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EDITORIAL

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The Evolution of Social Behaviour

Special Issue in honour of Michael Taborsky: Revealing the fundamental principles of social evolution

In July 2020, Michael Taborsky officially retired as Professor in Behavioural Ecology at the University of Bern, Switzerland. His scientific life has been, and still is devoted to revealing the fundamental principles of social evolution by natural selection, based on conflict and cooperation among individuals. Colleagues, collaborators and students celebrate this occasion with a symposium on the evolution of social behaviour in September 2021, in which former colleagues, collaborators and students present their current research. This special issue on *The Evolution of Social Behaviour* is a companion to this event and includes contributions of almost all symposium speakers. Having been trained as a classical behavioural ecologist, during his further scientific life Michael recognized the central necessity to study ultimate and proximate causation of behaviour in conjunction. The breadth of the contributions to this special issue nicely mirrors the multifaceted interests and integrative scientific approach of Michael to animal behaviour. The contributors to this special issue selected *Ethology* as outlet because this journal represents and encourages this integrative approach ever since its foundation, and not the least because Michael served as Editor-in-Chief of *Ethology* for 11 years, from 1999 to 2010.

Ethology offers their authors a wide spectrum of article types. Accordingly, this special issue contains a bouquet of contributions. The issue includes Perspective and Reviews papers asking how cooperative breeding may help or hinder coping with environmental change (Komdeur & Ma, 2021), highlighting the possibility that sociality is more widespread in marine habitats than usually assumed (Mazzei & Rubenstein, 2021), or how individual social competence may further the evolution of sociality and vice versa (Taborsky, 2021). Oliveira and Bshary (2021) propose to include interspecific relationships into social behaviour, and Bender (2021) outlines the potential for ethology to improve the evolutionary understanding of human medical problems. Original Research papers ask whether naked mole rats express caste differentiation (Siegmann et al., 2021), whether rats are aware of the ability of partners to reciprocate food donations (Schweinfurth, 2021), propose novel imaging techniques in the study of sociality (Jungwirth et al., 2021), show how collective actions can lead to diversification of behaviours (Green et al., 2021) and illustrate the importance of the early social environment for learning abilities in cichlids (Fischer et al., 2021) and later life attraction to conspecific odours (Schneeberger & Eccard, 2021). Tebbich et al., (2021) provides the first quantitative account of self-anointment in birds. Two Species-in-the-Spotlight articles provide comprehensive insights into the social systems and sociality of crotophagine cuckoos (Riehl, 2021) and vampire bats (Carter, 2021). Finally, an Ethological Methods article explores the usefulness of mirrors to score aggression across cichlids (Josi & Frommen, 2021).

The compilation of articles for this special issue underlines the extraordinary diversity of Michael's research on the evolution of social behaviour. Beyond that, it mirrors one of Michael's fancies to dive deeply into discussions on exciting scientific questions, no matter whether it concerns his own fields of research or entirely unrelated topics.

Among his colleagues, Michaels is certainly best known for his large body of research on the evolution of cooperation. Cooperation has been considered one of the most fundamental questions of biology ever since Darwin, and current consensus in primary literature and biology textbooks has been that kin selection is generally responsible for the evolution of cooperation among social partners. Michael's research on different vertebrate and invertebrate study systems demonstrated, however, that this focus is way too narrow. His work revealed that cooperation originates by an interaction of several evolutionary mechanisms, involving kin selection, negotiation and trading, and enforcement, depending on social and ecological forces of natural selection. Michael further measured the fitness consequences of males and females in two very different fish systems both exhibiting three alternative male mating tactics allowing to understand how such multiple morphs can evolve and be maintained; and he deciphered the intricate decision rules Norway rats use when reciprocating help received by others.

In the era of the "phenotypic gambit," when Michael was trained in behavioural ecology, mechanisms of behaviour were considered to be unnecessary for understanding evolution. However, very early on Michael adopted an integrative angle on animal behaviour. Building on Tinbergen's famous "four questions" (Tinbergen 1963), Michael was convinced that to understand the function ("why") one also has to know "how" animals accomplish their behaviour (e.g., Hofmann et al., 2014; Taborsky et al., 2015; Taborsky & Taborsky, 2015). Above all, he wanted to understand the decision rules animals use when expressing social behaviours, exemplified by his work on Norway rats, but Michael also strived to understand the sensory (Gerber et al., 2020; Schneeberger et al., 2020), energetic (Grantner & Taborsky, 1998; Taborsky & Grantner, 1998) and hormonal (Bender et al., 2006, 2008) underpinnings of social behaviour.

