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EDITORIAL

How Giant honeybees and Assam came to Graz

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Epilogue: Visual functions in urodela and sound production in fishes. After my doctoral thesis on retinal functions in *Salmandra atra* (Urodela) (Kastberger, 1975) a research grant from Austria brought me to the Instituto Nacional de Pesquisas da Amazonia (INPA) in Manaus (Amazonia, Brazil) to study sound production and, later in Graz, hearing capacities in Amazon fishes (Siluriformes: Kastberger, 1977, 1978a; Characiformes: Kastberger, 1978b, 1981a,b; Stabentheiner and Kastberger, 1983; Stabentheiner, 1988). That time, the director of INPA was Warwick Estavam Kerr, the creator of the hybrid Africanized bees, commonly termed "killer bees". In a consecutive short episode I was concerned with cave crickets which show specific gating of their locomotor behaviour by the steepness of the natural substrate (Kastberger, 1982, 1984, 1985). In the late 1980's, I came to the bees and started to analyze the functional role of the ocelli (the accessory visual system of hymenopterans) in the Western honeybee *Apis mellifera*, This research project was endorsed by Herbert Heran, the former head of the institute and a former scholar of Karl von Frisch (who won the Nobel prize 1973 for the decoding of the dance language of honeybees, and who was head of the Zoology department in Graz immediately after World War II). The data we were supposed to gain under tethered flight conditions should substantiate the findings of Karl Kral in his doctoral thesis (Crailsheim, 2005) which had been collected years before from walking honeybees (concerning the ocellar influence on the orientational decisions under T - shaped light channels). We were now able to separately stimulate each of the three ocelli and the compound eyes and to utilize the tarsal reflex to provoke flight in the honeybees, which were fixed to a torque transducer. From the opened front of the specimens, we recorded intracellularly on- and off-responses of ocellar interneurons evoked by the light stimuli. That time, such experimental approaches were en vogue and, along with the booming electrophysiology, „everybody" was convinced that the knowledge about the role of complex systems such as the ocellar flight control could be comprehensively expanded with those invasive treatments under artificial stimulation.

The right approaches? Though banal but fundamental, it took me several years that it became clear to me that creatures capable of fast flight would behave differently under walking or tethered conditions. Moreover, the data gained under tethered conditions hardly provide access to the real nature of the ocellar system (which has been, without much doubt, evolved to support in fast flight control). I had to reconsider the particular scientific approach and started developing alternatives without the constraints of fixing bees to transducers, of recording signals from the brain under mimicked flight condition, and collecting data without understanding the real motivation of the animal. Honeybees with intact and covered ocelli were then trained to visit a feeder, and they were now observed in special flight chambers on their way towards or from the feeding station, and the responses to side light flashes were filmed and successfully analysed (Kastberger, 1990a,b, 1992; Kastberger and Schuhmann, 1993).

My first contact with giant honeybees. It happened on my first visit to India on behalf of the International IUSSI congress in Bangalore 1990, where I reported on the outcome of these prettily unconventional free-flight experiments on ocellar functions: I saw, for the first time, giant honeybees on a big old fig tree which gave me a feeling like little Buddha. Before I started with honeybee research, I was used to work on animals, which are considered icons of danger, such as the piranhas of the Amazon. But now, it seemed that the giant honeybees were serious competitors of the piranhas, and I took the challenge to expand my knowledge in the Western honeybees to the giant ones. On my post-congress tour around India I came across Mohammad Habibulla in New Delhi, that time dean of the science compartment at the Jawaharlal Nehru University. At the JNU, I also found giant honeybee nests hanging from the projecting roofs of the buildings.

Starting my personal giant honeybee research. Only a few years later I came back to India to start a research project about the ocellar flight control in giant honeybees. Together with Habib we organized flight chambers for training bees which should come from their nests just outside the window sills to the feeding places inside the chambers.

