which illustrates the diverse reactions of orienting honey bees to UV light. Jacob-Jessen (1959) carried out very interesting comparative studies on hymenopteran orientation and communication. Important here are her experiments in which she trained honey bees to depart from their hive by walking from the center of a uniformly marked disc in a specific compass direction. Besides the disc, the walking bees could see only the sky, and they quickly learned to use the sun and skylight polarization

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26. In addition, I have frequently noted that if a bee is shown (in serial order) a white, polarized light (to which she exhibits solar orientation), then a UV polarized light (sky orientation) and then finally a white, polarized light again, she is much more likely to notice the polarization of the white light and tends to dance as if the (white) source was a part of the sky.

patterns to determine the (fixed) compass direction in which they could leave the hive. Her data for bees trained in this way show very definite peaks opposite to the sun (e.g., 1959; Figure 5D, p. 604), as well as in the trained direction. It is well known that bees are strongly phototactic when leaving the hive and press towards lights which are maximally stimulating for them. On this basis, one would expect that they would move toward the sun. But the behavioral observations show clearly that they do not.

For reasons not important here, I repeated Jacob-Jessen's experiment using Italian honey bees (Apis mellifera ligustica). Although my bees never learned how to escape from the disc and leave the hive very well, (even after months of training), they showed an antisolar tendency in their walking to an extreme degree.[27] In fact, under clear skies, virtually all of my bees streamed in the antisolar direction. Interesting details of the behavior could be easily shown by the following manipulations. Bees entered the disc at the center, climbing out of an opaque tube. A partition was placed in the vicinity of the exit hole, perpendicular to the plane of the solar vertical so that for emerging bees, half of the sky was obscured. Bees entering the disc would be as likely to emerge under either sky section and could not see the other. Bees entering the section without a view of the sun immediately walked towards the antisolar direction until they were stopped by the edge of the disc. Reflected images (by use of a first surface mirror) of the sun did not affect their orientation. However, bees which entered on the side from which the sun could be seen tended to walk towards the sun until they

27. Perhaps this is a major racial difference between the two subspecies of bees.

passed out of the shadow of the partition. Often these bees then reversed their direction and walked back towards the antisolar sky (i.e., the partition). When they entered the shadow of the partition again, they turned around and walked back towards the sun. Some bees would pass back and forth like this essentially trapped by their phototactically mediated behavior. By raising or lowering an opaque plate at the edge of the disc, I was able to determine that the bees were attracted by a part of the sky about 90° from the sun in the antisolar vertical. Examination of this sky area with the polarimeter described in Chapter III showed that it possessed the greatest relative UV flux of any point visible in the sky. When this point was covered, the bees tried to escape in another, non-solar direction which seemed to correspond to the bluest spot still visible to them in the sky.

With several large celluloid filters of various colors, I determined that only short wavelengths were responsible for this phototactic behavior. It could be shown in a number of ways that bees were not responding to the <u>polarization</u> of the skylight. For example, a large, UV transmitting polarizing filter did not change the direction in which the bees spontaneously tried to escape. In addition, ultraviolet transmitting mylar could be placed over the disc in any orientation without changing the escape direction adopted by the bees. This could only happen if the light used by the bees was unpolarized, since mylar is a high-order wave-plate (measured in this case to be about one-quarter wavelength for 350 nm) and thus would generally change the patterns of skylight polarization.

In summary, the results of these experiments and observations suggest strongly not only that bees can identify certain sections of the sky on the basis of color, but also that the processing of ultraviolet information in the central nervous system is probably flexible and depends upon multiple factors. In this processing, ultraviolet receptors clearly do not seem to have a independent, straight-line route into the central nervous system, since long wavelength masking effects clearly show that information from other color receptors interact strongly with ultraviolet input, in so far as they determine whether the polarization information is used. In many cases, it is likely that the specific conditions determine how the light is ultimately analyzed and used as an orientation cue.

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Appendix A.

Geometry of orientation and skylight polarization.

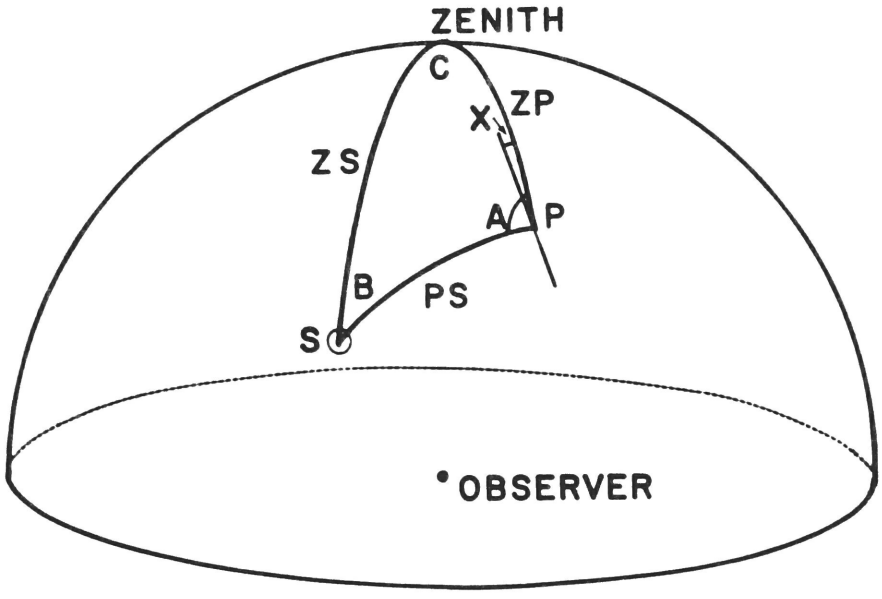


Figure A-1. The scattering triangle.

In Chapter II a geometrical description of skylight polarization was developed using the scattering triangle. For convenience, it is illustrated again here as Figure A-1. A principal use of the scattering triangle is for thinking about and calculating various skylight parameters which (assuming primary Rayleigh scattering) may act as cues in animal orientation. Table VI-I summarized some of the expected behavioral possibilities which can be deduced by considering the geometrical relationships of various parts, and is derived in analytical detail below along with more extensive comments about the behavioral implications. This development is not intended to be exhaustive and focuses only on some

basic relationships. In this treatment, a "known" quantity is one which an animal measures, calculates, or remembers and can directly use in its orientation. That is, experimental manipulation of these variables is expected to modify an animal's orientation, while changes in other variables should be ineffective. The six variables used in this analysis are described in detail in the section on the scattering triangle in Chapter II:

ZP = skypoint zenith distance

ZS = solar zenith distance

PS = scattering angle

$A = 90^{\circ} \pm X$; where X is the E-vector orientation

B = angle between the sun's vertical and the scattering plane

C = the relative azimuth

Analysis is separated into two cases: 1) only information about the point in the sky (sky point) is known and 2) information about both the sky point and the sun are known. Since most orientation behavior observed, e.g., the flights of honey bees or dances on horizontal surfaces, concerns movements in the horizontal plane, the azimuth angle is the important variable. In addition, there are instances where animals use vertical angles which refer the the horizontal plane (such as the usual dances of honey bees on vertical comb). Therefore, azimuth is treated here as a dependent variable. Obviously, these procedures could also be applied to any other part of the scattering triangle just as easily, depending on the observed behavioral characteristics.

I. Only Skypoint Information Known

Case i: Skypoint zenith distance and E-vector orientation known.

If only the sky point zenith distance (ZP) and E-vector orientation (X) are known, these two parts of the scattering triangle cannot uniquely specify other parts.

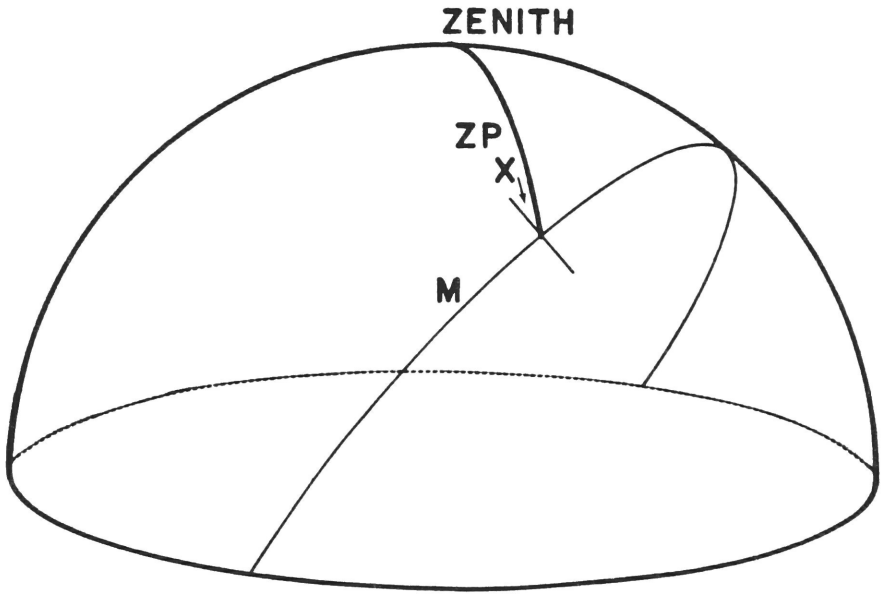


Figure A-2. Skypoint zenith distance and E-vector orientation known.

The geometrical reason for this can be appreciated by referring to Figure A-2. Given only the zenith distance of the point (ZP) and the E-vector orientation (X), the sun could be located anywhere along great circle M. The specific relationship is found using the law of transposed cosines written for ZS, PS, ZP, and A. Now,

$$\sin(ZS)\cos(C) = \cos(PS)\sin(ZP)-\sin(PS)\cos(ZP)\cos(A).$$

But, $A = 90^{\circ} \pm X$; so $\cos(A) = \pm \sin(X)$. Thus,

$$\cos(C) = \frac{\cos(PS)\sin(ZP)}{\sin(ZS)} \pm \frac{\sin(PS)\cos(ZP)\sin(X)}{\sin(ZS)}.$$

This equation describes analytically what Figure A-2 illustrates geometrically: all that can be deduced from this information is that the sun lies somewhere along the great circle perpendicular to the E-vector orientation at the sky point. For example, for an E-vector orientation X = 30° and ZP = 15°, a few possible sun positions are:

ZD	relative azimuth (degrees)
10	9.98
50	46 or 105.4
50	47 or 121.4
30	88 or 158.6

Thus, the solar position can only be fixed somewhere along the great circle M, and the relative azimuth can take on a large range of values. Therefore, an animal analyzing a skypoint only on the basis of its E-vector orientation and zenith distance would be unable to determine the relative azimuth of the point they observed.

Case ii: Skypoint zenith distance and scattering angle known. Knowledge of the scattering angle (PS) and zenith distance of the skypoint (ZP) fix the position of the sun somewhere along a circle (of arc radius = the scattering angle) centered on the sky point, as shown in Figure A-3. This is summarized mathematically be using the law of cosines written for ZP and PS:

$$\cos(PS) = \cos(ZP)\cos(ZS) + \sin(ZP)\sin(ZS)\cos(C).$$

Because the solar position is constrained to lie on the circle around P, possible azimuth values vary from 0° (when the sun is in the same vertical as the skypoint) to a maximum when ZP = ZS (scattering angle = 90°).

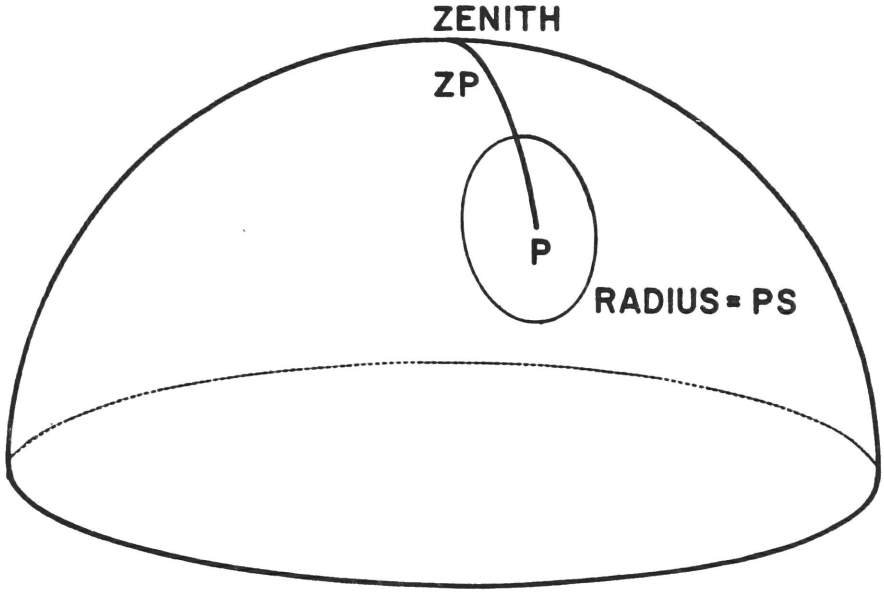


Figure A-3. Skypoint Zenith distance and scattering angle known.

Obviously, as described by the equation above, as the scattering angle diminishes, the range of possible solar azimuths does likewise.