While Michael developed mastery in the art of testing ultimate and proximate concepts by sophisticated experiments in the field and in the laboratory, often involving targeted behavioural manipulations of particular focal or stimulus individuals, he combined his empirical work with theoretical modelling to understand cooperative behaviour on evolutionary time scales. Rather than heuristic proof-of-concept models with a high degree of abstraction, Michael aimed at informing the models by biological insights gained from his empirical work, even at the cost of greater model complexity (e.g., van Doorn &Taborsky, 2012; Hamilton & Taborsky, 2005; Quinones et al., 2016).

Few people may know that Michaels started his career in fact as a Lorenzian style "goose maid," working as a volunteer at the Max-Planck Institute for Behavioural Physiology in Seewiesen. When he joined this institute in the late 1970s, he hand-raised bar-headed geese (*Anser indicus*) for a project of Jürg Lamprecht. The goslings imprinted on Michael and followed him all day at every turn. Michael stayed in Seewiesen to start his PhD, dwelling deeply into the costs and benefits of cooperative breeding. It was the time when the first functional studies on cooperatively breeding birds (Emlen, 1982; Koenig, 1981; Reyer, 1980) and mammals (Rasa, 1977) caused quite some excitement: cooperative breeding was considered a major evolutionary riddle, because it seemed to contradict the maximization of individual fitness to forgo own reproduction in order to raise foreign young. When Michael came to Seewiesen, Kalas (1976) just had described the basics of the social system of an apparently cooperatively breeding cichlid fish from Lake Tanganyika, *Neolamprologus brichardi*. Sociality of these fish were chosen as PhD topic of Michael and his colleague Dominique Limberger, who used the fantastic opportunities this system offers to study cooperative breeding experimentally in the laboratory and in the field. Michael's thesis, handed in at the University of Vienna in 1982, contained a most detailed cost–benefit analysis of helping behaviour from the perspectives of subordinates and dominant breeders (Taborsky, 1984, 1985; Taborsky & Limberger, 1981). He would return for an in-depth study of this cichlid system only several years later.

When I met Michael in Seewiesen in 1981, I was an ornithologist aiming for a scientific career studying birds. I did not consider fish as super-exciting, to say the least. However, I was taught better. As first postdoctoral project, Michael studied alternative male reproductive tactics (ARTs) in Mediterranean ocellated wrasses, *Symphodus ocellatus*. I joined him as a field assistant and was truly astounded to see that fish have diverse and fine-tuned means of behaving and communicating, form stable, individual relationships and recognize each other. Ocellated wrasses feature three male ARTs, nest-building burgeois males, tolerated satellite males that help defending against sneakers, and female mimic sneakers, which steal fertilizations. Remarkably, satellites parasitically spawn themselves and therefore do not enhance the net fertilization success of nest males. Yet, nest males benefit from satellites, as their presence indicates a successful nest to females (Taborsky et al., 1987).

Michael's second postdoc project, still at the MPI in Seewiesen, was on birds—much to my delight. However, these particular birds were unusual in almost any respect and on top of that they were pretty much invisible. Michael became hooked to a species featuring one of the most extreme parental investments among animals, the flightless and fully nocturnal North Island brown kiwi, *Apteryx mantelli*. Females of the size of a small chicken lay yolk-rich eggs weighing up to half a kilo, incubated by males for 3 months. Reproduction drives both sexes to their critical limits of energy expenditure (Taborsky & Taborsky 1993). The question was why such extreme investment pattern would evolve. Also, should one not expect that during this long male incubation, female partners would seek their chances of multiple matings? This project, aspects of which became my diploma and doctoral topics, challenged the limits of technical feasibility and required all our investigative skills to obtain quantitative data on the behaviour and energetics of this secretive species. Our first, fruitless weeks of the first field season we spent trying various more or less sophisticated methods to catch kiwis, until we had to accept that the only way to catch a kiwi is by trying to run faster than it and catch it by hand. Needless to say that more often than not the kiwis were winning the race. It turned out that kiwis live in stable pairs and are socially and genetically monogamous (Taborsky & Taborsky, 1991, 1992, 1999). Males need a long recovery time after incubation, during which they lose all their energy reserves. But why are females 100% faithful to their male partners? Simply because they cannot lay more of these jumbo eggs. Egg formation also greatly depletes their reserves, and so they cannot compensate energy loss fast enough to engage in mating with other males (Taborsky & Taborsky, 1993).

