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50 years of the Nobel Prize to Lorenz, Tinbergen, and von Frisch: integrating behavioral function into an ethology for the 21st century

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The 50th anniversary of the awarding of the Nobel Prize to Konrad Lorenz, Niko Tinbergen, and Karl von Frisch, arguably one of the most significant events in the history of ethology, has gone virtually unnoticed. Students and newcomers to the field may be wrongly led to believe that ethology has lost its prominent role as the leading discipline at the forefront of studies of animal behavior with a biological foundation. However, the decline of ethology is more apparent than real, in part a consequence of tying the discipline to a particular theoretical approach (i.e., that of classical ethology), but also due to the historical amnesia affecting many areas of science and the uneasy relationship of ethology with some of its own subdisciplines. Behavioral ecology emerged in the 1970s as an ethological subdiscipline devoted to the study of behavioral function, one of the four aims of ethology famously identified by Tinbergen. Behavioral ecology became extremely popular, but was criticized due to its narrow focus on behavioral function. With the new millennium came a return to a more balanced approach to the study of animal behavior, with frequent calls to recover the balance between the different areas of study and the integrative spirit that many consider one of the most distinctive features of ethology. Still, some behavioral ecologists contend that ethology disappeared shortly after Lorenz, Tinbergen, and von Frisch's Nobel Prize award and has been replaced by behavioral ecology, and offer revisionist narratives of the aims and scope of both disciplines in support of this contention. Contrary to this view, modern ethology remains a necessary and coherent endeavor that encompasses and subsumes all four of Tinbergen's aims, including those considered to be part of the agenda of behavioral ecology. The challenge for the next 50 years will be to preserve the ethological legacy of pursuing the four aims and their integration across levels of biological organization, taxa, methodologies, and interdisciplinary boundaries for a complete understanding of animal behavior.

KEYWORDS

ethology, behavioral ecology, four aims of ethology, Tinbergen, Lorenz

From Nobel Prize to the "e" word

Fifty years ago, the 1973 Nobel Prize in Physiology or Medicine was awarded to Konrad Lorenz, Niko Tinbergen, and Karl von Frisch for their studies of animal behavior and for being "the most eminent founders of a new science, called 'the comparative study of behaviour' or 'ethology' " (Burkhardt, 2022, p. 192). This was the first, and so far the only instance of the prize being awarded for purely behavioral research, and marked the coming of age of ethology as a scientific discipline, "from a quiet backwater of natural history to the forefront of the biological sciences" (Durant, 1986; Burkhardt, 2005). In his banquet speech, Lorenz, reflecting on the consequences of the award, remarked that "under certain circumstances, world opinion about the importance of an entire branch of research can be influenced by this judgment" (Bueno-Guerra, 2021). Lorenz's prediction was fulfilled, and in the wake of this landmark event, ethology achieved unprecedented popularity and international recognition: students enthusiastically embraced the burgeoning discipline, university departments and graduate programs in ethology flourished worldwide, new research centers and field stations were erected, and ethological societies were established in many countries.

Fast forward to 2023. Interest in animal behavior has not diminished (Snowdon, 2007; McCallen et al., 2019), and the study of behavior is regarded as one of the most dynamic and exciting areas in all of biology (Kappeler, 2010; Strassmann, 2013; Breed, 2017). Ethology is not dead or on the brink of extinction, as some have suggested (Alcock, 2003; Giraldeau, 2003; Greenberg, 2012), but 50 years after its founders were awarded the Nobel Prize, the discipline seems to have lost a lot of steam. At the time of writing, not a single paper commemorating the Nobel Prize award has been published in any of the major behavior journals. This contrasts with the flurry of papers and book chapters published to celebrate the 50th anniversary of Tinbergen's famous "four whys" paper. Although "ethology" was the term of choice for referring to the biological study of animal behavior in the 1960s and 1970s, today many researchers eschew it and instead use other terms, such as "animal behavior", "behavioral ecology", or "behavioral biology" (Taborsky, 2006a; Hogan and Bolhuis, 2009; Bateson, 2012; Drickamer, 2019; Bueno-Guerra, 2021; Bolhuis et al., 2022; Kappeler, 2022). None of the major animal behavior textbooks published in the last two decades include the term "ethology" in their titles, and some make only a passing reference to ethology, often just for the sake of historical completeness (e.g., Rubenstein and Alcock, 2019; Nordell and Valone, 2021). Students and researchers working on animal behavior are more likely to identify themselves as "evolutionary biologists" than as ethologists (Taborsky, 2006a). Even Tinbergen is more often characterized as a "biologist and ornithologist" than as an ethologist, as a quick internet search reveals. When representatives of several European ethological societies convened in 2001 to launch a series of international conferences, they decided to name them the "European Conferences on Behavioural Biology" rather than refer to ethology (Thierry, 2007). Starting in 2011, the biennial International Ethological Conferences, established in 1952, were renamed "Behaviour", followed by the year in which the conference was held.