Aside these experiments which verified the importance of the ocellar system in fast flight control (Kastberger and Habibulla, 1994a,b; Kastberger *et al*., 1996, 1997; Kastberger and Kranner, 1998), we also observed a series of aspects of the daily life of the giant honeybees just outside Habib's lab. We tagged bees with color codes to trace them back to their maternal nests, and watched the spectacular arriving or absconding of colonies. We brought with us a 6 m extension arm to fix an Hi8 camera, sufficiently long and stiff, to film the nests outside Habib's lab also from the sun-exposed side. So we recorded bats that regularly fed on drones during their mass flight in the dusk, and also the

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shimmering waves as one of the remarkable behaviors in the display of giant honeybee colonies. Shimmering occurred when birds passed by but also when wasps scanned in front of the nests and tried to grab bees off the nest surface. We then used dummy wasps built of styrofoam of different sizes with differently colored stripes to stimulate the colonies under more controlled conditions. Steadily, the list of questions we asked in context of giant honeybee behaviors grew exponentially. One of the first findings dealing with shimmering was that the social Nasonov pheromone is released by the abdomen lifting action during shimmering, possibly to avoid that guard bees start individual counterattacks (Kastberger *et al*., 1998).

In the meantime, the research team grew with Otmar Winder, Christian Kropf, Ernst Hüttinger, Thomas Hötzl and Ilse Kranner, completed by various Indian doctoral students. After the experimental sessions we used to plan field trips to see tigers, wild elephants, rhinos, gaurs or golden langurs in the many of the great Indian National parks, and we also wanted to find giant honeybees in the wild. However, while we chose the Sunderbans south of Calcutta as target, a cyclone around Orissa made this visit impossible. As a second choice, Habib proposed Assam and contacted D.K. Sharma of the Gauhati University who should pick us up at Gauhati airport. This was the time when my personal fairy tale of the "Magic trees of Assam" started (Kastberger *et al*., 1999).

In the following years, we have visited Northeast India for 8 times, and we can proudly present a number of scientific paper and outreach on giant honeybees. We focussed on the distribution of giant honeybee colonies in lower and upper Assam on both sides of the Brahmaputra (Paar *et al*., 2002, 2004a,b; Wattanachaiyingcharoen *et al*., 2003), investigated aspects of migration and colony aggregation (Paar *et al*., 2004), the queen's mating frequencies (Wattanachaiyingcharoen *et al*., 2003), the drifting of workers in nest aggregations (Paar *et al*., 2002), but also the individuality of wing patterns (Kastberger *et al*., 2003). For the first time, we confirmed that one and the same queen revisited the same nesting site over more than four years (Paar *et al*., 2000; see also the back-to-back paper of the competing group: Neumann *et al*., 2000) and analyzed the interaction between the honeybee colonies and predatory birds such as the bee eater (Kastberger & Sharma, 2000). We also filmed of the private live of the honeybees and initiated an international production of a natural documentary film (Kastberger, 1999) (with Sir David Attenborough as the narrator; meanwhile, this „our" film was viewed by more than 300 or even 400 millions of people world-wide).

Broadening up giant honeybee research. We then expanded the scientific research on giant honeybees and included the cliff bee *Apis laboriosa* (Kastberger *et al*., 2003; Paar *et al*., 2004), for which we also visited Himalayan valleys in India (Himachal Pradesh, Arunachal Pradesh) and Nepal. Nepal was, at the time, much easier to travel for an European scientist than India. For support regarding logistics we found a mentor in the UNESCO organization ICIMOD with its headquarter in Kathmandu, and with two former members, S.R. Joshi and Madhusudan Man Singh, two competent colleagues who helped us along with the bureaucracy while establishing cooperational ties with the Tribhuvan University Kathmandu. Lastly, we organized four expeditions to Nepal and have collected a big data set for both Giant honeybees (*A. dorsata dorsata* and *A. d. laboriosa*).