In 1985, Michael took up a permanent research position at the Konrad-Lorenz Institute of Comparative Ethology (KLIVV) in Vienna, where he also served as deputy director since 1993. While waiting for a generous aquarium facility to be built at the KLIVV for cichlid research, he and myself started a project on another unusual bird. This time, the species was able to fly and active during the day—so far so good. But it was odd in another way: it was an obligate brood parasite. We started this project, because it was still unknown how females of the European cuckoo, *Cuculus canorus*, find the "correct" host species for which they lay a mimetic egg among the roughly 100 potential host species. Host imprinting, the most popular hypothesis at this time, according to which young learn the phenotype of their host as nestlings, was not supported in an experiment by Brooke and Davies (1991). We set out to perform a hand-rearing experiment, testing an alternative hypothesis—the habitat-imprinting hypothesis, proposing that cuckoo chicks learn the habitat type around their nest and return to this habitat as adults for egg laying. We hand-reared seven cuckoo chicks in differently shaped and coloured artificial "habitats." While cuckoo chicks are clearly early birds, neither Michael nor I are. So during the early morning hours, the chicks were placed next to our bed to ensure they get their hourly meals from 6:00 am, and in between we still could catch some additional sleep. As adults, the cuckoos were tested in the huge flying hall of the KLIVV for their habitat preferences. When given the simultaneous choice between all possible rearing habitats and a natural reed habitat, they indeed preferred to watch nest-building songbirds within the habitat they had been imprinted on (Teuschl et al., 1998). In a radio-telemetry study in the Czech Republik, further support for this hypothesis was accumulated (Vogl et al., 2002, 2004), and a recent cross-continental study using ringing data confirmed that after first migration, cuckoos return to habitats resembling the ones they grew up in (Kolecek et al., 2020).

In 2000, Michael was offered an ordinary professorship and chair of the Division of Behavioural Ecology at the Institute of Ecology and Evolution of the University of Bern, Switzerland, situated in the picturesque Ethological Station Hasli, a 300-year-old farm in a nature reserve next to the river Aare. During the two decades he worked in Bern, Michael's main focus remained on the study of social behaviour, in particular cooperative breeding in *Neolamprologus pulcher* and of alternative reproductive tactics in *Lepidiolamprologus callipterus*. In addition, he started to work on reciprocal interactions in wild-type Norway rats (*Rattus norvegicus*) and on cooperative breeding in ambrosia beetles. Parallel to experimental work in the laboratory, from 1995 on, Michael started yearly expeditions to Zambia, where he established a field station in Kasakalawe near Mpulungu, which is now open to cichlid research teams from all over the world.