Case iii: Skypoint zenith distance, E-vector orientation, and scattering angle known. Knowledge of these components corresponds to two sides and an included angle of a spherical triangle. This ordinarily would allow for a unique solution of the remaining parts. In this case, however, there is a 90° ambiguity of the included angle: $A = 90^{\circ} \pm X$. Thus, except for $X = 0^{\circ}$ or 90° (vertical or horizontal E-vector orientation), there are two possible solutions for solar position. These two points correspond to the intersection of the curves of Figure A-2 and Figure A-3

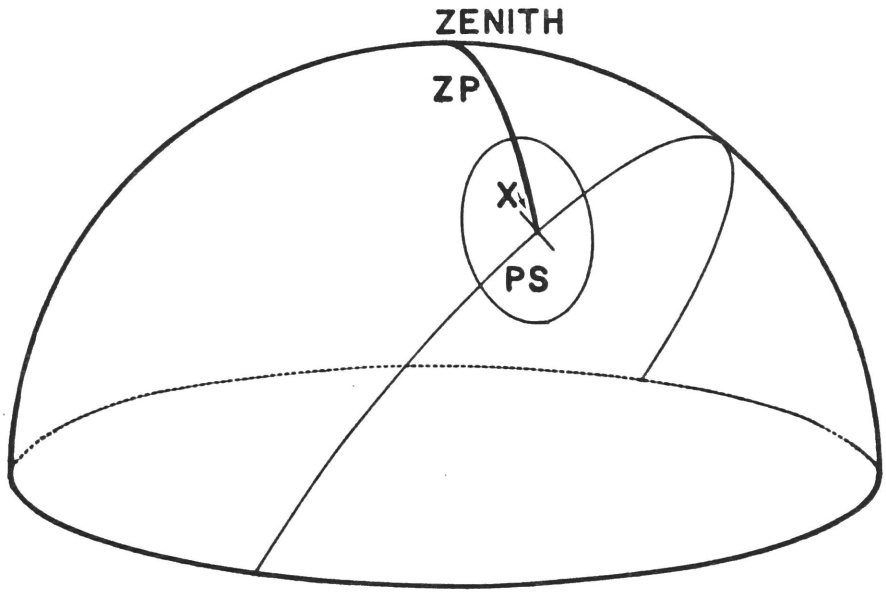


Figure A-4. Skypoint zenith distance, E-vector orientation, and scattering angle known.

as shown in Figure A-4. Notice that these two solution have, in general, different zenith distances. The facts can be mathematically summarized by the law of cosines written for the solar zenith distance:

$$\cos(A)\sin(PS)\sin(ZP) + \cos(PS)\cos(ZP) = \cos(ZS).$$

Since $A = 90^{\circ} \pm X$,

$$\pm\sin(X)\sin(PS)\sin(ZP) + \cos(PS)\cos(ZP) = \cos(ZS)$$

and in general, the two possible solutions are found by substituting the values of ZS into the law of sines:

$$\sin(C) = \frac{\sin(A)\sin(PS)}{\sin(ZS)}$$

Obviously, without additional information, a unique solution cannot be

obtained.

Unlike the previous two situations, there are only two possible azimuth values, rather than a range. Without additional information, an animal should not be able to differentiate between these two possibilities. The orientation behavior, therefore, is expected to reflect this situation: e.g., the animal should move bidirectionally, or an average between the two directions, and so on.

Summarizing the three cases just considered, analysis based on the polarization characteristics of the skypoint alone does not allow an unambiguous determination of solar position.

II. Solar position and skypoint information known.

Considering only the vertex of the scattering triangle formed by the sun, it is obvious that the only variable which can be directly measured is the solar zenith distance. Considered here are only those non-trivial cases where the sun itself is not visible, so a knowledge of the sun's zenith distance implies either that it is "remembered" or can be "calculated".

Case iv: Zenith distances of the sun and skypoint known

Figure A-5 illustrates that the sun's zenith distance only specifies a small circle parallel to the horizon plane (an "almucantar") and therefore the relative azimuth can be any value. It can be concluded that animals using such an orientation system would be disoriented.

Case v: E-vector and zenith distance of sun and skypoint known. As illustrated by Figure A-6, these three variables specify two sides and an

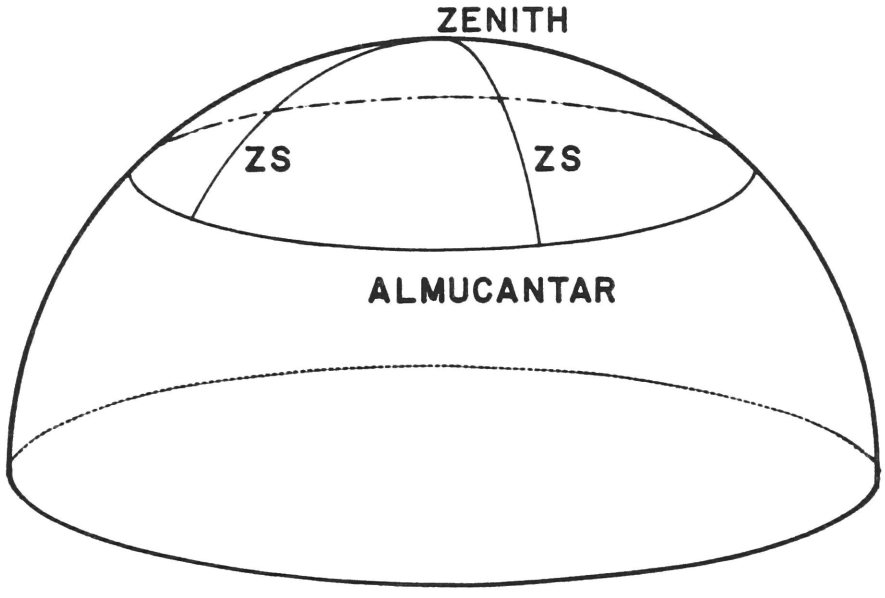


Figure A-5. Zenith distances of sun and skypoint known.

opposite angle of the scattering triangle. Geometrical solutions generally result in <u>two</u> solutions in this case, since it is not known whether the included angle or its compliment is included in the spherical triangle. A method of solution is described in detail in Chapter II and consists of two steps: 1) using the law of sines written for angle B,

$$\sin(B) = \frac{\sin(ZP)\sin(A)}{\sin(ZS).}$$

2) The Naperian analogy written for the azimuth gives:

$$\cot(\tfrac{c}{2}) = \frac{\tan((A-B)/2)\sin((ZS+ZP)/2)}{\sin((ZS-ZP)/2)}$$

One behavioral implication is that unless one of the two possible solutions can be eliminated, the orientation behavior expected should be

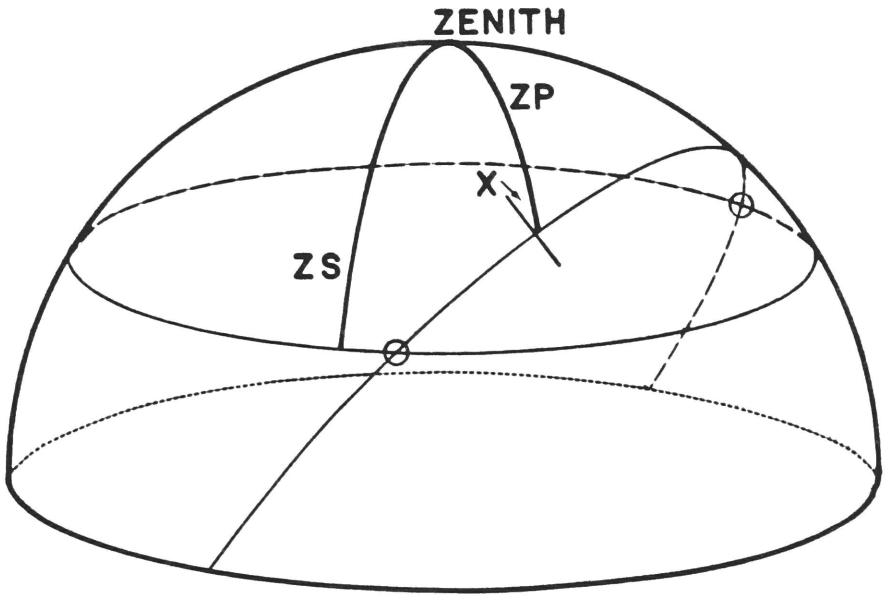


Figure A-6. Zenith distance of sun and skypoint and E-vector orientation known.

appropriate considering the equally possible azimuth directions.

Case vi: Scattering angle and zenith distances of sun and skypoint known.

These variables constitute three known sides of the scattering triangle, so all included angles can be determined unambiguously. By the law of cosines written for the scattering angle

$$\cos(PS) = \cos(C)\sin(ZS)\sin(ZP) + \cos(ZS)\cos(ZP)$$

and

$$\cos(C) = \frac{\cos(PS) - \cos(ZS)\cos(ZP)}{\sin(ZS)\sin(ZP)}.$$

Similar equations provide the solutions for the other angles. Of course

in this case, it is expected that animals possess the necessary information to perform unimodal orientation in predictable directions. Special cases can be conceived for some interesting circumstances. For example, if bees interpreted (because of the high degree of polarization) the artificial stimuli of the experiments reported in Chapter V as a part of the band of maximum polarization, they might determine the scattering angle to be 90° and cos(PS) = 0. Then the pertinent equations reduce to the simple form:

$$\cos(C) = -\cot(ZS)\cot(ZP)$$

which lead to much different behavioral predictions. What type of orientation behavior is actually observed would provide the data to evaluate whether this interpretation was performed by the bees.

Case vii: Zenith distances of sun and skypoint, E-vector orientation, and scattering angle known.

Analysis performed with four known parts of a spherical triangle is conveniently accomplished by use of the transposed cosine rule:

$$\sin(ZS)\cos(C) = \cos(ZS)\sin(ZP) - \sin(ZS)\cos(ZP)\cos(A)$$

and

$$\cos(C)=\frac{\cos(ZS)\sin(ZP)-\sin(ZS)\cos(ZP)\cos(A)}{\sin(ZS)}.$$

From these relationships unique solutions can be obtained. Like the previous case considered, an interesting case occurs when the light is completely polarized and the scattering angle is interpreted to be 90°. Then the equation reduces to:

$$\cos(C) = \frac{-\cos(ZP)\cos(A)}{\sin(ZS)}.$$

For any triangle, the angle opposite a smaller side must be smaller than an angle opposite a larger one. In this case, ZS is generally less than

PS (since PS = 90°, which is the maximum possible zenith distance). Thus, the relative azimuth must be greater than the skypoint angle A. Since A = $90^{\circ} \pm X$, this means that C must be greater than X.

Summarizing, only when variables pertaining to solar position are known can the scattering triangle be analytically solved for a unique azimuth value. Further, in each case where such a unique solution is geometrically possible, the scattering angle must be known. In all other cases, the solutions are ambiguous, and it is expected that the orientation behavior should mirror this situation.

Appendix B.

Responses of bees to the earth's magnetic field.

When an observation hive was placed horizontally, the initial control observations in a diffusely lighted room clearly showed that the waggle dances were generally randomly oriented.

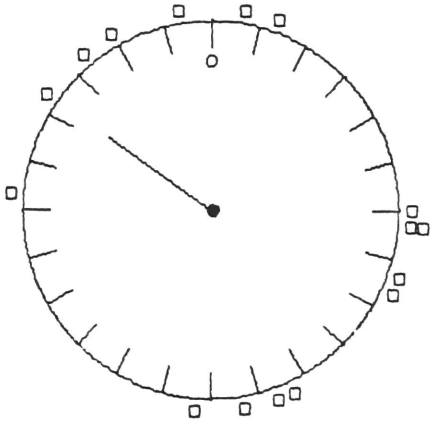


Figure B-1. Single bee dancing in diffusely lighted room under an unpolarized light source with a Corning Glass Works #3390 filter inserted into the beam (absorbs all wavelengths from 0.2 to 5.0 micrometers. The long vector is the expected direction for the source interpreted as the sun.

When a "black glass" Corning Glass Works #3390 filter, which is nearly opaque to all wavelengths from 0.2 to 5.0 micrometers, was inserted into the beam of a high intensity quartz-halogen lamp, the waggle dance appeared to be somewhat bimodally oriented (Figure B-1). Under these conditions in a diffusely illuminated room, the bees exhibited obvious difficulty in orienting themselves--they turned round and round before performing a waggle run.

Initially, controls of this type generally elicited only disoriented dances resembling those described by von Frisch (1967; p. 134; Fig. 116). However, confused bees were observed only for a short time after placing

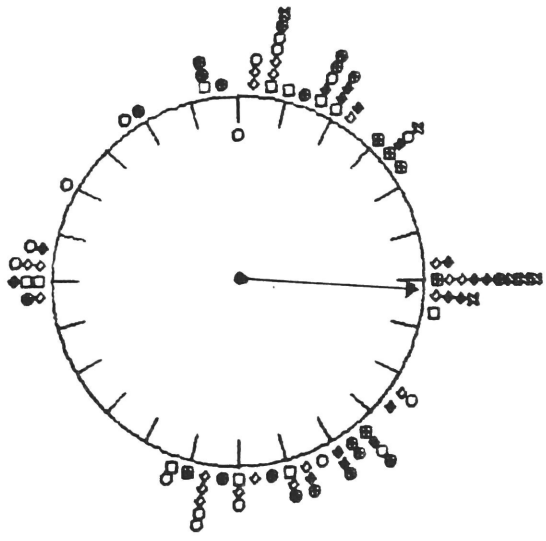


Figure B-2. Each different symbol represents a separate bee dancing in a diffusely lighted room. The vector corresponds to magnetic North, as measured at the surface of the comb.

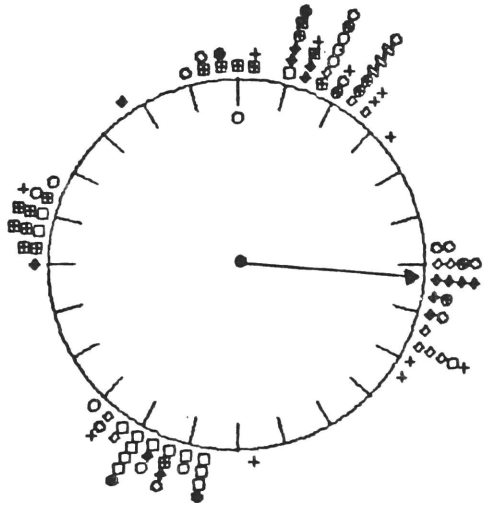


Figure B-3. Separate bees dancing in the dark (underneath a dim, deep-red light suspended in the zenith). The vector corresponds to magnetic North, as measured at the surface of the comb.

the hive horizontally, and were not seen in controls performed a month

later. Then, the waggle dances were no longer completely disoriented but pointed in four directions about 90° apart, as shown by Figure B-2. This quadrimodal orientation was even more dramatic when the bees were in the dark. For example, Figure B-3 summarizes the waggle orientations of dancers under a 25 watt deep-red lamp (directly above the dance floor) in a horizontal hive covered by a black cloth so that no stray light could be seen by the bees. Even if the bees could perceive this red light, (due to some shorter wavelengths leaking through the filter), it could have provided no orientation cues since it was located in the zenith. However, it did provide enough illumination to videorecord the dances observed through a very small hole cut in the cloth. Unlike the earlier controls, bees which showed this quadrimodal orientation demonstrated no hesitation in selecting a dance direction.

