Entomol. Gener.	14 (3/4): 223—232	Stuttgart 1989-07	ISSN: 0171-8177

EGT-Nr 621 IX

Factors Affecting Diurnal Activities of Solitary Wasps (Hymenoptera: Sphecidae and Pompilidae)

István Karsai

Received: 1988-06-14/1988-08-29 Accepted: 1988-09-29

Karsai, I. [Dep. Zool., JATE Univ., Szeged, Pf. 659, 6701 Hungary]: **Factors Affecting Diurnal Activities of Solitary Wasps (Hymenoptera: Sphecidae and Pompilidae).** — Entomol. Gener. 14 (3/4): 223—232; Stuttgart 1989. — [Article].

Factors affecting the diurnal activities of 2 solitary wasps species, *Bembecinus tridens* (Fabricius 1781) and *Pompilus cinereus* (Fabricius 1775), were investigated in a sandy grassland area of the Great Hungarian Plain. The temporal distribution of activity values in relation to different physical parameters rules out the role of wind in the regulation of diurnal activity, but clearly demonstrates the roles of soil temperature and air temperature. On principal component analysis of potentially effective factors, 2 factors, climate and time scale, prove to be important. When represented in factorial space, the activity values of the wasp species reflect the fact that, besides the climate, the time scale corresponding to the internal clock of wasps is an important factors. This may be connected with the reproduction strategies of solitary wasps.

Key words: Diurnal activity — field experiment — principal component analysis — *Bembecinus tridens* (Fabricius 1781) [Sphecidae] — *Pompilus cinereus* (Fabricius 1775) [Pompilidae].

1 Introduction

Most publications on the diurnal cycles of insects deal with species that are regulated by only 1—2 factors [Schwerdtfeger 1963]. In these cases the factor determining the activity can easily be recognised; in general it can be identified with temperature or relative humidity [e g: Chand 1987, Gallé 1976, Caldas & de Ameida 1985, Nyrop & Simmons 1986, Kon 1986, Ilosvay 1982, Warburg 1987, Warburg et al 1984]. In the activity of certain flying insects, the role of the light intensity may also be important [Gilbert 1985, Kapyla 1974, Singh et al 1984, Pivnick & McNeill 1987]. In certain groups of insects, other important factors may act in addition to physical ones, e g: body length [Kapyla 1974], competition [Abe 1971, Baroni-Urbani 1969, Stebaev & Reznikova 1972], avoidance of parasitism and predation [Evans et al 1980, Ottesen 1985] or the internal clock [Dreising 1986, Joern et al 1986].

Solitary wasps perceive changes in weather very sensitively. Just before rain, some species return to the nest from the searching flight without prey and close the entrance [Nachtigall 1983]; the activity decreases if the previous day or night was rainy [Miller & Kurczewski 1976]. In many papers dealing with the daily activity of solitary wasps, the air temperature [Evans & O'Neill 1987, Abraham 1982] or the soil temperature [Hager & Kurczewski 1986] are considered to be determinants. The important role of the light intensity was discovered in a more complex analysis of factors affecting the digging [Brockmann 1979] and flying [Kapyla 1974] activities.

Other studies on diurnal activity have described the time schedule of the different behaviour forms of wasps [e g: Gwynne 1980, Hager & Kurczewski 1985/a, 1985/b, O'Neill & Evans 1983, Nilsson et al

0171-8177/89/0014-0223 $ 2.50

1986]. The importance of temporal processes is emphasized by the fact that wasps sometimes show typical activity in bad weather [O'Brian & Kurczewski 1976].

Solitary wasps display involved behaviour patterns; the daily activities can be specified as pollinating activity [Nilsson et al 1986], flying activity [Abraham 1982, O'Neill & Evans 1983], digging activity [Brockmann 1979, Gwynne 1980], provisioning activity [Evans et al 1980] and general activity [Hager & Kurczewski 1985].
The aim of this paper is to reveal the factors that are important in the regulation of the general activity of *Bembecinus tridens* (Fabricius 1781) [Sphecidae] and *Pompilus cinereus* (Fabricius 1775) [Pompilidae].