Neolamprologus pulcher (see Cover Illustration of this issue) is certainly Michael's most intensively studied and best understood study system. It is a cooperatively breeding cichlid, in which a dominant breeder pair and helpers jointly care for eggs and larvae produced by dominants until free-swimming, guard them from egg and fish predators, and maintain the quality of breeding territory. Several features diverge significantly from those of most other cooperative breeders. (a) Michael's team found that one particular ecological factor—predation pressure—predominantly triggers sociality in this species (Groenewoud et al., 2016; Heg et al., 2004; Taborsky, 1985) whereas resource availability, habitat saturation or climatic unpredictability play less of a role for sociality in these fish. The risk to be predated, mainly by large piscivores, explains why *N. pulcher* breed in colonies (Jungwirth et al., 2015), have extended natal philopatry (Heg et al., 2004), why helpers strategically adjust their growth (Heg et al., 2004b) and why helpers pay to stay to be accepted by the dominants of a group (Taborsky, 1985). Cooperative breeding in *N. pulcher* reflects a system of negotiation and reciprocal trading of commodities (Quinones et al., 2016). Safety of subordinates is traded against energetic load-lightning of breeders (Taborsky et al., 2007; Zöttl et al., 2013a) and offspring survival (Brouwer et al., 2005), and this is stabilized by a latent threat of punishment and eviction (Fischer et al., 2014). (b) Another peculiarity of *N. pulcher* is their marked size-dependent division of labour (Taborsky & Limberger, 1981; Taborsky, 1984; Taborsky et al., 1986, Bruintjes & Taborsky 2011), which is possible because many different sizes are present in a social group due to indeterminate growth. (c) Finally, *N. pulcher* groups consist of a mixture of related and unrelated individuals. Relatedness to breeders declines with helper age, so that large adult helpers, which are most efficient in providing help, are usually unrelated to the breeder's offspring and beneficiaries of help (Dierkes et al., 2005). Opposite to cooperative systems driven by kin selection, but in accordance with the pay-to-stay mechanism, in *N. pulcher* relatedness reduces cooperative effort (Zöttl et al., 2013b).

Cooperative breeding can take entirely different forms in certain invertebrates. Next to fish, Michael worked on a cooperatively breeding beetle system exhibiting division of labour by age (age polyethism; Biedermann & Taborsky, 2011), and in which the relatedness between sisters is exceedingly high due to haplodiploidy and nearly obligate full-sib mating. Ambrosia beetles are a group of tiny bark beetles practising agriculture by cultivating fungi cultures (Biedermann et al., 2009), which they grow and harvest in a burrow system in the wood of dead trees. Due to high inbreeding, genetic conflict in these beetles is low; outbreeding even reduces their fitness (Peer & Taborsky, 2004, 2005). Additionally, sociality in ambrosia beetles may be furthered by the need to socially defend against pathogens, allowing the beetles to grow edible fungi, but not to be overgrown by harmful germs (Nuotcla et al., 2019). Moreover, humidity of the wood influences the viability of fungi and the timing of beetle dispersal (Nuotcla et al., 2021).

With one of his first PhD students in Bern, Claudia Rutte, Michael sought for a system suited to study reciprocity and trading between animals more directly—they decided to study wild-type Norway rats, *Rattus norvegicus*, which turned out to be a lucky pull. In the past two decades, Michael's team unfolded an unforeseen diversity of simple as well as complex decision rules how Norway rats exchange goods and services. After demonstrating that rats use direct reciprocity, requiring to remember previous co-operators or defectors (Rutte & Taborsky, 2008), these authors showed that rats can also reciprocate by a much simpler rule: In generalized reciprocity, help is triggered by receiving help by any other individual, a mechanism requiring minimal cognitive capacity (Rutte & Taborsky, 2007). While in rats direct reciprocity generates a higher propensity for cooperation than generalized reciprocity, a study in dogs revealed that here both direct and generalized reciprocity trigger similar cooperation levels (Gfrerer & Taborsky, 2017). Several theoretical models showed that generalized reciprocity can be evolutionary stabilized by social relationships or by state (Barta et al., 2011; van Doorn & Taborsky, 2012; Pfeiffer et al., 2005).

Rats exhibit direct reciprocity when exchanging goods (e.g., food; Rutte & Taborsky, 2008) or services (allogroming; Schweinfurth et al., 2017) of the same commodity, when interaction partners use the same or different methods for the exchange (e.g., pulling a bar for pushing a lever, Schweinfurth & Taborsky, 2017), and also when exchanging different commodities (e.g., food for allogrooming, Schweinfurth & Taborsky, 2018a). They can remember cooperative and defective partners over several days (Schweinfurth & Taborsky, 2020) and likewise remember the actions of different cooperative or defective partners (Kettler et al., 2021). Remarkably, reciprocal cooperation is lower between related than unrelated rats (Schweinfurth & Taborsky, 2018b). Mechanistically, reciprocal exchange of food in rats is triggered by the smell of helpful (Gerber et al., 2020) or of hungry partners (Schneeberger et al., 2020). In the work on rats as well as in extensive reviews across animal taxa, Michael proved the long held belief wrong that reciprocity is rare in nature (Taborsky et al., 2016, 2021).