Ethology: the old and the new

What has happened in the 50 years since the founders of ethology were awarded the Nobel Prize? Is ethology dead or senescent? Is it an outdated science? A thing of the past? It has been argued that skepticism about the current status of ethology has more to do with the discipline's name rather than with its scientific credentials (Taborsky, 2006a). Some researchers may feel uncomfortable with the label ethology, which they associate with classical or Lorenzian ethology (Taborsky, 2019). In 1999, Peter Slater, a well-known ethologist, changed the title of his introductory textbook from "An Introduction to Ethology" to "Essentials of Animal Behaviour". The author justified the change as follows:

"… the word "ethology" to describe animal behaviour, and "ethologist" for someone who studies it, while admirably concise, have rather fallen from use. Unfortunately they have tended to be tied in people's minds to the particular school of study and theories that emanated from Europe in the middle years of this century. Many of these theories have not been supported by later work, and the word ethology has tended to sink with them." (Slater, 1999, p. ix).

Although some are still useful in amended form (e.g., Burghardt and Bowers, 2017; Bueno-Guerra and Amici, 2018; Burghardt and Burkhardt, 2018), many of the core theoretical concepts of classical ethology, such as instinct theory, fixed action patterns, innate releasing mechanisms, action-specific energy, appetitive and consummatory behavior, and functional circles have been superseded by newer conceptual frameworks. What we might call ethology today is very different from the work conducted in the first half of the 20th century during the heyday of classical ethology. In fact, during the 1980s, ethology had already lost most of its original meaning, and its identity was closer to the aims and scope outlined by Tinbergen in his programmatic 1963 paper (see below) than to classical ethology (Barlow, 1989). Sociobiology, the selfish gene, game theory, kin selection, memes, the cognitive revolution, evolutionary psychology, mathematical models, phylogenetic comparative methods, epigenetics, neuroscience, and omics, among others, have transformed and enriched contemporary ethology. But this only shows that, rather than becoming stagnant, the discipline has matured and moved forward as more refined theories, empirical data, and novel methodologies have become available. Much of the work currently being done by geneticists and neurobiologists would probably be unrecognizable to their mid-20th-century predecessors. Yet apparently neither geneticists nor neurobiologists feel compelled to find alternative names for their disciplines. On the other hand, even those who shed doubts on the currency of ethology admit to the existence of a "modern ethology", different from classical ethology, that is practiced by "modern ethologists" (Barnett, 1981; Slater, 1999; Martin and Bateson, 2007; Bateson and Martin, 2021).

So ethology may be dead, but only if one thinks of ethology as classical ethology as practiced in the 1930s and 1940s (Barlow, 1989). If judged by the work of contemporary ethologists, ethology is alive and thriving (Klopfer and Polemics, 2002; Burkhardt, 2005; Ord et al., 2005; Bekoff, 2015; Stuhrmann, 2022). Thus, its apparent demise is only word deep and misrepresents the modern field of animal behavior and its ethological legacy. The transformation in some areas has been so profound that one might think that the animal behavior studies currently being conducted have no relation to the ethology of Lorenz and Tinbergen, but, in reality, this is not the case. There is a clear continuity between the work of the early ethologists and that of modern ethologists (e.g., Burkhardt, 2005; Bolduc, 2012). The focus on the behavior of intact animals in their natural environment, the breadth of topics and approaches, and the integration of studies on ultimate and proximate causes of behavior are key elements of that continuity.