The four principle directions in the dance orientation correspond well to the cardinal points of the earth's magnetic field, as seen when compared to the direction of magnetic North (indicated in the diagram by the labeled vector) which was recorded at the surface of the comb. It is particular interesting to note that although large numbers of bees made the quadrimodal distribution seem relatively evenly distributed, individual bees tended to "favor" particular directions.

Sensitivity of bees to the earth's magnetic field was first reported by Lindauer and Martin (1972; p. 565), who found that the influence of the earth's magnetic field on horizontal dances were not observed until about 3 weeks after the hive had been placed horizontally. My observations of quadrimodal orientation may confirm that weak magnetic fields (on the order of the earth's strength) are detected by Apis mellifera

ligustica (Italians). Although such bees are "oriented", elsewhere in this thesis the term "disoriented" has been applied to such quadrimodal dances, since the dance orientation does not depend upon light as a directional cue.

Several interesting pilot investigations were attempted, but they produced only negative results. First, a pair of Helmholtz coils was constructed which enabled the direction and magnitude of the magnetic vector to be easily changed, and yet remain on the order of the earth's field strength. The form of the field was easily monitored by several sensitive dip needles, which measured the field line directions in three dimensions. Because of the close proximity of massive steel girders to the hive, however, the gradient of the field at the surface of the comb was very large, and the field could not be nulled over large areas. No effects of this disturbance of the local magnetic field were obvious in the quadrimodal dances. Similarly, a series of changes of the local field for bees dancing under a red light produced no significant changes in the quadrimodal dance orientation compared to controls. Second, a 60 Hz degaussing coil (tape recorder head demagnetizer) was held very close to a dancing bee, and produced no obvious changes in the quadrimodal dance orientation.

Although these experiments need to be refined and repeated in detail, their negative results may mean that bees do not use permanent magnet detectors for their quadrimodal orientation in the earth's magnetic field and that the response characteristics of their detectors may be very slow.

APPENDIX C

Additional measurements of skylight parameters.

This appendix provides additional examples of measurements of skylight parameters, particularly under marginal atmospheric conditions and high reflectance from the underlying surface (snow covered ground). For these data, the half-hemisphere of the sky measured by the polarimeter is collapsed into a plane with concentric circles of radii equal to the zenith distances of the corresponding sky points, as illustrated by Figure C-1. Here, the measured half-hemisphere is shown in the upper half of Figure C-1, where lines of equal elevation are labelled. This half-hemisphere is compressed into a plane, giving the lower half of the figure. In this form, the solar vertical is on the left and azimuth increases from 0° to 180° clockwise. Although data were taken at 5° intervals, in order to clarify this representation, they are displayed only every 10° of azimuth and elevation.

The plots of relative intensity and degree of polarization show the actual numerical value recorded at each 10° location on the skyvault. For relative intensity, the maximum possible value was 102, which corresponded to saturation of the photocell amplifier. In the E-vector orientation plots, the angle between the small line segment and the radius drawn through it (i.e., from the zenith point) is equal to the E vector orientation seen in the sky. This representation illustrates the striking symmetrical form of the sky patterns with respect to the position of the sun. For example, in the top half of Figure C-2, point M corresponds to an observer looking at a skypoint 10° in elevation, 30° to the left of the sun. The E-vector seen there would be about -45°. The theoretical E-vector distributions (assuming Rayleigh scattering) were calculated by spherical trigonometry (see Chapter II) and displayed in

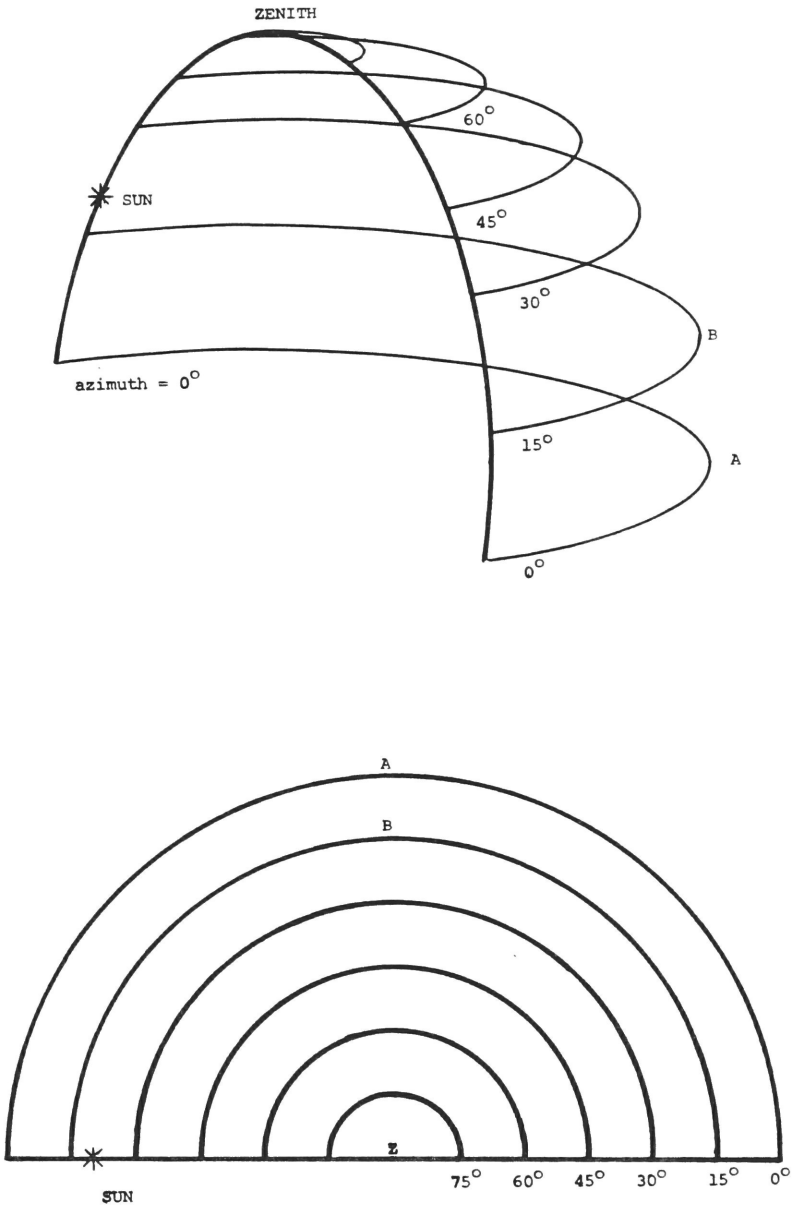


Figure C-1. Half of the skyvault is collapsed into a plane. Solar position is always on the left, indicated by a *. In these diagrams, azimuth refers to the left of the sun. Points A and B are mapped into the plane for illustration.

the same manner as actual measurements. Thus, by superimposing theoretical and measured values, one can see at a glance how well these values

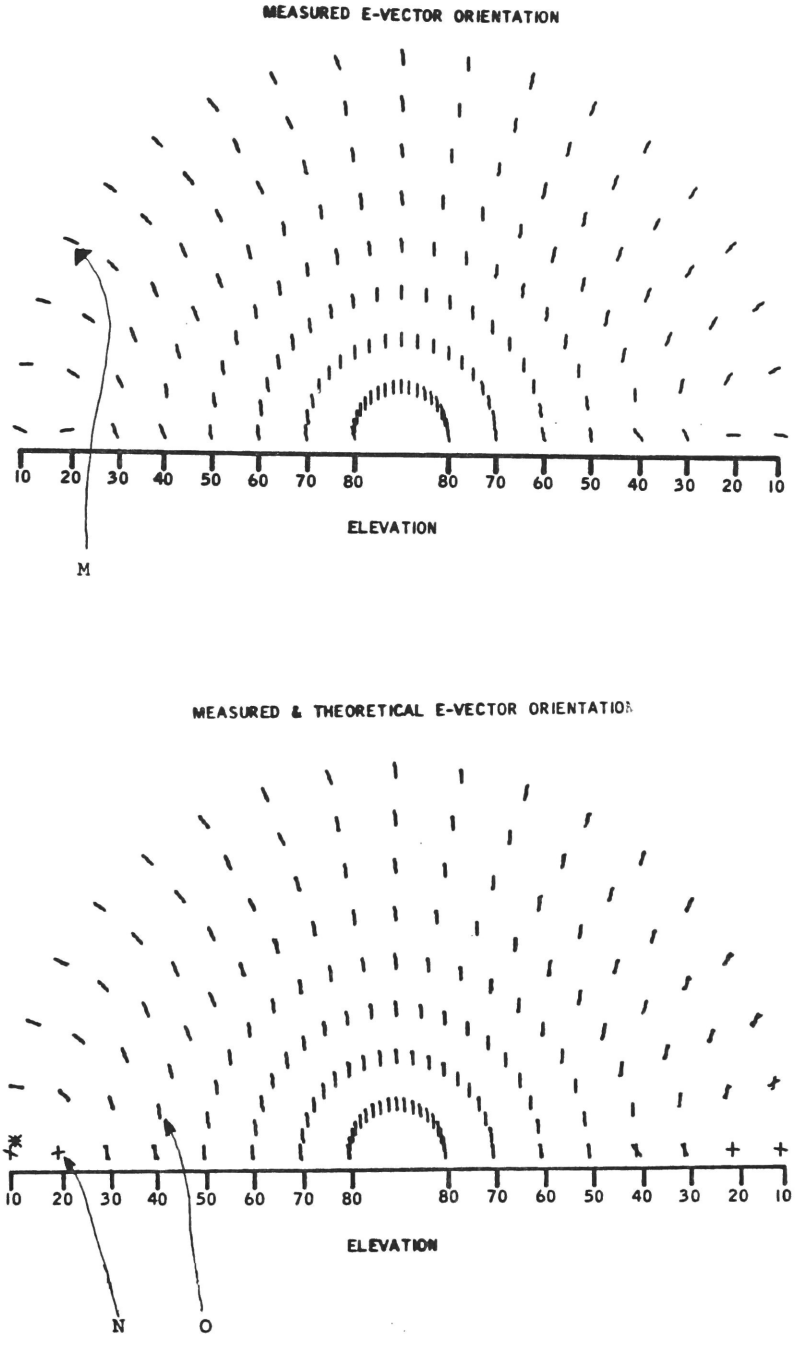


Figure C-2. Example of measured and theoretical E-vector skyplots.

compare as a function of position on the skyvault. When theoretical and measured values are equal, only a single line segment can be seen at each

point on the diagram. When two segments are observed, the angle between them is equal to the deviation. For example, in the lower half of Figure C-2, Point N (elevation 20°, azimuth 0°) has about an 80° divergence between the measured and theoretical E-vector orientations, while Point O (elevation 40°, azimuth 10°) has none and the measured E-vector orientation equal the theoretical. Figures C-3 through C-18 summarize the relative intensity, degree of polarization, and E-vector orientation for a variety of conditions, as explained in each figure legend. Table C-1 lists the conditions for data presented in these figures.

TABLE C-1

List of Sky Plots

Date	Time (EST)	Fig.	Wavelength (nm.)	Sky Conditions
18 Nov. 1977	1555	C-3	650	quite clear
18 Nov. 1977	1620	C-4	500	clear
1 Dec. 1977	1445	C-5	350	completely overcast; very dark; slight mist
1 Dec. 1977	1535	C-5	500	completely overcast; very dark; slight mist
1 Dec. 1977	1510	C-5	650	completely overcast; very dark; slight mist
3 Dec. 1977	1340	C-6	350	sun or blue sky not visible; uneven, complete overcast
3 Dec. 1977	1420	C-7	500	sun or blue sky not visible; uneven, complete overcast; light rain falling
3 Dec. 1977	1440	C-8	650	sun or blue sky not visible; uneven, complete overcast; light rain falling
3 Dec. 1977	1540	C-9	350	heavy, uneven clouds; slight clearing at horizon
15 Jan. 1978	1415	C-10	350	sky filled with patchy strato-cumuli
15 Jan. 1978	1500	C-11	650	clear at small ZD; patchy cumulus near horizon
15 Jan. 1978	1620	C-12	350	virtually clear; light currus near horizon
28 Jan. 1978	1335	C-13	350	no blue sky; snow falling making solar disc just visible; radiance seemed quite uniform
28 Jan. 1978	1400	C-14	650	no blue sky; snow falling making solar disc just visible; radiance seemed quite uniform
28 Jan. 1978	1420	C-15	500	no blue sky; snow falling making solar disc just visible; radiance seemed quite uniform

TABLE C-1 (continued)

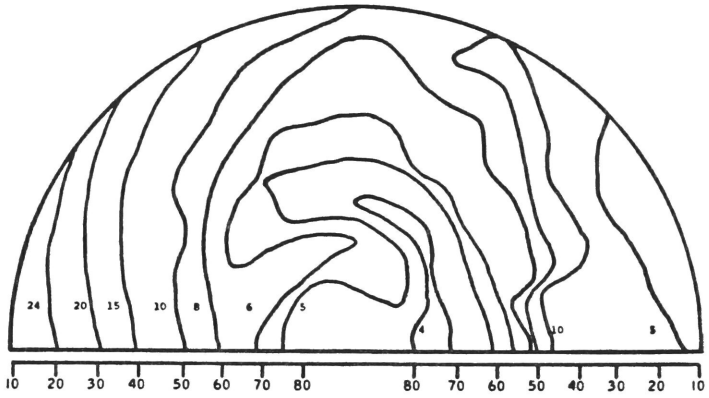
List of Sky Plots

Date	Time (EST)	Fig.	Wavelength (nm.)	Sky Conditions
28 Jan. 1978	1440	C-16	350	no blue sky; snow falling making solar disc just visible; radiance seemed quite uniform
28 Jan. 1978	1455	C-17	650	no blue sky; snow falling making solar disc just visible; radiance seemed quite uniform