Ever since his first postdoctoral project on Mediterranean wrasses, Michael kept being fascinated by the question how ARTS are evolutionary stabilized. Similar to the wrasses, the cichlid *Lepidiolamprologus callipterus* exhibits three alternative male types. Large bourgeois males build and vigorously defend nests made of hundreds of empty snail shells. The much smaller females use these shells to deposit their eggs, and they care for their offspring for two weeks in the shells. Bourgeois males and females of *L. callipterus* exhibit the most extreme sexual size dimorphism in animals in this direction: males are 12 times heavier than females. A series of meticulous experiments (Schütz & Taborsky, 2000, 2005) and a theoretical model (Schütz et al., 2006) revealed that divergent selection pressures—with males being selected to grow large enough to carry shells during nest building and with females being selected to remain small enough to fit into the shells—are driving this extreme dimorphism.

Nest males inseminate eggs through the shell opening, a tactic also followed by intermediate-sized sneakers. However, there is also a tiny dwarf male morph able to pass by females and to inseminate offspring while sitting in the tip of the snail shell. Dwarf males that make it to the shell tip achieve on average 78% of fertilizations, but are rarely successful in reaching this favourable position (Wirtz-Ocana et al., 2014). A breeding experiment revealed that unlike most ARTS in other vertebrates, bourgeois and dwarf tactics represent genetic morphs that are inherited on the y-chromosome, whereas females are monomorphic (Wirtz-Ocana et al., 2013, 2014). The different male types and females engage in intricate behavioural interactions, which can even end deadly for females when a new bourgeois male takes over an existing nest (Maan & Taborsky, 2008). But different male types also heavily compete via sperm competition (Schütz et al., 2010, 2017; Taborsky et al., 2018).

Michael summarized his insights gained from this species and other systems exhibiting ARTs in several conceptual articles (Taborsky, 1994, 1997, 1998). In 2008, Rui Oliveira, Michael and Jane Brockmann compiled a comprehensive edited book about ARTs (Oliveira et al., 2008), presenting 20 contributed chapters summarizing the most recent knowledge on all major taxa featuring ARTs.

In the past years, Michael and his colleagues Mike Cant and Jan Komdeur set out for the major endeavour to write a book explaining the evolution of the stunning diversity in social systems and behaviours in animals. Arguably, most social behaviour results from competition. Grounded in evolutionary theory, their book synthesizes the current knowledge on cooperation and conflict into a simple framework for predicting how animals cope with competition. The authors argue that individuals can succeed in resource competition by "racing" others, that is being faster than others in accessing resources, "fighting" for exclusive access or "sharing" both the efforts and gains. After many years of intense writing and discussions among the authors, sweetened by a few writing retreats in the Swiss Alps or the Dutch Atlantic coast, this comprehensive work appeared in August 2021 (Taborsky et al., 2021).

Being at a university, Michael also was involved in a number of duties as university administrator. Apart from being a member of countless commissions, he had been Director of the Institute of Ecology and Evolution, Acting Director of the Biology Department and Vice-Dean of the Phil.-Nat. faculty, some of these duties repeatedly.

As a teacher, in the many lectures, seminars and practical courses Michael gave and organized, a major aim was to make students engage in scientific discussions, rather than just consuming contents. As supervisor of his almost 40 PhD students, 17 Post-Docs and countless master and bachelor students, he focussed on training young researchers in all aspects of the scientific method, including the use and development of evolutionary concepts and asking critical questions. An integral part of his student training was to encourage everyone, including master students, to publish their results. He spent uncountable hours to correct manuscripts and to get them ready for publication.

Last not least Michael substantially inspired and motivated me throughout my own career. Therefore, I would like to end on a personal note. I have been asked several times how it is possible to not only share table and bed with someone, but also to work with that person next doors all days. I can only say: it worked perfectly well. I cannot imagine a more inspiring and supportive partner in life, in science or in any of the small and large everyday challenges we are confronted with.

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