2 Material and Methods

Investigations were carried out in the E' part of the Bócsa-Bugac region of the Kiskunság National Park (Hungary) on 1986-06-17/18 and 1986-07-17. The experimental site consisted of 3 small neighbouring plots: a sandy road, bare or covered with a Cynodonti-Poetum angustifoliae plant association; 2 plots that were earlier denuded, one with a Festucetum vaginatae association, the other with a mixed community of Festucetum vaginatae and Brometum tectorum (names after Soó [1964]). In this area the summer is generally extremely warm and dry [Körmöczi et al 1981]. The microclimatic differences between the study plots were insignificant.
The digger wasp *B. tridens* and the spider wasp *P. cinereus* were chosen for investigation because of their high density [Karsai 1988] and easy recognizability in the field. Since the outdoor recognition of the ♂♂ of spider wasps is very difficult, only the ♀♀ were used in the study. Since the differential recognition of the sexes of *B. tridens* in the field is impossible, the activities of both sexes were examined jointly. As shown by other authors [Simon Thomas & Simon Thomas 1972, Gwynne 1980], the activity differences between the 2 sexes are characteristic mainly of territorial species.
To determine the activity of the wasps, 6 permanent quadrats of 4 m^2 were placed on each subplot. The air temperature [A-T][1], soil temperature [S-T][2] (at a depth of 5 cm), relative humidity [R-H][3], light intensity [L-I][4] and wind speed [W-S][5] (at a height of 1 m) were measured at 2 h intervals.
Since the wasps spend a considerable part of their active period under the soil surface, e g: with digging [Simon Thomas & Simon Thomas 1972], longer and repeated observations were necessary. One observation in each quadrat lasted 4 min. In min-1 the number of individuals appearing in the quadrat was counted (appearance number), in min-2 the number of flights was observed at a 2 m or 1 m line. In min-3 and min-4 the observations were repeated. The data for all quadrats were then pooled to obtain information about the general moving activity of the wasps.
To analyse the common effect of the time scale and other potential factors on the diurnal activity, principal component analysis [PCA][6] was used. The measured factors were the attributes and the subsequent points of time were the objects of the analysis. The objects were plotted in 2-dimensional PCA space, and the activity values were added to them.

3 Results

The activity of both species was unimodal on temperate day (1986-07-17) and bimodal on hot summer days (1986-07-17/18). This difference is more definite as concerns the number of

[1] air temperature; in further text: A-T — [2] soil temperature; in further text: S-T
[3] relative humidity; in further text: R-H — [4] light intensity; in further text: L-I
[5] wind speed; in further text: W-S — [6] principal component analysis; in further text: PCA

flights: on less hot days the number of flights decreases more than the number of appearances. (Though the 2 types of activity are highly correlated with r = 0.92 for *B. tridens* and r = 0.89 for *P. cinereus*, the number of flights reflects the searching behaviour.) The peak activity is in the morning hours (Fig 1).

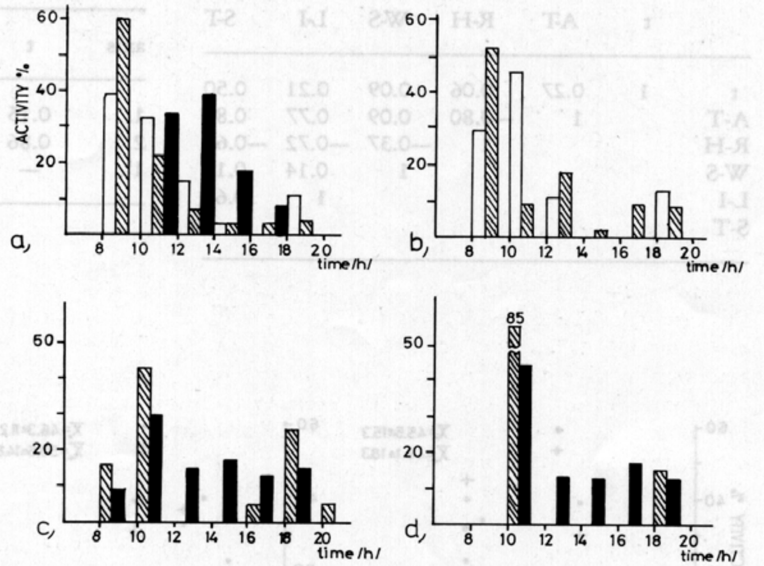

Fig 1: Daily activity of *Bembecinus tridens* (Fabricius 1781) (**a, b**) and of *Pompilus cinereus* (Fabricius 1775) (**c, d**) (presence: **a, c**; flights: **b, d**). Date codes: 06. 17.: empty column; 06. 18.: striped column; 07. 17.: black column.

