OBITUARY

Martin Lindauer (1918–2008)

Prime mover in behavioural physiology and sociobiology.

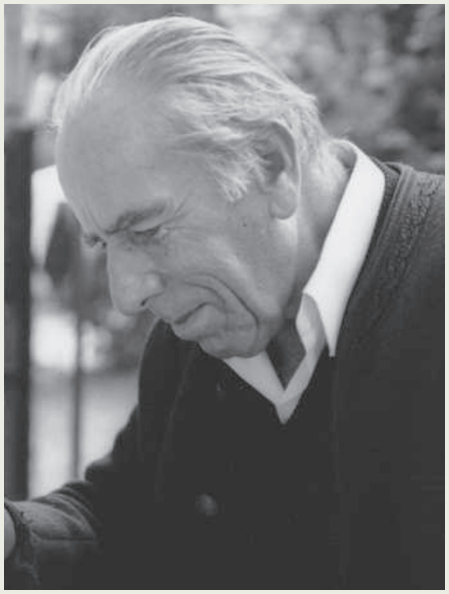
Martin Lindauer, who died on 13 November 2008, was a leading light in the discovery of how honeybees communicate and learn, sense the world, find their way, and live in societies. His enduring influence will also be felt through his success in nurturing a generation of German neurobiologists and behaviourists during his tenure, from 1963 to 1973, as a professor of zoology at the University of Frankfurt.

Lindauer was born in a tiny village in the foothills of the Bavarian Alps, the next to youngest of 15 children in a poor farming family. Here he grew up close to nature — including the bees in his father's hives — but he was also an outstanding student, and won a scholarship to a distinguished Bavarian boarding school in Landshut. In April 1939, he was drafted into Hitler's Work Service to dig trenches, but six months later was transferred to the army and assigned to an anti-tank unit. In July 1942, on the Russian front, he was badly wounded. This was to prove his salvation. He was removed from the front, but the other 156 men in his company went on to the Battle of Stalingrad. Only three returned alive.

While recovering in Munich, Lindauer attended a lecture delivered by Karl von Frisch, a distinguished zoology professor at the university. Lindauer later recalled the occasion, saying that when he heard von Frisch talking about cell division, he felt he had returned to "a world of humanity", where humans create rather than destroy. He resolved to study biology, ultimately starting his PhD research on honeybees, with von Frisch as his adviser, in the spring of 1945.

The previous summer, von Frisch had made a revolutionary discovery, one for which he would eventually receive the Nobel prize: an insect, the worker honeybee, can inform her hive mates of the direction and distance to a rich food source by means of dance behaviour. Von Frisch wanted to press forward with this research, so he assigned Lindauer a relevant (but less exciting) topic, namely, how these communication dances are affected by food scent and taste.

Lindauer had a knack for noticing some anomaly or behavioural quirk that would turn out to be important. So, while pursuing his assigned topic on how bees tune their dancing in relation to the properties of a food source (nectar sweetness, abundance and so on), he noticed that the bees' assessment of a food source's desirability, as indicated by their willingness to advertise the source, depends not only on its profitability as an energy source, but also on how badly the colony



H. HEILMANN

needs the food the bee is providing.

On cool, cloudy days, when the delivery of nectar to the hive was slow, Lindauer's bees would dance for the slightest taste of sugar; by contrast, on hot, sunny days, when nectar was flowing heavily into the hive, his bees would dance only if he made his feeder super sweet. How could a forager, working out in the fields, keep herself informed of her colony's changing needs? Lindauer discovered the answer: the speed with which a forager is unloaded of nectar tells her whether the colony's need is high (fast unloading) or low (slow unloading). These findings proved a springboard for numerous studies of how 'queuing delays' are used to control processes in animal societies.

Between 1945 and 1960, Lindauer repeatedly demonstrated his ability to detect the subtle features that enable coherence to emerge from the apparent tumult in a beehive. He discovered how individuals stay informed of their colony's labour needs. This process rarely involves bee-to-bee signalling; instead, each bee is mostly her own informant, devoting much time to reconnoitring inside the hive. He discovered how a colony regulates its water intake to avoid dehydration: when the need for water increases, any bee that enters the hive with a droplet of water receives a stormy welcome, with several hive bees eagerly taking her water from her, and she is thereby inspired to dance and activate additional water collectors. And he discovered how a honeybee swarm chooses its new home: house-hunting bees fly out, locate several candidate sites, then return to the swarm where they perform dances to advertise their findings to uncommitted house hunters. The more highly a site is valued, the more strongly it is advertised and the more supporters it gains. Eventually, the best site dominates the discussion and is occupied.

While blazing trails in sociobiology in his own studies, Lindauer was also solving mysteries in behavioural physiology in collaboration with von Frisch. Their most notable joint project was investigating whether bees can calculate, using knowledge of the time of day and the Sun's diurnal course, a specific compass direction according to the Sun's position. Von Frisch doubted that bees were capable of this. But Lindauer persisted, and devised a clever experiment for testing the idea: bees were trained to find food in one direction (south, say) on one afternoon, then were taken overnight to an unfamiliar location and tested the next morning for the ability to orient to the south to find food. Lindauer found that they did indeed fly south on the morning of the test.

In 1963, Lindauer accepted a professorship at the University of Frankfurt, where he attracted a constellation of students — including Bert Hölldobler, Eduard Linsenmaier, Hubert Markl, Randolf Menzel and Rüdiger Wehner — who became his successors in advancing behavioural physiology and sociobiology in Germany. Lindauer nurtured his students by giving them the freedom to prove their talent, providing due praise and encouragement, and also guidance in writing clear and enjoyable scientific papers. Lindauer left Frankfurt in 1973 to take up a professorship at the University of Würzburg. There he devoted himself primarily to administrative work until his retirement in 1987.

In summarizing his work, Lindauer published a small volume entitled *Communication Among Social Bees*, based on lectures he had delivered at Harvard University. In the preface, he expressed his pleasure in discovering how "common problems and interests within biology [had] built new bridges ... that span the wrongs of the past". His life's work leaves us not just with a legacy of discoveries, but also with the lesson that the study of nature, such as the social order of bees, can bring sweetness out of chaos.

Thomas D. Seeley
Thomas D. Seeley is in the Department of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853, USA.
e-mail: tds5@cornell.edu