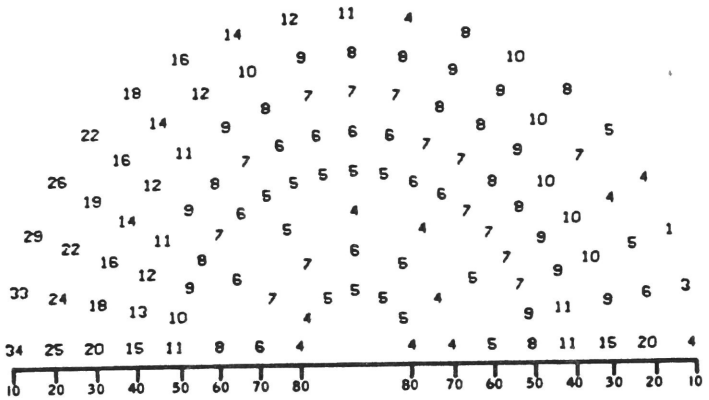
Figure C-3

500 nm.
18 November 1977
1620 EST
solar ZD = 85°
solar AZ = 239°
clear

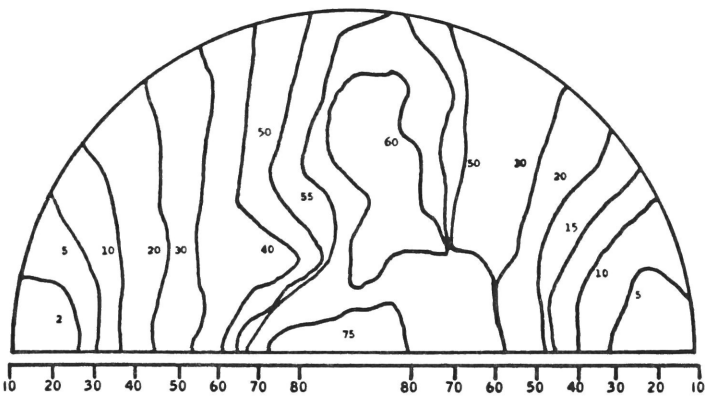
EQUAL INTENSITY



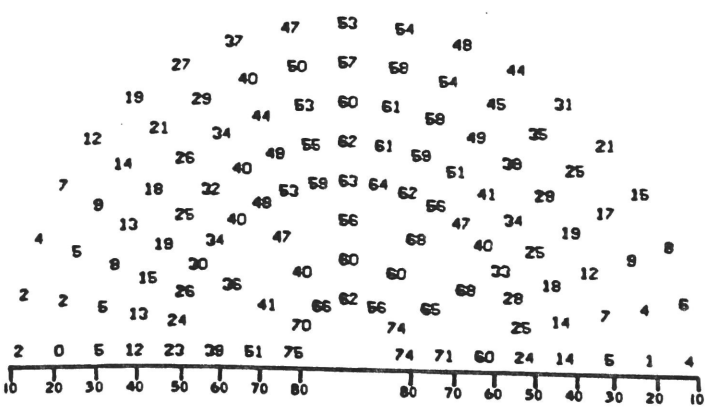
RELATIVE INTENSITY



EQUAL DEGREE OF POLARIZATION



DEGREE OF POLARIZATION



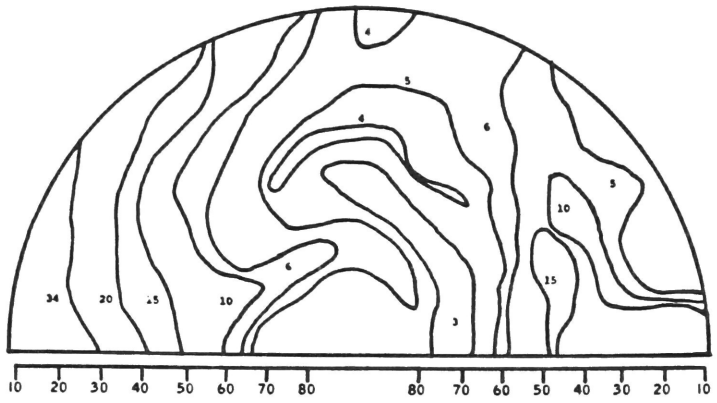
ELEVATION

Figure C-4

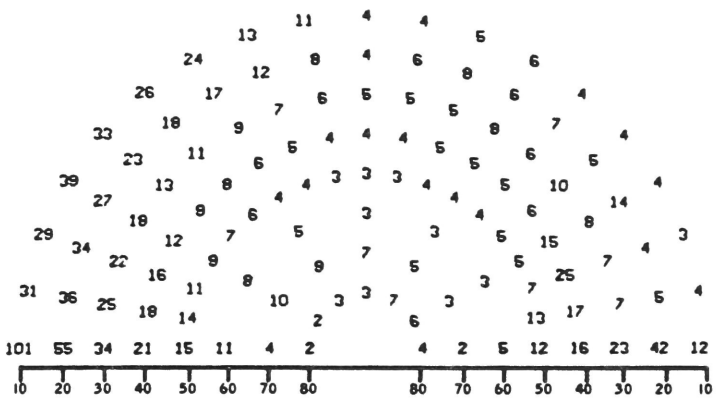
650 nm.
18 November 1977
1555 EST
solar ZD = 81°
solar AZ = 233°

quite clear

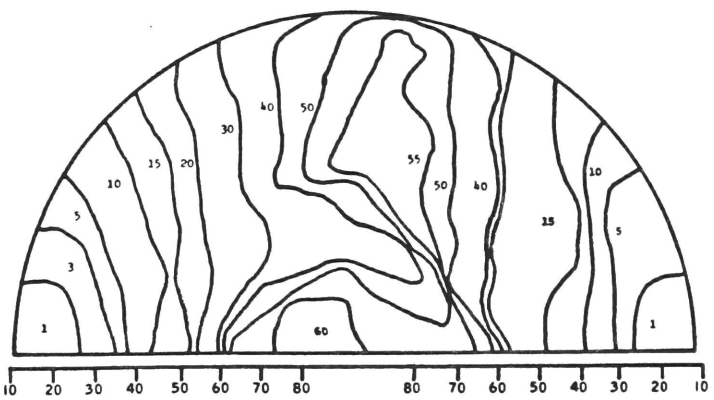
EQUAL INTENSITY



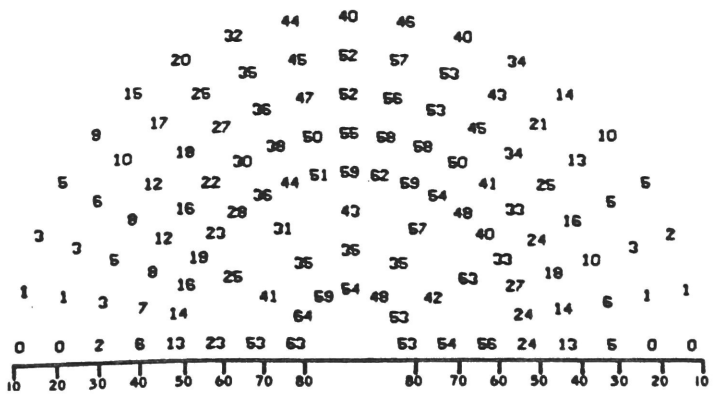
RELATIVE INTENSITY



EQUAL DEGREE OF POLARIZATION

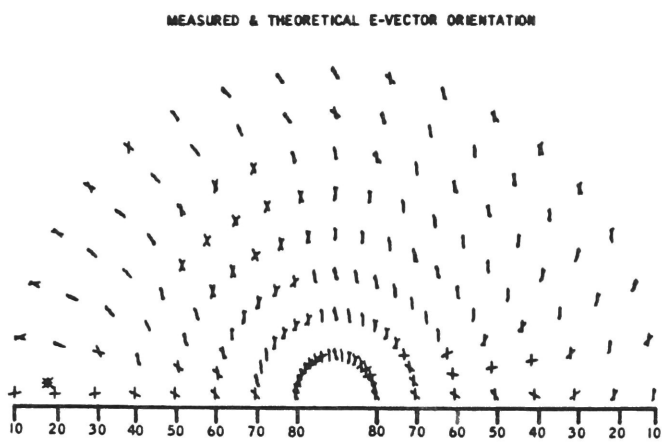


DEGREE OF POLARIZATION



ELEVATION

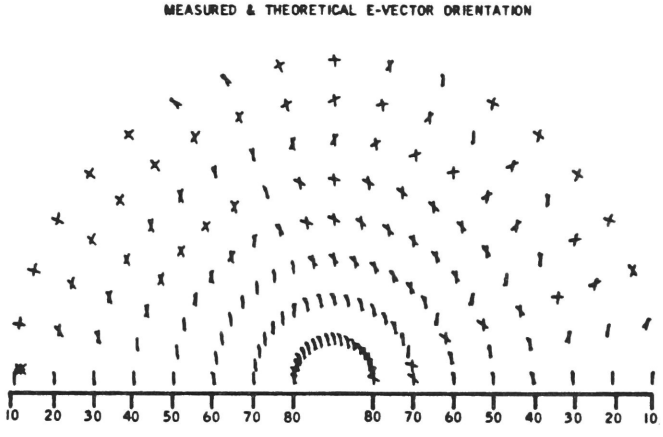
Figure C-5



350 nm.
1 December 1977
1445 EST

solar ZD = 73°
solar AZ = 220°

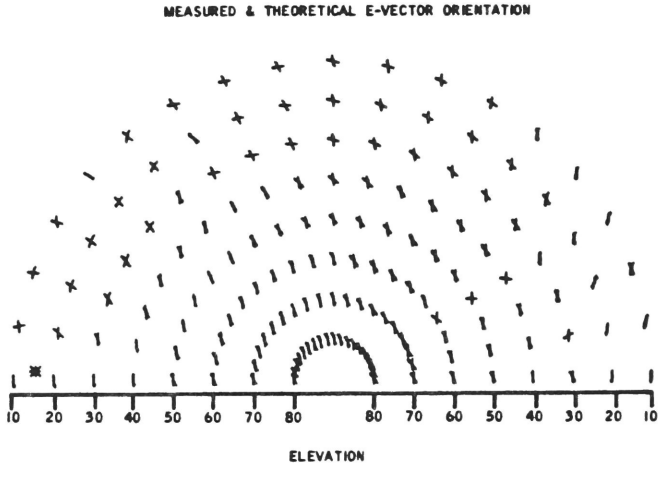
completely overcast; very dark; slight mist



500 nm.
1 December 1977
1535 EST

solar ZD = 80°
solar AZ = 230°

completely overcast; very dark; slight mist



650 nm.
1 December 1977
1510 EST

solar ZD = 76°
solar AZ = 225°

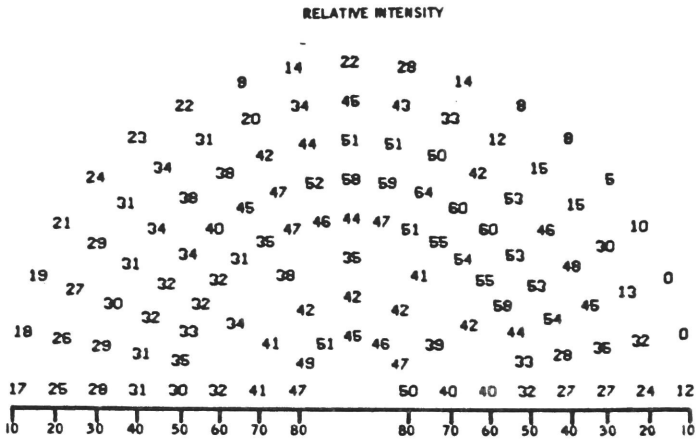
completely overcast; very dark; slight mist

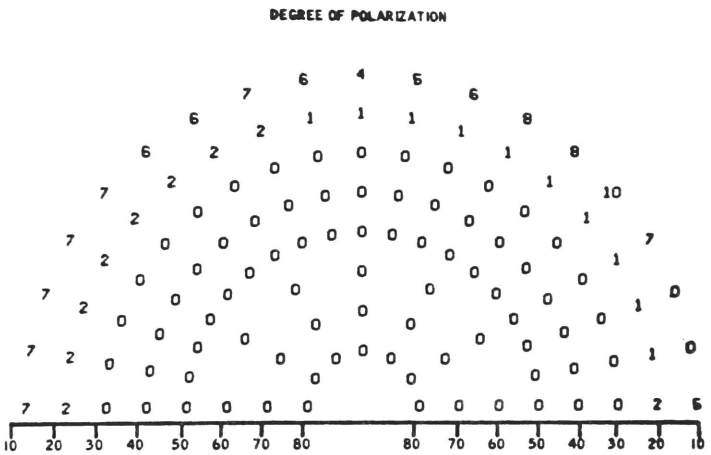
Figure C-6

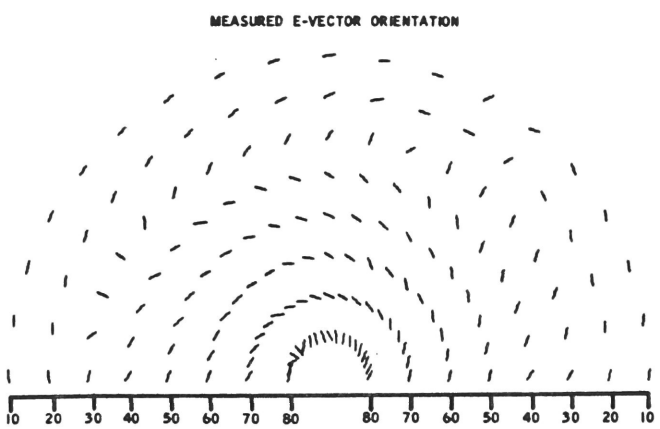
350 nm.
3 December 1977
1340 EST

solar ZD = 67°
solar AZ = 205°

sun or blue sky not visible; uneven, complete overcast







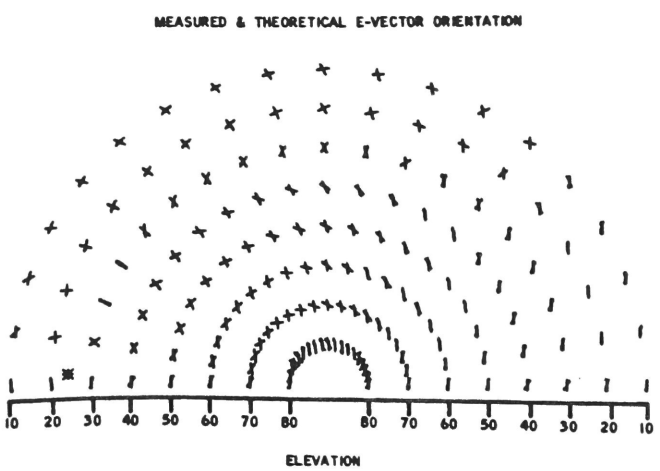
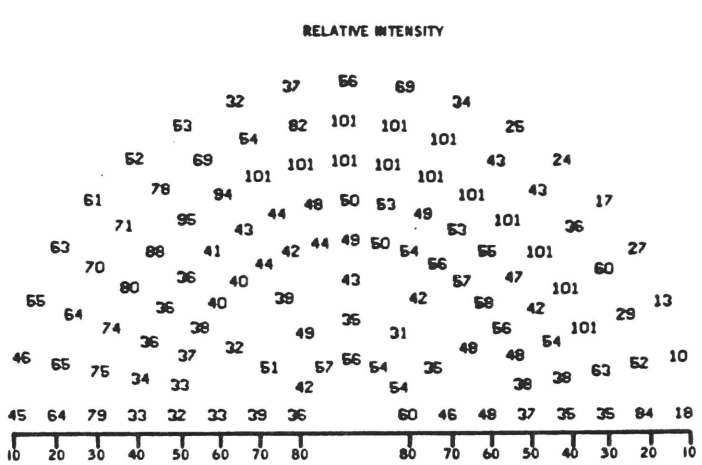