The effects of different environmental parameters on the activities are similar in both species (Fig 2, 3). The high standard deviations of L-I and R-H imply that these factors have less effect on the activity, while the low standard deviations of A-T and S-T reflect their greater importance. W-S does not significantly influence the activity in the intervals measured. This is probably due to the low wind intensities, a usual phenomenon on the steppe during the early mornings and late afternoons, when both wasps are less active. The very different activity levels relating to similar values of temperature, humidity, etc indicate that no one of the factors is determinative in itself.

Among the potential factors, A-T, S-T, L-I and R-H exhibit significant correlations ($p < 0.01$) with each other, but W-S does not correlate with any of them (Tab 1). Since W-S does not considerably affect the activity either (Fig 2, 3), it may be excluded from further considerations.

The sample points are separated by 2 factors in the PCA computed from the potential factors. Axis-1, accounting for 66 % of the variance, includes A-T, S-T, L-I and R-H, while axis-2, accounting for 25 % of the variance, contains the effect of the time scale. It is also apparent from an analysis of the eigenvectors that the extents of participation of the 4 factors in axis-1 are nearly identical (with a certain predominance of S-T and A-T), and this does not alter when the time scale is removed from the analysis. Axis-2 can be clearly identified with the time scale.

The groupings of the activity values of the 2 wasp species represented in factorial space are similar (Fig 4, 5). The activity decreases to a minimum in response to extreme cold or heat.

Tab 1: Correlations of factors potentially effective on activity. Codes: **t** time; **A-T** air temperature; **S-T** soil temperature; **W-S** wind speed; **L-I** light intensity; **R-H** relative air humidity.

	t	A-T	R-H	W-S	L-I	S-T
t	1	0.27	0.06	0.09	0.21	0.50
A-T		1	—0.80	0.09	0.77	0.89
R-H			1	—0.37	—0.72	—0.63
W-S				1	0.14	0.13
L-I					1	0.69
S-T						1

Tab 2: Eigenvector values of potentially effective factors from principal component analysis. Codes: **t** time; **A-T** air temperature; **S-T** soil temperature; **W-S** wind speed; **L-I** light intensity; **R-H** relative air humidity; 1' time as factor is excluded.

axis	t	A-T	S-T	R-H	L-I
1.	0.15	0.53	0.51	—0.47	0.46
2.	0.86	0.03	0.26	0.19	—0.41
1'.	—	0.53	0.49	—0.48	0.49