We proved that shimmering behavior is a defence trait against wasps (Kastberger *et al*., 2008) and also against foreign conspecifics (Weihmann *et al*., 2014) and discovered that shimmering waves are triggered by "special agents" in the nest surface (Schmelzer & Kastberger, 2009; Kastberger *et al*., 2010). We developed a 3-dimensional imaging tool for analyzing behaviors of surface bees (Kastberger *et al*., 2011a), measured the thermogenetic behaviors of colonies by infrared thermography (Waddoup, 2014; Kastberger and Stachl, 2003) and the comb vibrations elicited by shimmering with the method of Doppler vibrometry (Kastberger *et al*., 2013). We explained in great details how collective decision-making occurs in shimmering by initiating and spreading signals for intrinsic and extrinsic purposes (Kastberger *et al*., 2008, 2010, 2011a,b, 2012, 2013, 2014a,b; Schmelzer & Kastberger, 2009; Weihmann *et al*., 2012, 2014). Towards external addressees, the colonies deliver signals at variable shimmering strength by controlling the participation of surface bees and the repetition rate of the waves (Kastberger *et al*., 2008). They also direct the waves by controlling their spreading direction to follow preying wasps in front of the nest (Kastberger *et al*., 2014b) (this was the first evidence! for a mobbing response in arthropods). Intrinsically, shimmering waves provoke vibrations at the comb (Kastberger *et al*., 2013a) which continuously channel the information of the arousal state at the active side of the nest towards the colony members of the contralateral, passive nest side.

Our research activities in Southeast Asia over the last twenty years led to fascinating stories about the collective behaviors of giant honeybees. However, they also motivated us to consider *Apis mellifera* ecotypes in the tropics (*A. m. scutellata*, *A. m. capensis*) and in the temperate climate (*A. m. carnica*) (Kastberger *et al*., 2009). This brought me to South Africa, to the US and back to Brazil where, 25 years later, Kerr was director for a third period. We filmed two documentaries, one on the Africanized bees in both the Americas (Kastberger *et al*., 2002) and one on the African Small hive beetle *Aethina tumida* (Kastberger *et al*., 2003) which has become a serious pest attacking the Western honeybee *Apis mellifera* in the temperate zones.

Summarizing, the scientific research on honeybees was only possible with the help of collaborators in India, Nepal, Thailand, South Africa and Australia. The resulting papers ranged from behavioral sciences of colony structure (Paar *et al*., 2002), collective management of information transfer (Kastberger *et al*., 2008, 2010, 2011a,b, 2012, 2013, 2014a,b; Schmelzer & Kastberger, 2009; Weihmann *et al*., 2012, 2014) - involving high-end methodology (Kastberger *et al*., 2011a, 2013, Waddoup, 2014) - to defence behavior (Kastberger *et al*, 2008, 2009, 2012, 2014; Kastberger & Sharma, 2000), migration (Paar *et al*., 2000), reproduction (Wattanachaiyingcharoen *et al*., 2003; Paar *et al*., 2004a,b) and self organization (Kastberger *et al*., 2011b). They also addressed the fields of systematics

(Paar *et al*., 2012; Kastberger *et al*., 2003), genetics (Kastberger *et al*., 2002; Paar *et al*., 2004), physiology (Kastberger *et al*., 1993, 1996, 1997, 1998; Kastberger & Habibulla, 1994a,b; Kastberger & Kranner, 1998), thermobiology (Kastberger & Stachl, 2003; Waddoup, 2014), parasitology (Kastberger *et al*., 2003) and also of environmental science (Sulzer *et al*., 2010). They additionally gave rise to the production of several documentary films (Kastberger *et al*., 1999, 2002, 2003) which received highest global awards and were aired to an audience of hundreds of millions of people worldwide.

I want to stress that the research on giant honeybees would reflect the link between fundamental science and conservation. Only on the basis of a broader knowledge of the role of a species in its natural environment are we able to understand how creatures evolve and adapt. Our multifaceted experiences with giant honeybees have led us to the conclusion that because of the dramatically escalating ecological situation in Southeast Asia (caused by the extraordinary increase of the human impact through agriculture and urbanization) the giant honeybee species *Apis dorsata* with all its ecotypes has to be included in the red list of endangered species.

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