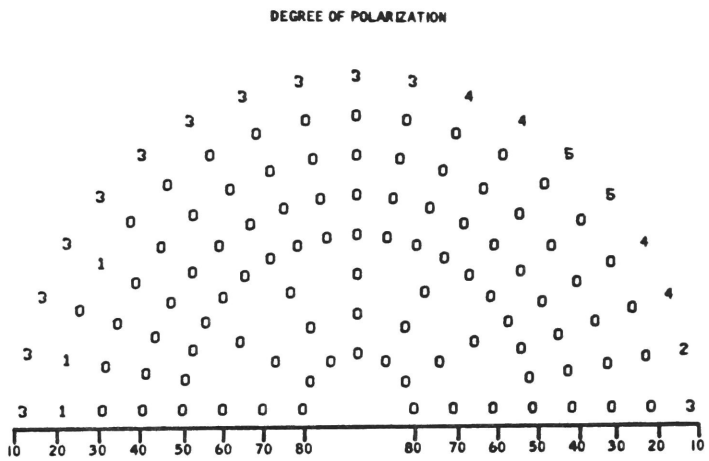
Figure C-7

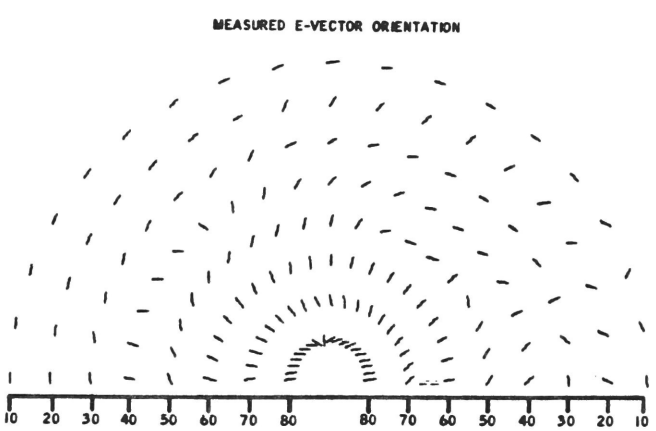
500 nm.
3 December 1977
1420 EST

solar ZD = 70°
solar AZ = 214°

sun or blue sky not visible; uneven, complete overcast; light rain falling







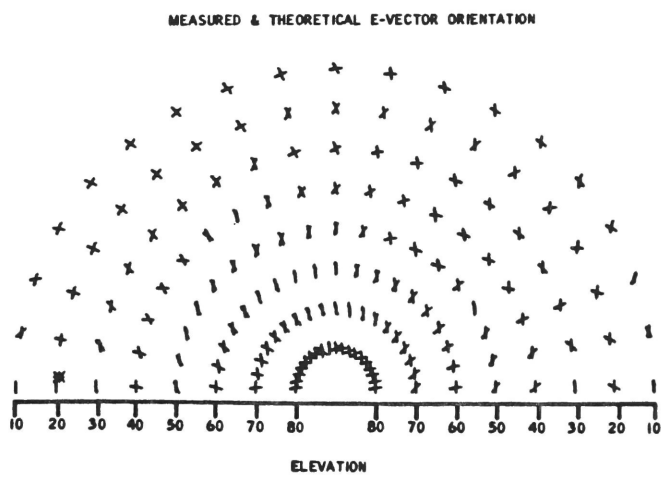
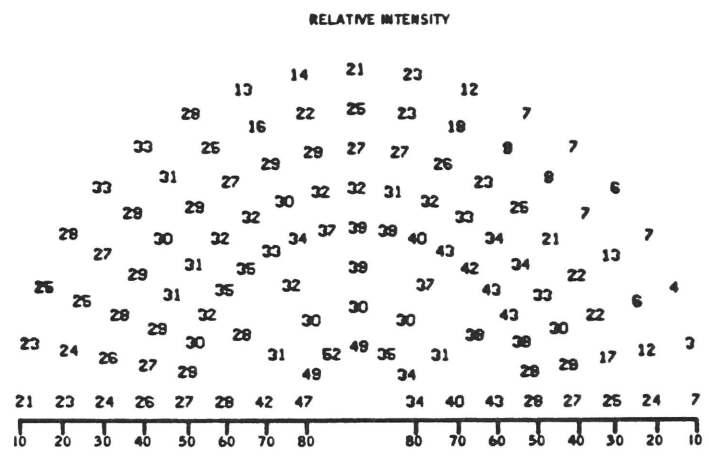


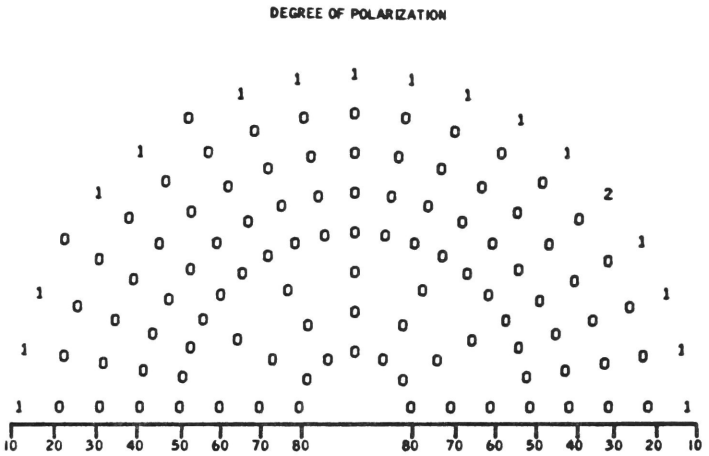
Figure C-8

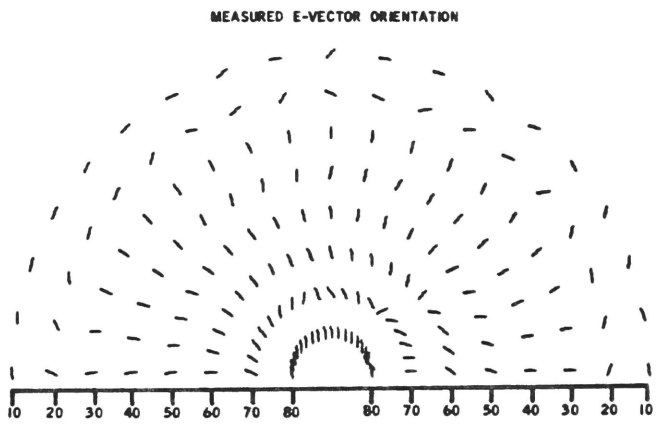
650 nm.
3 December 1977
1440 EST

solar ZD = 73°
solar AZ = 219°

sun or blue sky not visible; uneven, complete overcast; light rain falling







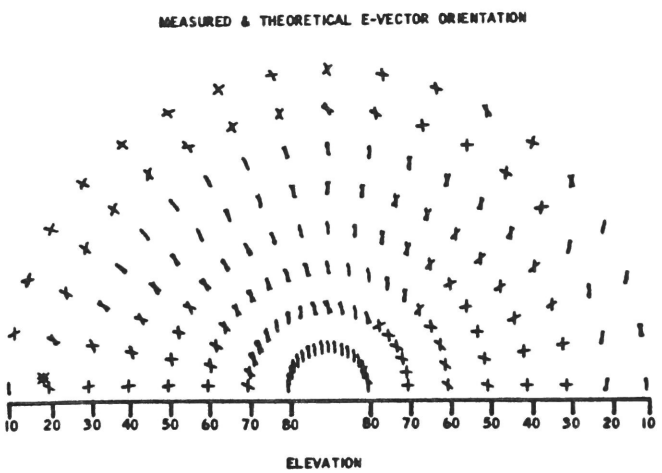
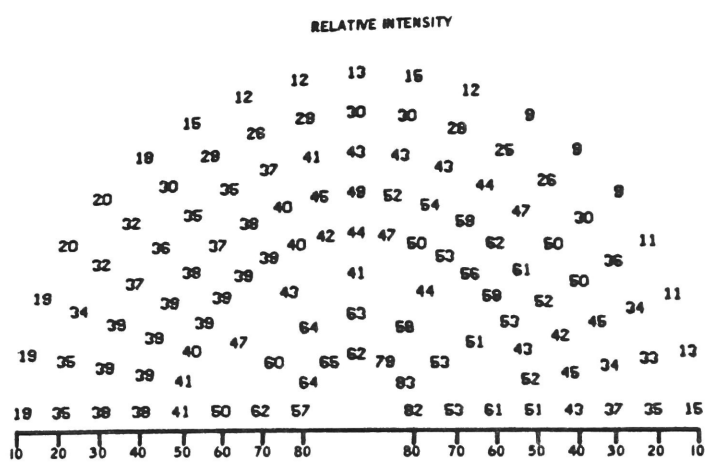


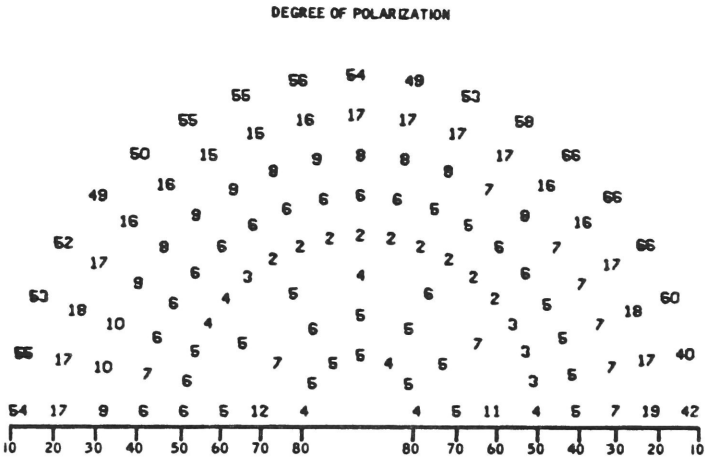
Figure C-9

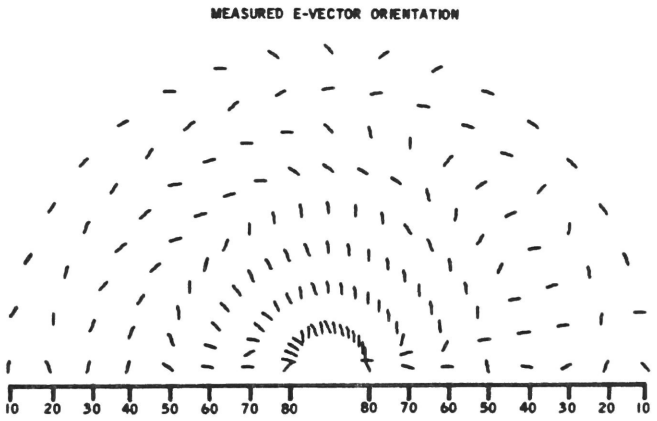


350 nm.
3 December 1977
1540 EST

solar ZD = 81°
solar AZ = 230°

heavy, uneven clouds; slight clearing at horizon





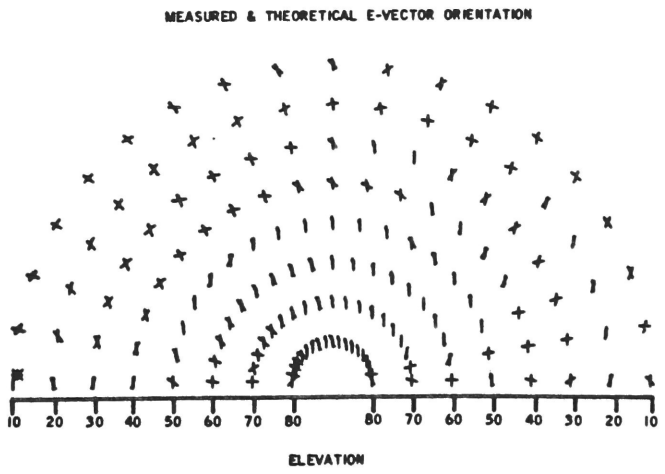
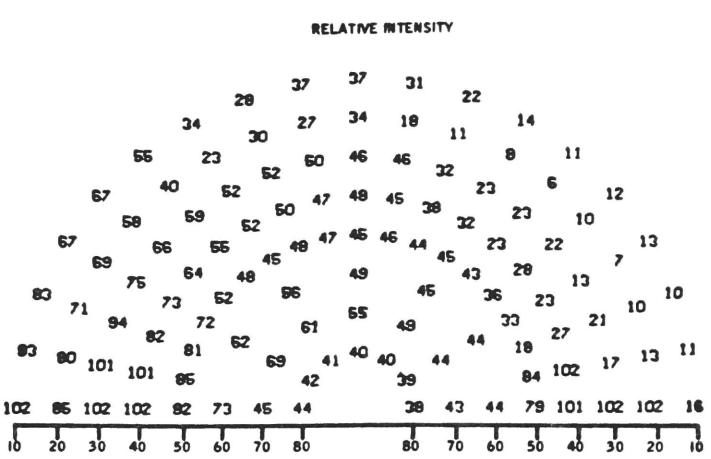