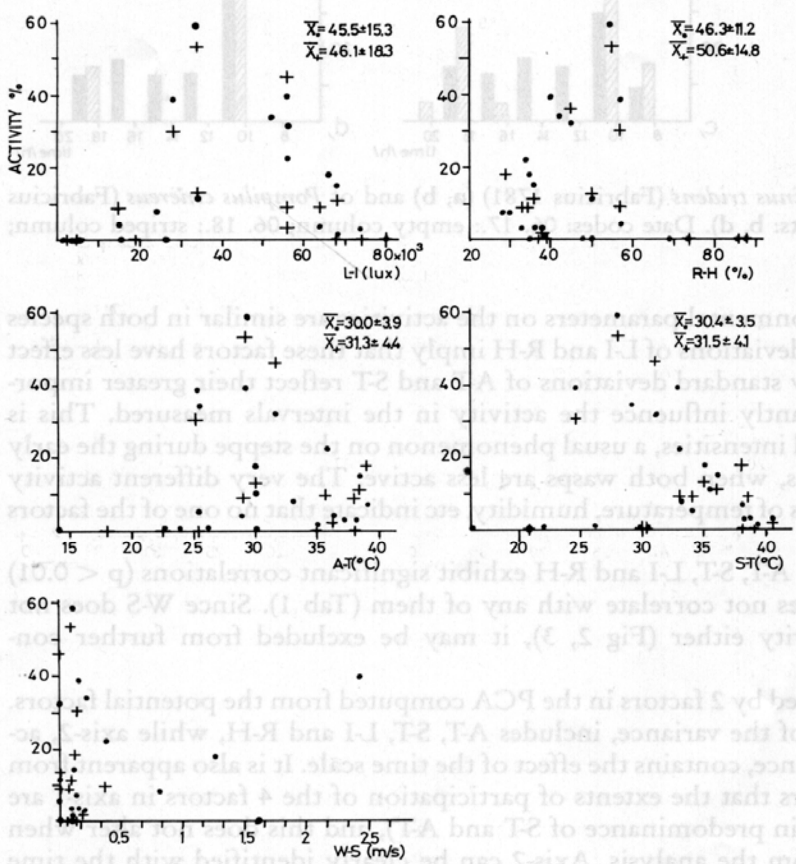

Fig 2: Effects of environmental factors on daily activity of *Bembecinus tridens* (Fabricius 1781). Codes: **L-I** light intensity; **R-H** relative air humidity; **A-T** air temperature; **S-T** soil temperature; **W-S** wind speed; **o** presence; **+** flights.

It increases abruptly to a maximum in the morning, and then gradually decreases as the temperature rises. In this projection the climate axis has the main importance, while the movement along the time axis is less pronounced, whereas the latter is more substantial in the afternoon hours. At this time the activity is also much less in the case of weather characteristic of the maximum activity. The peaks of the two activity types coincide. The flights of *P. cinereus*, however, are more inhibited by extreme weather than those of *B. tridens*. Digging, which indicates nest building, is characteristic mainly of high and medium level activities.

4 Discussion

In general, the temperature is regarded as the effective factor influencing the behaviour of solitary wasps. The ecofaunistical classification based on temperature and R-H is widely used nowadays [Móczár 1948, Westrich 1979, Józan 1986]. Steiner [1978] refers to the importance

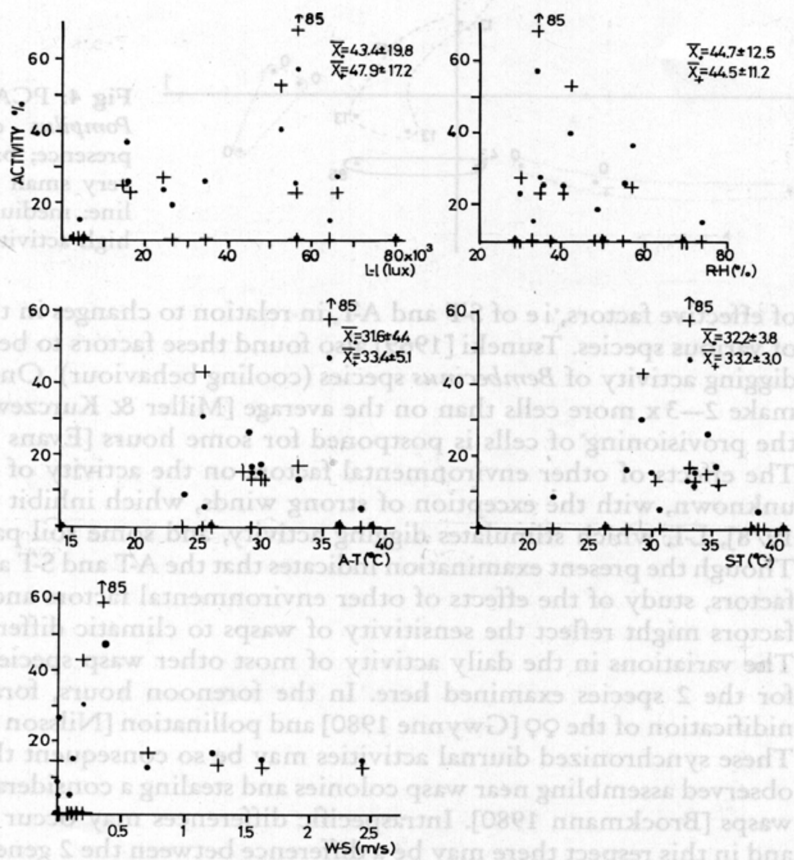

Fig 3: Effects of environmental factors on daily activity of *Pompilus cinereus* (Fabricius 1775). Codes: **L-I** light intensity; **R-H** relative air humidity; **A-T** air temperature; **S-T** soil temperature; **W-S** wind speed; **o** presence; **+** flights.

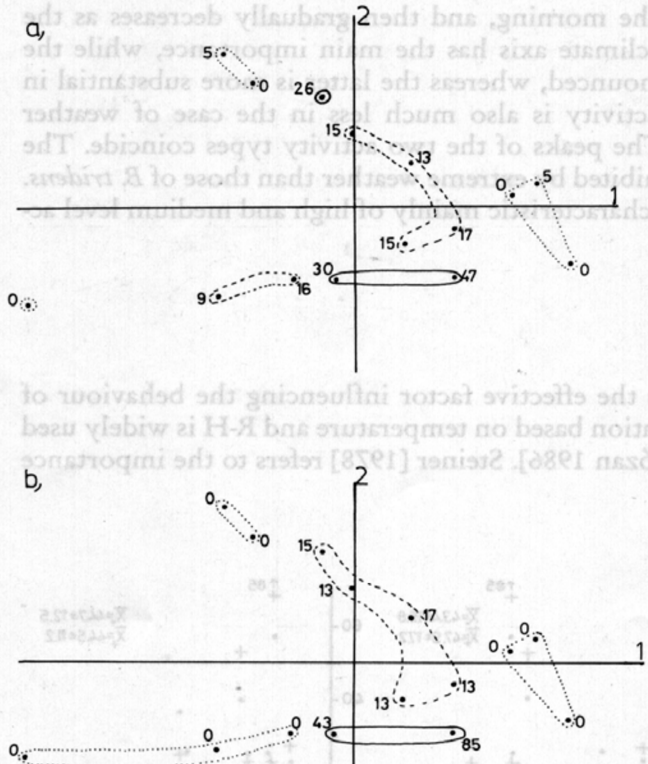

Fig 4: PCA scatter diagrams of activity of *Pompilus cinereus* (Fabricius 1775) (**a:** presence; **b:** flights). Codes: dotted line = very small or no activity (0—5 %); broken line: medium activity (5—20 %); solid line: high activity (> 20 %).

of effective factors, i e of S-T and A-T, in relation to changes in the territory-guarding activity of various species. Tsuneki [1969] also found these factors to be effective in alterations in the digging activity of *Bembecinus* species (cooling behaviour). On hot days certain species may make 2—3 x more cells than on the average [Miller & Kurczewski 1976]. In cooler weather the provisioning of cells is postponed for some hours [Evans et al 1980].

The effects of other environmental factors on the activity of solitary wasps are practically unknown, with the exception of strong winds, which inhibit territorial behaviour [Steiner 1978], L-I, which stimulates digging activity, and some soil parameters [Brockmann 1979]. Though the present examination indicates that the A-T and S-T are among the most important factors, study of the effects of other environmental factors and of correlations between the factors might reflect the sensitivity of wasps to climatic differences.

The variations in the daily activity of most other wasp species studied are similar to those for the 2 species examined here. In the forenoon hours, foraging [Evans et al 1980], the nidification of the ♀♀ [Gwynne 1980] and pollination [Nilsson et al 1986] are more intensive. These synchronized diurnal activities may be so consequent that house-sparrows have been observed assembling near wasp colonies and stealing a considerable amount of the prey of the wasps [Brockmann 1980]. Intraspecific differences may occur in diurnal time partitioning, and in this respect there may be a difference between the 2 generations [Hager & Kurczewski 1986]. The question arises as to the extent to which this is attributable to climatic causes. Because of the complicated ethology of digger wasps and spider wasps, the activity values could differ markedly not only intersexually [Gwynne 1980, Simon Thomas & Simon