Figure C-10

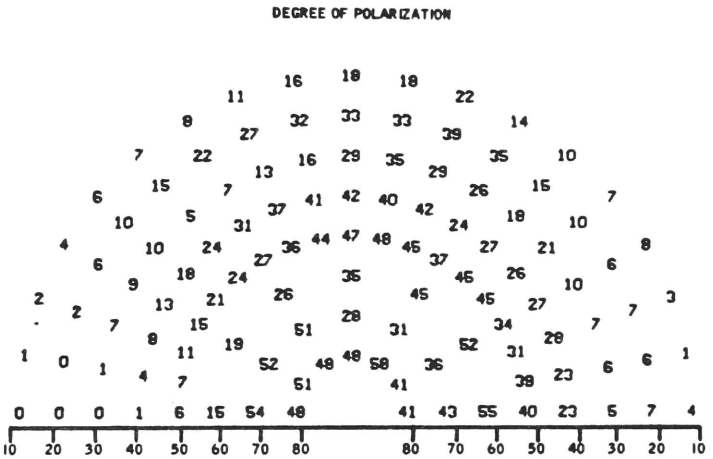


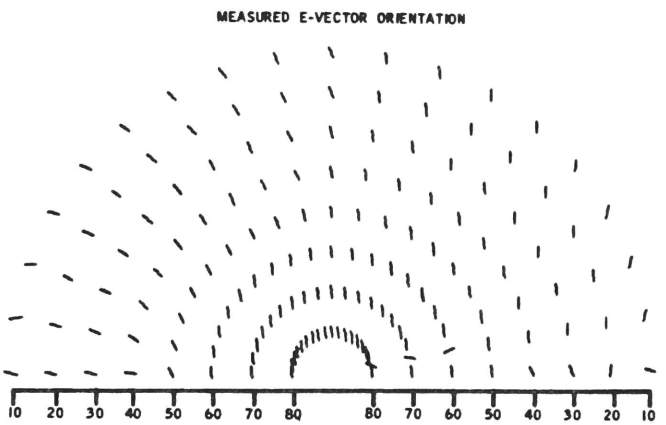
350 nm.
15 January 1978
1415 EST

solar ZD = 69°
solar AZ = 214°

sky filled with patchy strato-cumuli

heavy ice over light snow





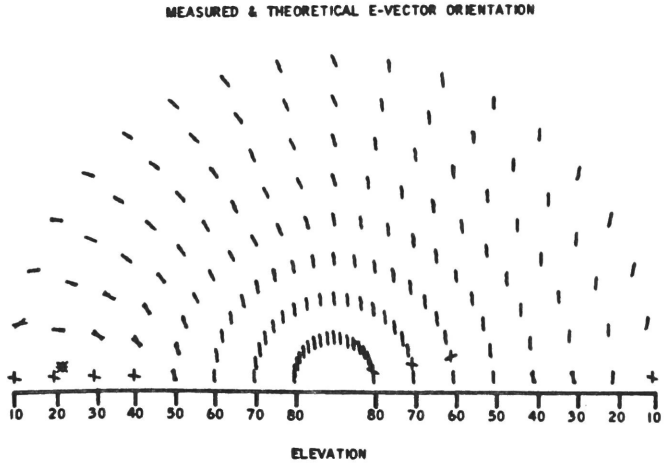


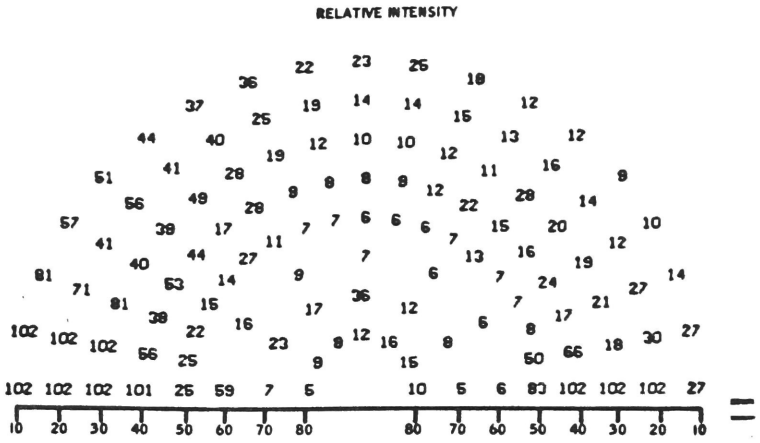
Figure C-11

650 nm.
15 January 1978
1500 EST

solar ZD = 74°
solar AZ = 223°

clear at small ZD; patchy cumulus near horizon

heavy ice over light snow



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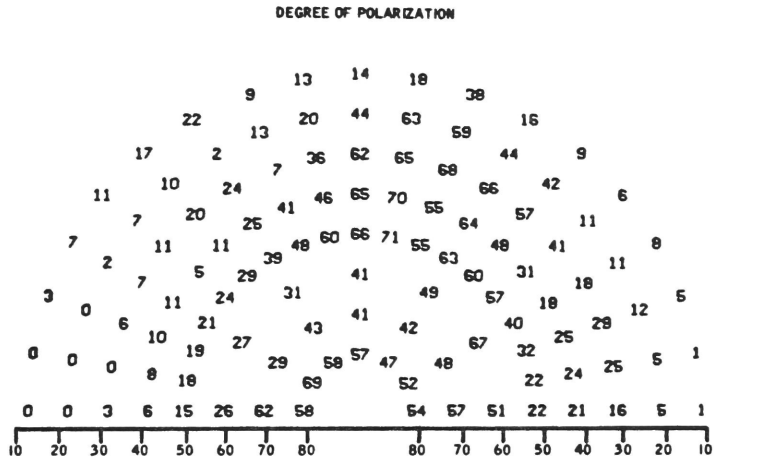
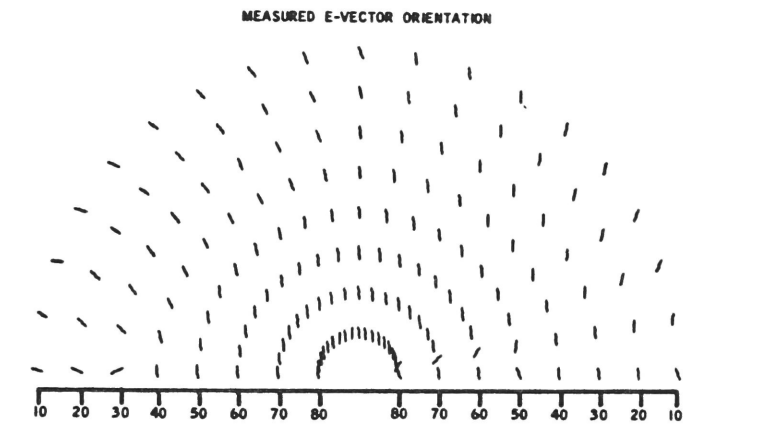
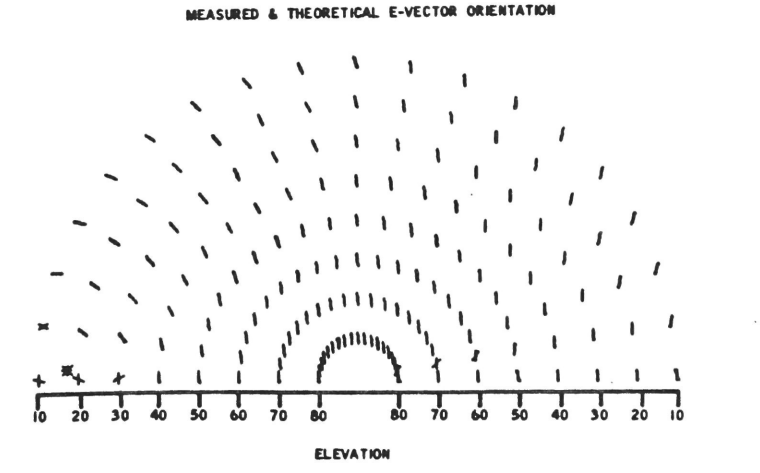
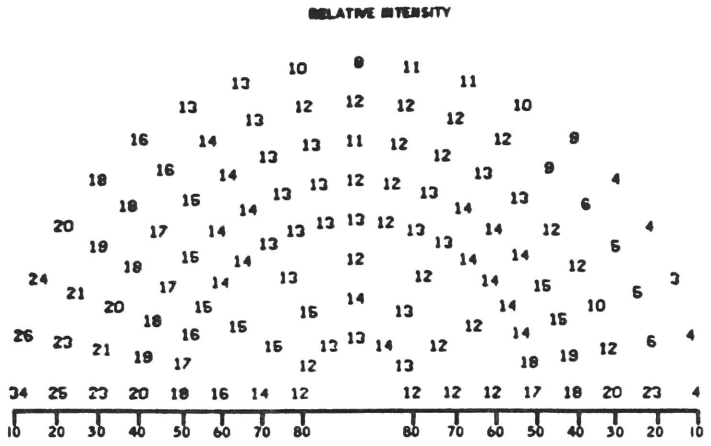
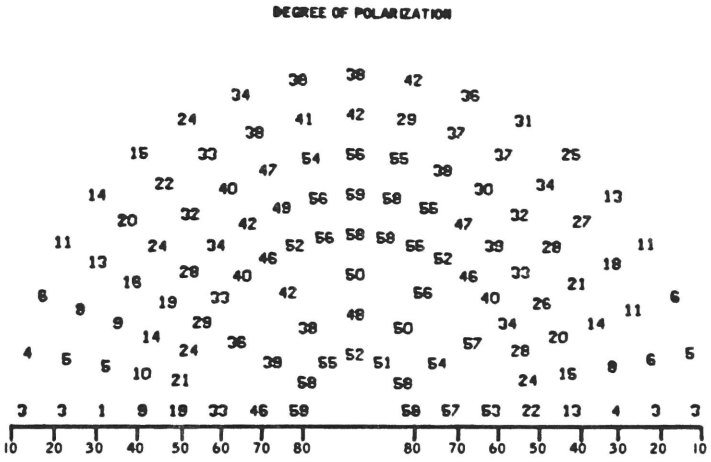
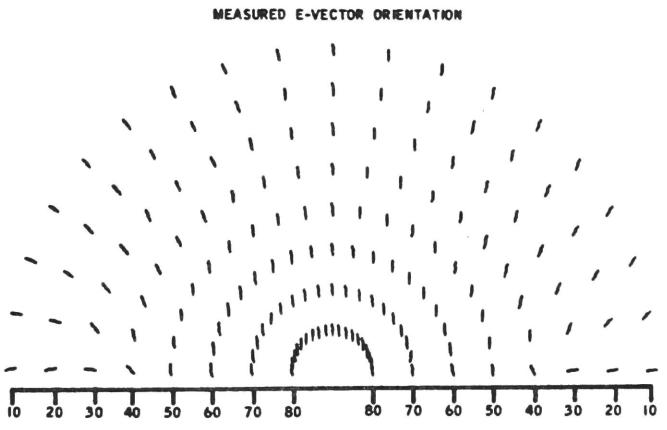












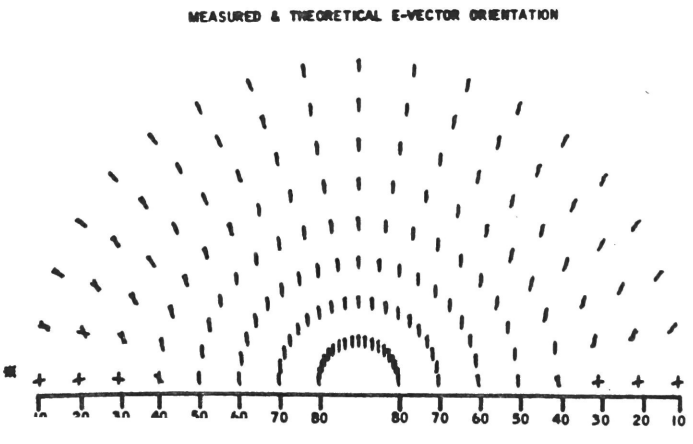


Figure C-12

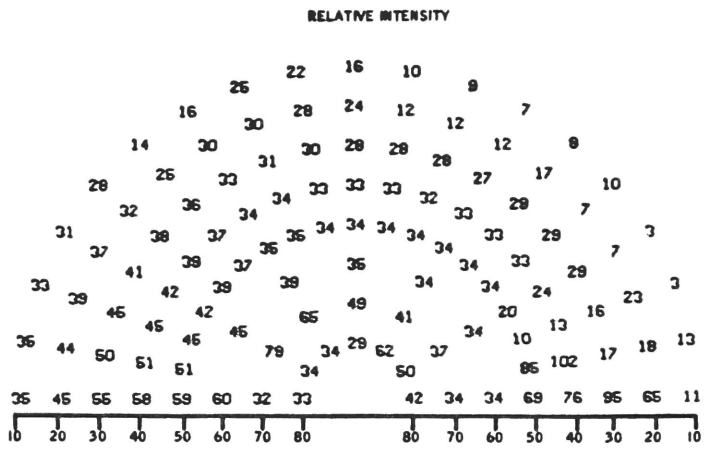
350 nm.
15 January 1978
1620 EST

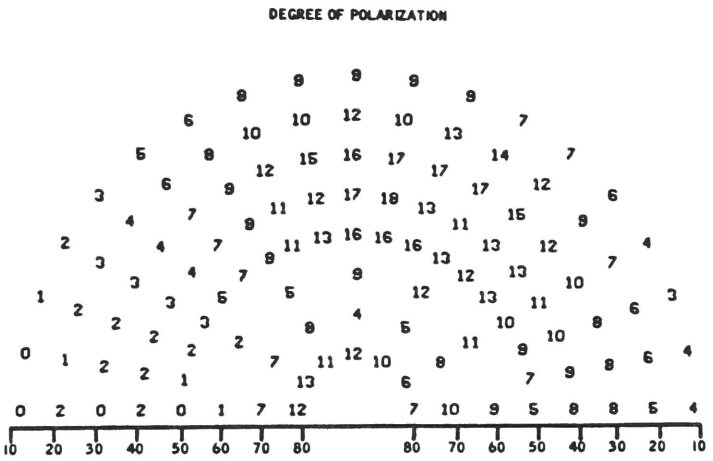
solar ZD = 86°
solar AZ = 239°

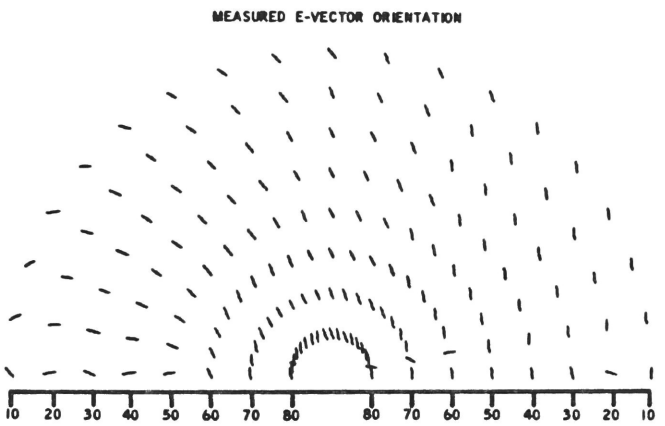
virtually clear;
light cirrus near
horizon

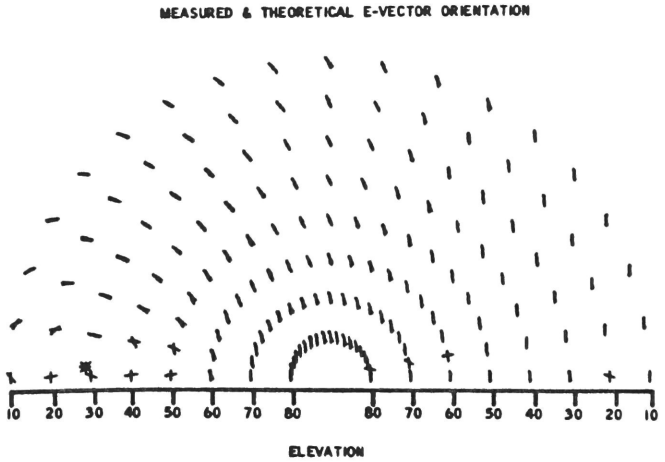
heavy ice over
light snow

Figure C-13









350 nm.
28 January 1978
1335 EST

solar ZD = 62°
solar AZ = 203

no blue sky; snow falling making solar disc just visible; radiance seemed quite uniform

light, dirty snow with many icy spots

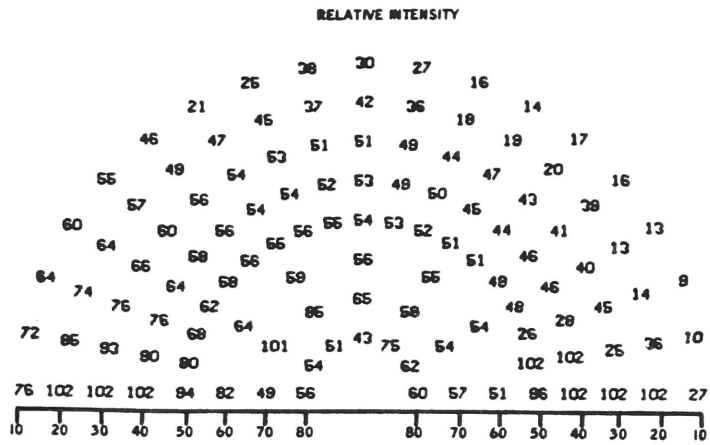
Figure C-14

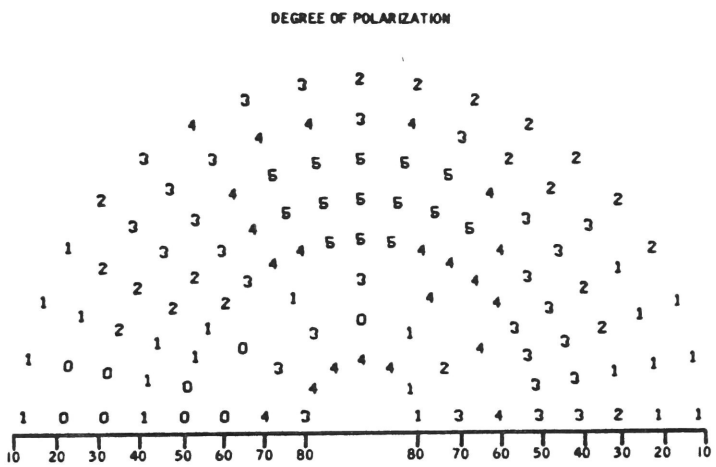
650 nm.
28 January 1978
1400 EST

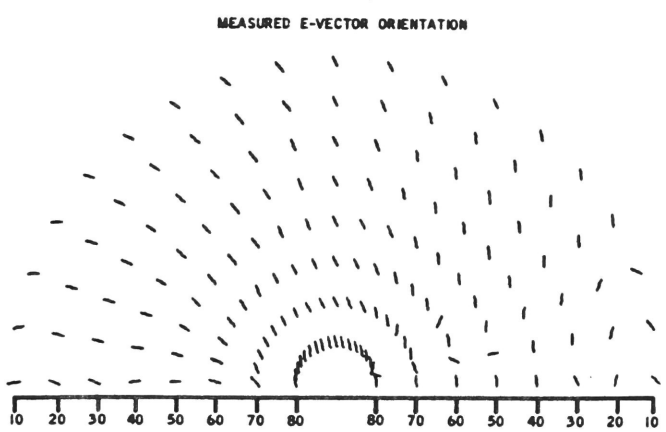
solar ZD = 65°
solar AZ = 212°

no blue sky; snow falling making solar disc just visible; radiance seemed quite uniform

light, dirty snow with many icy spots







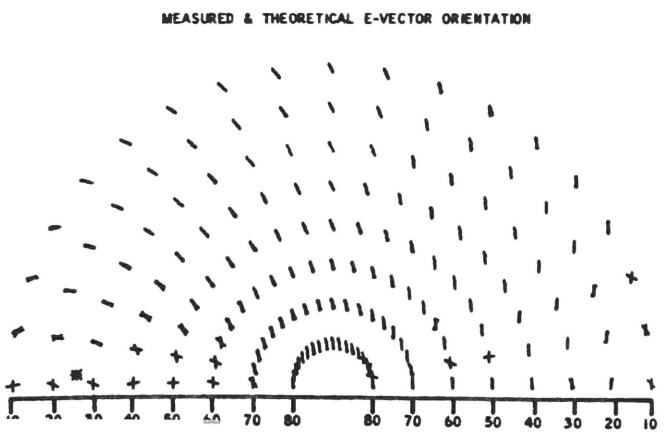
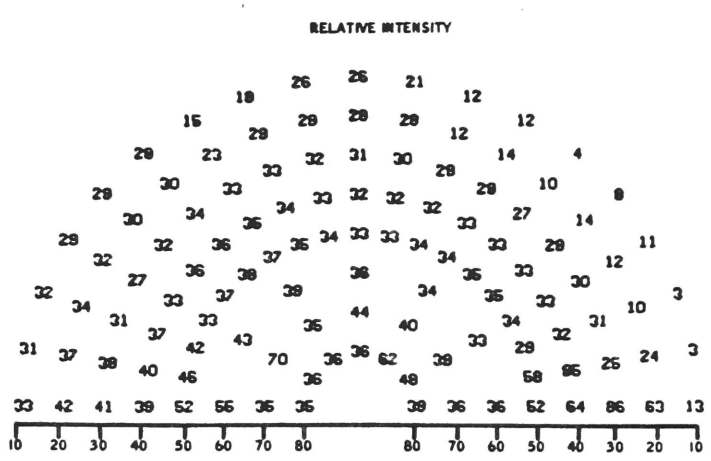
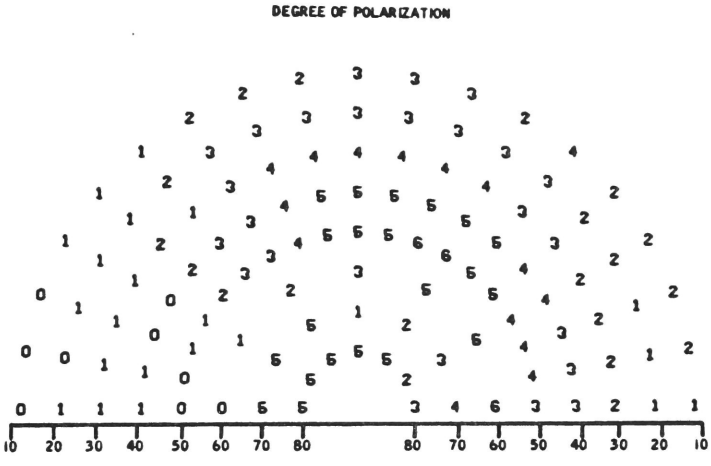
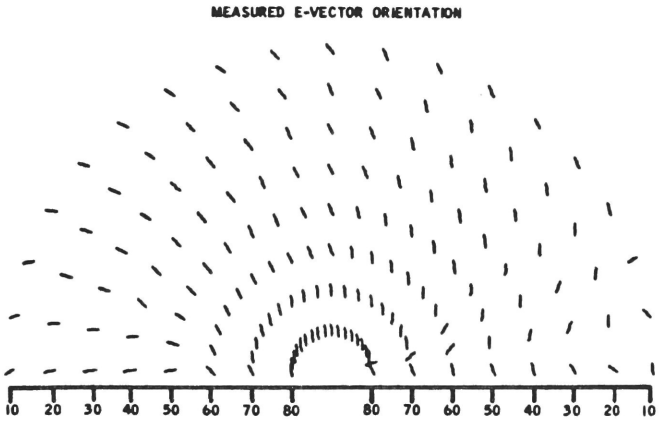
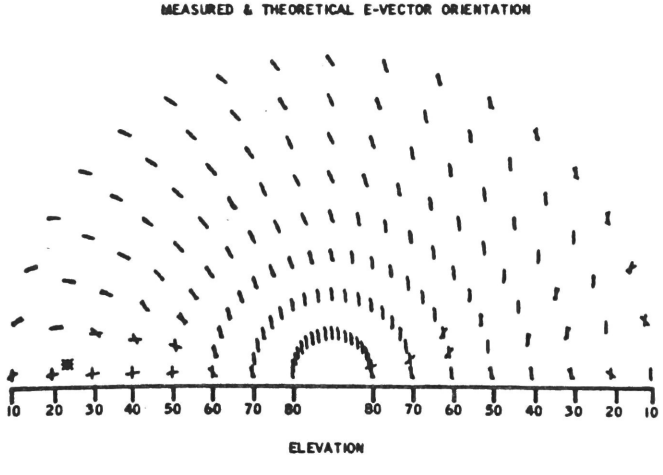


Figure C-15









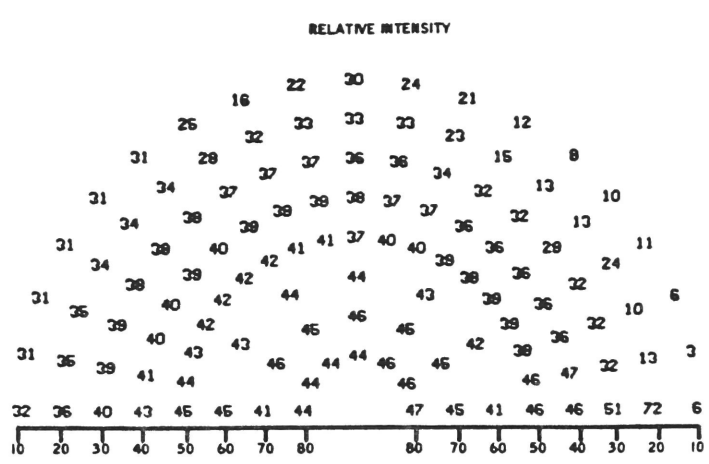
500 nm.
28 January 1978
1420 EST

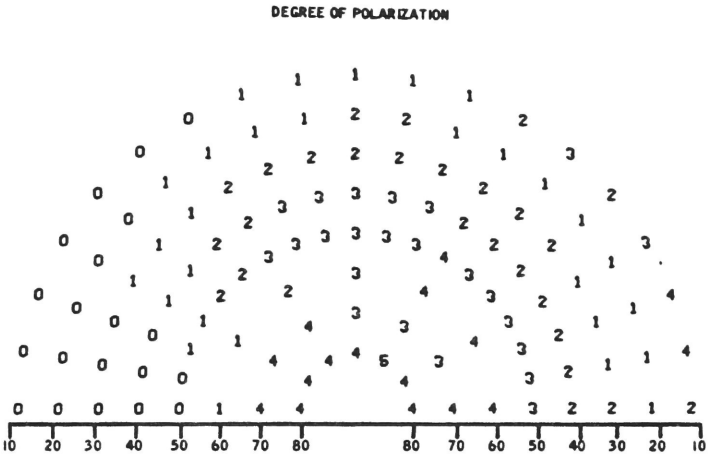
solar ZD = 67°
solar AZ = 216°

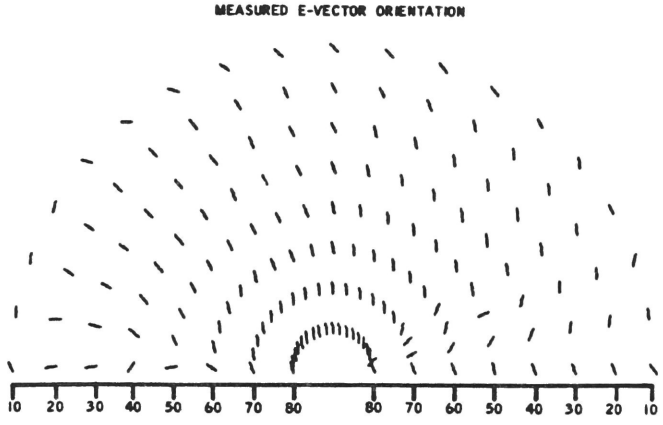
no blue sky; snow falling making solar disc just visible; radiance seemd quite uniform