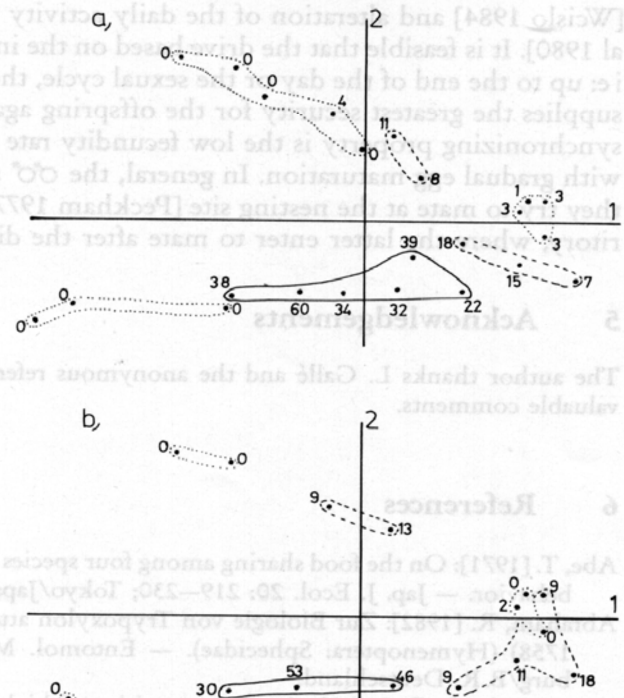

Fig 5: PCA scatter diagrams of activity of *Bembecinus tridens* (Fabricius 1781) (a: presence; b: flights). Codes: dotted line: very small or no activity (0—5 %); broken line: medium activity (5—20 %); solid line: high activity (> 20 %).

Thomas 1972], but also between individuals within the sexes. One reason for this is that the individuals that have not mated or do not produce eggs behave in a different manner. The other reason is that the diurnal rhythm is an integral part of the nesting cycle; i e: it is also influenced by the previous activity state [Steiner 1968]; thus, the daily nesting pattern depends on the different condition stages of the nests [Hager & Kurczewski 1986]. In the present study, behaviour sequences and the differences originating from this were concealed because of the examination of general activity, but those properties were studied that are characteristic of most behaviour sequences (presence, moving).

Time, as the other relevant factor in the diurnal activity, probably plays an important role in the reproductive strategy of wasps. The ♀♀ have to fulfil some cycle up to the end of the day (e g: they have to make or provide a given number of cells and also to close one cell). The Bembecini carry prey into the nest not on the day when the nest is made and the eggs are laid, but on the next day. Up to that time they leave the nesting area [Tsuneki 1969]. This behaviour may be of importance in the defence against parasites, since the parasite pressure on solitary wasps is substantial [Jacob-Remacle 1986, Danks 1971]. There is a significant correlation between the provisioning activity of wasps and the entry of parasites into the nest.

Miltogramminea flies are most active when the wasp species provide the cells most actively [Wcislo et al 1985, Hager & Kurczewski 1985/b]. It is not known whether this is an evolutionary response of the parasites or whether it is connected with environmental parameters. There is some evolutionary response of solitary wasps against parasitic infestation: continuous provisioning [Hager & Kurczewski 1985/b, Evans 1977], driving of parasites by the ♂♂ [Peckham 1977], collective nesting as the selfish herd response to being parasitized

[Wcislo 1984] and alteration of the daily activity until the parasites are less active [Evans et al 1980]. It is feasible that the drive based on the internal clock of wasps is a similar response, i e: up to the end of the day or the sexual cycle, they have to fulfil a behaviour sequence that supplies the greatest security for the offspring against parasites. The other, less special time synchronizing property is the low fecundity rate of the ♀♀ [Danks 1971], which is coupled with gradual egg maturation. In general, the ♂♂ are adaptable to the cycle of the ♀♀: either they try to mate at the nesting site [Peckham 1977] or they wait for the ♀♀ in their own territory, where the latter enter to mate after the digging of the nests [Gwynne 1980].

5 Acknowledgements

The author thanks L. Gallé and the anonymous referees for reviewing the manuscript and offering valuable comments.

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Author's address — Anschrift des Verfassers: István Karsai, József Attila Tudományegyetem, Állattani Tanszék, Szeged, Egyetem u. 2, Magyarország, H-6722 — Ungarn — Hungary.

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At the beginning of the century, Karl von Frisch inaugurated the experimental analysis of bee behavior with his studies on form and color vision. Since then, experimental analysis of bee behavior has been extended to their orientation in space and time, sensory capabilities, and communication within a social group. How does a creature with a brain volume of scarcely one cubic millimeter generate such varied and complex behavior? This volume represents the latest research on the behavior and neurobiology of bees. Topics include: dance communication, foraging and search bahavior, decision making, color vision, learning and memory, structure and function of brain neurons, immunocytological characterization of neuropils and identified neurons, and neuropharmacological studies of stereotyped and learned behavior. Together these papers illustrate the challenge that bee behavior presents to the neuroethologist as well as the progress that this field has made in recent years in the tradition of von Frisch's pioneering work.