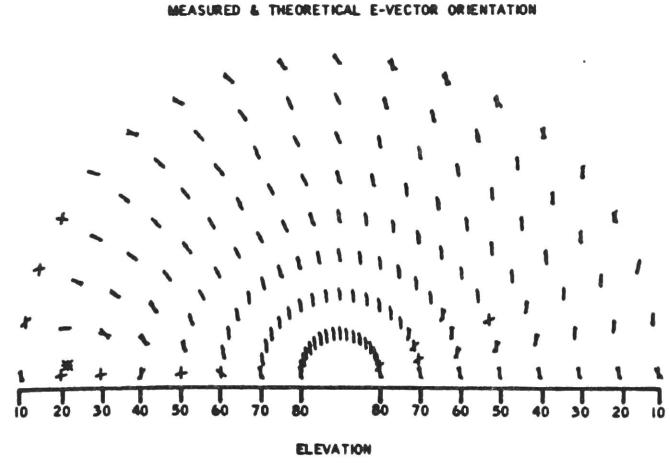
light, dirty snow with many icy spots

Figure C-16









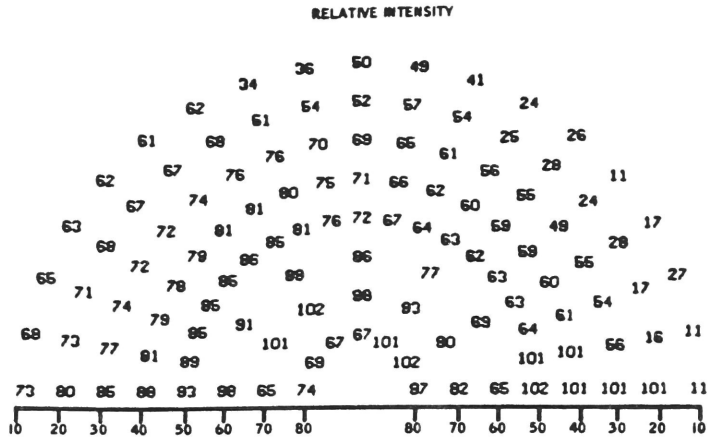
350 nm.
28 January 1978
1440 EST

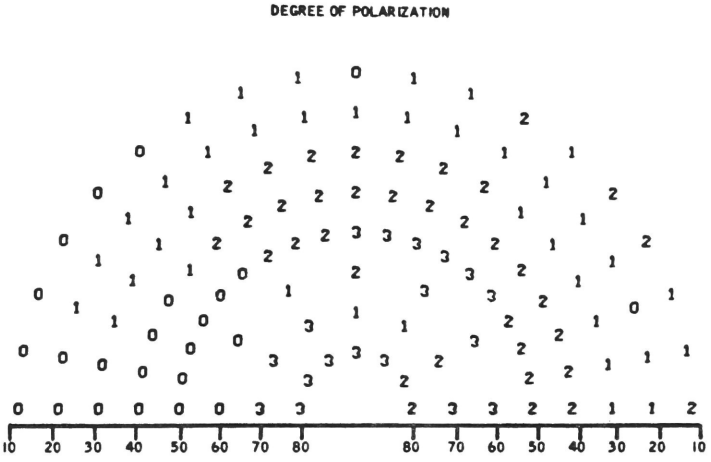
solar ZD = 69°
solar AZ = 221°

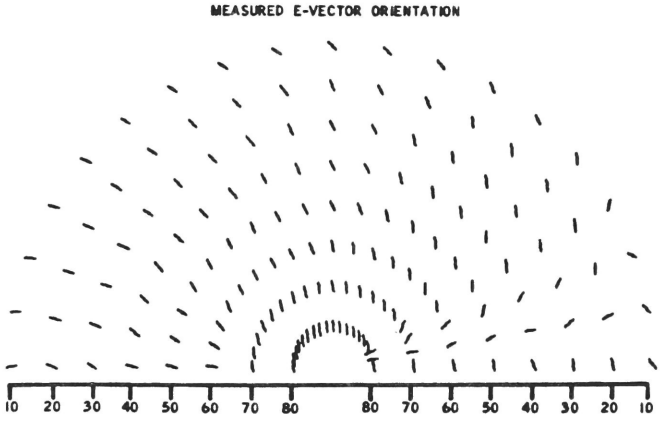
no blue sky; snow falling making solar disc just visible; radiance seemed quite uniform

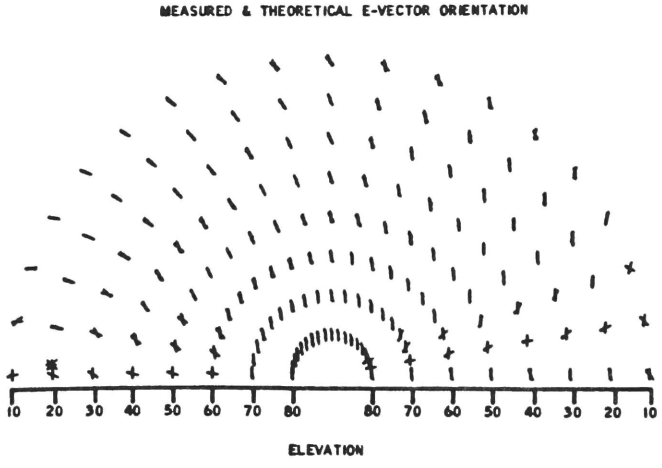
light, dirty snow with many icy spots

Figure C-17









650 nm.
28 January 1978
1455 EST

solar ZD = 71°
solar AZ = 224°

no blue sky; snow falling making solar disc just visible; radiance seemed quite uniform

light, dirty snow with many icy spots

APPENDIX D

Transport experiments.

Considering the success in carrying bees to new feeding locations (described in detail in Chapter IV), it was of interest to know how bees danced when they returned to the hive after being transported. Von Frisch was also interested in such problems--e.g., whether the flight to or away from a goal (or both) determined the direction of the waggle runs in the dances. He performed some interesting experiments and noticed several contributing factors (e.g., a bee flying into a head wind indicates a distance farther that she actually flew to the food source [reviewed by von Frisch, 1967; pp. 79-81; pp. 116 ff.]), from which he concluded that the flight out essentially determined the distance indicated by the dance communication.

Unlike the distance component, investigation of whether indication of direction in the dance is influenced by the outward or return flights has so far been conducted in an unbiological manner: bees are displaced laterally as they feed so that the outward and return flights occur in different directions. Observation of the resulting dances of such transported foragers should show which trip is the more important. Von Frisch's practical problems were that after such displacements transported bees return to the hive only after long delays--they tended to be greatly disturbed and did not usually dance. A partial explanation of the source of this disturbance was first noted by Wolf (1927): bees departing a displaced feeder fly away in a direction appropriate to the feeder's former position (i.e., the place to which they flew), and thus along a parallel path and travel a distance appropriate to return them to the hive. Once there and not finding the hive, they return only after long periods of time.

Otto (1959) observed similar behavior: the bees he transported did not seem to notice that they were at a new place and flew in the old (now incorrect) direction. He was able to overcome this problem, however, by training bees to fly back from the displaced position. He did this by repeatedly transfering individually marked bees to the displaced position whenever they landed on the feeder. Eventually these bees learned how to return to the hive directly after transport.

Some interesting facets of bee orientation processes were discovered. For example, when the flight path along the two directions was about equal in terms of distinguishing visual features (trees, fences, etc.) Otto's bees clearly danced the bisector of the angle between the direction of the outward and return flights. Otto (1959) and von Frisch (1967; p. 170) point out that this makes sense only if it is assumed that the bees transpose the angles flown on their return by 180°. By making one of the fight paths visually more distinctive (e.g., along a fence line) the direction indicated in the waggle dance was weighted more heavily in favor of the distinctive direction. In fact, by arranging optical cues properly, Otto could make waggle dance communication indicate any angle between the outward and return flights.

As pointed out by von Frisch, these experiments do not of themselves prove that bees use both directions of the foraging flight to derive the waggle dance orientation. The fact that the bees had to learn the return flight (since it wasn't just the reverse of the outward flight) meant that the return may have actually been interpreted as an "outward" flight (von Frisch, 1967; p. 172). This factor could explain the observed behavior because it is well known that two legs of an outward flight are

averaged in exactly the manner just described.

Lindauer (1963; reviewed by von Frisch, 1967; pp. 172 ff.) used several tricks to demonstrate that when a bee does not have to learn the flight back to the hive (the usual situation of course) only the direction of the outward flight determines the waggle dance direction. One successful procedure was to use only foragers which arrived at the feeder for the first time. If such bees were displaced laterally, they returned to the hive with only a little delay; they had not made a return flight to the feeder and were for reasons unknown, less "confused" than bees which had made many returns.[1] These new foragers, however, will not ordinarily dance in the hive until they have made several successful foraging flights. Lindauer induced them to do this, however, by starving the hive. Under these extreme conditions, bees will dance readily for even very meager food sources. Lindauer observed that all of the dances of these transported foragers showed unambiguously that the outward flight determined the direction indicated in the dance communication.

Returning to the work discussed here, it was obvious from the results of my training procedures (Chapter IV) that the bees remembered the return flight since they returned readily to the location of the displaced feeder. But my methods were different from the others just mentioned because the feeder at the old position was removed along with the feeding bees, and the foragers transported were actually already established foragers. Only after bees visited its old position would they then come to its new (displaced) position. All of these observations

1. Presumably both kinds of bees were familiar with the surrounding environment because of previous foraging activity and extensive orientation flights.

indicated that the bees knew both locations well. A displacement experiment was therefore used to determine whether the return flight of transported bees under some conditions affected the waggle dances of returned foragers.

Procedure

It seemed likely that the direction component would show clearer results than distance, since a displacement angle of about 35° was easily accomplished, and any resulting changes in dance direction could be measured. To this end, bees were trained to forage from a feeder located 450 m at an azimuth of 60°. Individually marked bees were transported as they drank sugar water (described in Chapter IV) by automobile to a point 500 m and azimuth 95°. Upon their return to the hive, the bees could dance only on a horizontal surface under a small, white, unpolarized light source which they used as the sun in their dance orientation. The dances of all bees were recorded on videotape and analyzed as described in Chapter IV. The expectations were: 1) if only the outward flight was important in determining the direction for the dances, then no difference would be observed in the direction indicated (if any) by controls and experimentals. 2) If, however, the return flight was important, a divergence in dance direction proportional to the influence of the return flight should be observed for the displaced bees.

Results.

An experiment was carried out on 19 August 1977 from 1800 to 1900 EDT, under relatively cloudy (cumulus) sky. The temperature was moderate and a light, variable wind was blowing. Most transported bees were

well-established foragers, which flew directly away from the feeder without orientation circles. Covering the feeder and transporting it by automobile to the new release point took only about one minute but unfortunately bees were never observed to be still feeding upon arrival.[2] In this case, as soon as they were released the bees never oriented around the feeder, and, as far as could be seen, departed in a direction appropriate for the feeder position to which they had flown (i.e., the reverse of the outward flight).

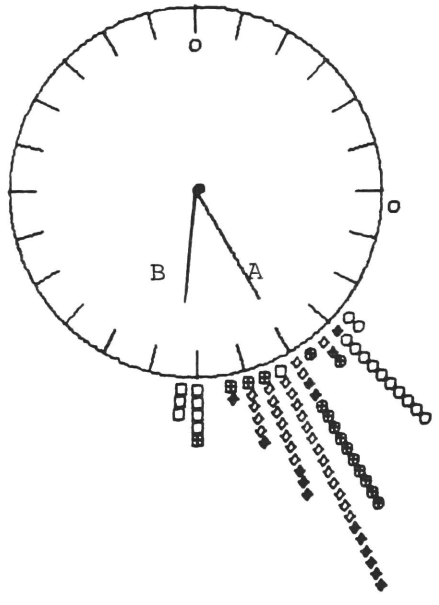


Figure D-1. The waggle directions of displaced bees dancing on a horizontal hive to a small, white, unpolarized light. Vector A indicates the dance direction appropriate for the feeder flown to; B is appropriate for the displaced feeder location. Only a single bee danced in the displaced feeder direction.

This observation agrees with those of Meder (1958), Wolf (1927), and Otto

2. As discussed in Chapter IV, bees had to feed while at the new position in order to assure that they would return to it. Only undisturbed bees performed characteristic orientation flights around the feeder before departing.

(1959). In contrast to their results, however, my displaced bees always returned to the hive with very little delay, and danced very readily.[3]

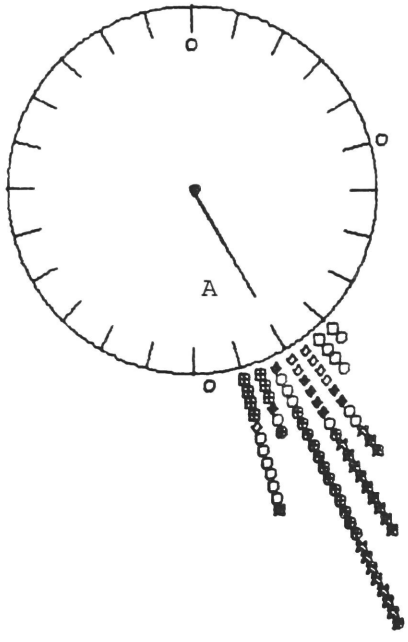


Figure D-2. The waggle directions of control bees (not transported), dancing on a horizontal hive to a small, white, unpolarized light. The vector is the direction of the feeder during the outward flight.

The results are given in the form of a polar histogram in Figure D-1 (displaced experimentals) in which each symbol represents a different bee. For comparison, Figure D-2 summarizes the dances of bees which were not displaced (controls).

Although the dance dispersion of the experimentals seems slightly greater, the basic direction indicated by the waggle dances is clearly not different from the controls, except for a single bee. This individual (open squares) seemed to have used the return flight alone in deter-

3. The differences in rate of return cannot be explained simply by the race of bees used for the experiments, because Otto also used Italian bees in his work.

mining her dance orientation. Of particular importance, in my opinion, is the fact that none of these bees finished feeding at the displaced feeder location. Maybe the single bee affected by the transport had just finished feeding when the cover was removed and therefore was able to perform nearly normal flight departures. Perhaps if the bees arrived at the displaced position while still feeding, they would have exhibited dances derived in some degree from the return flight.

Further experiments were carried out with bees transported directly from the hive and therefore lacking any outward flight. The procedure of transport has been described in detail in Chapter IV and individually marked bees were carried 150-200 m from the hive. Special care was taken to make certain that all bees had not finished feeding before they were released. These transported bees returned to a horizontal hive to view various light cues (polarized or nonpolarized). Only the first return to the hive was used in the data analysis, and transports were carried out on relatively clear days.

Although such transported bees readily returned to the hive after their transport, only a small proportion (about 10%) danced on the first return. Without exception these bees oriented their dances using either unpolarized lights (the "sun") or polarized UV lights (the "sky") to indicate the goal to which they had been moved. The accuracy of these dances was comparable to those observed for well established foragers dancing to the same feeder location. Therefore, for these bees lacking an outward flight, a single return is sufficient for them to obtain orientation information with respect to cues visible in the sky. Of particular interest was the observation that the bees "reversed" the

direction flown on their return flights by 180° so that they referred to the outward flight. In this regard these observations confirm the previous work already discussed. Further experiments along these lines should clarify additional details.

End