Early opposition to ethology and the current reluctance to use the term may also be related to Lorenz's connections with the Third Reich prior to and during World War II, definitely a dark cloud over the history of ethology (Dewsbury, 2003; Strassmann, 2013). Ethologists who knew Lorenz and historians are unclear about the extent of his commitment with the Nazi doctrine (Richards, 1987; Klopfer, 1994; Burkhardt, 2005). After the war, Lorenz emphatically denied having any Nazi sympathies. He apologized in an autobiographical statement prepared for the Nobel Prize ceremony and justified his authoring of papers supportive of Nazi ideology as a naive and irresponsible attempt to secure research funding and facilities in difficult times (Klopfer, 1994; Dewsbury, 2003). Regardless, it would be unfair to use Lorenz's wrongdoings to portray ethology as Nazi antiscience. It should also be noted that the other two Nobel Prize recipients were targeted by the Gestapo, and that Tinbergen spent 2 years in a German prison camp for Dutch intellectuals (Kruuk, 2003).

A permanent identity crisis

The question of disciplinary identity has been a constant in the history of ethology (Burkhardt, 2022; Stuhrmann, 2022). In their efforts to carve out a niche for themselves in the behavioral sciences, ethologists have had noisy territorial disputes with practitioners from other disciplines. At first, ethology's main rival was comparative psychology (Dewsbury, 1989; Barlow, 1991; Dewsbury, 1992; Font et al., 1998; Burghardt and Drickamer, 2022). More recently, however, the conflicts have come from within ethology itself, which has seen its disciplinary integrity threatened by the rise of behavioral ecology, the most fractious and prolific of all ethological subdisciplines (Barlow, 1989; Griffiths, 2008b; Stuhrmann, 2022). The proliferation of subdisciplines and the establishment of bridgeheads with other disciplines are important hallmarks of contemporary ethology (Hinde, 1982; Hinde, 1985). Neuroethology, cognitive ethology, comparative cognition, human ethology, applied ethology, conservation behavior, animal welfare, and comparative evolutionary psychology are but a few of the growing catalog of ethological subdisciplines. However, the emergence of new subdisciplines is not always characterized by the cordiality and mutual tolerance of their practitioners.

The irresistible allure of functional studies

Although the history of the ascent of functional studies in ethology has been told many times, it is worth repeating it here (for more detailed accounts see Segerstråle, 2000; Alcock, 2001; Parker, 2006; Griffiths, 2008a; Birkhead and Monaghan, 2010; Drickamer, 2014; Simmons, 2014; Brown and Choe, 2019; Grodwohl, 2019; Taborsky, 2019; and Stuhrmann, 2022). In 1963, a full decade before the Nobel Prize, Tinbergen published, on the occasion of Lorenz's 60th birthday, an influential paper entitled "On aims and methods of ethology". In this paper, known to many ethologists as the "four whys" paper, Tinbergen outlined the four central aims, problems, or questions of ethology (i.e., the "four whys"), and stressed the need to devote equal attention to all of them and to their integration. He also lamented that ethologists had by and large neglected one of the four aims, namely that having to do with the function or adaptive value of behavior. Tinbergen's lament did not go unheeded and during the ensuing decades, research on the adaptive value of behavior grew explosively to the point of completely dominating the agenda of animal behavior research. This new field of study, essentially a recasting of Tinbergen's functional question with contributions from ecology, evolutionary biology, and economics (Krebs and Davies, 1993; Birkhead and Monaghan, 2010), came to be known as sociobiology in the United States and behavioral ecology in the United Kingdom, although the term that has prevailed worldwide is behavioral ecology (Parker, 2006; Birkhead and Monaghan, 2010; Stuhrmann, 2022).

The early reception of behavioral ecology was surrounded by controversy. In the United States, Edward O. Wilson's book "Sociobiology: The New Synthesis" (Wilson, 1975) ignited, primarily due to Wilson's extensions to human behavior, the sociobiology debate, the ramifications of which are felt to this day. Interestingly, researchers in Europe did not see political intent in Wilson's "Sociobiology" or in Richard Dawkins' "The Selfish Gene" (Dawkins, 1976), and the sociobiology debate reached this side of the pond in a much subdued form (Segerstråle, 2000). In the 1970s, relatively unmolested by the noise coming from across the Atlantic, some of Tinbergen's own students and disciples in Oxford were already concocting their own new brand of ethology centered on behavioral function, which they named, in part to distance themselves from the havoc generated by sociobiology, behavioral ecology (Segerstråle, 2000; Birkhead and Monaghan, 2010; Stuhrmann, 2022). Although behavioral ecology had a lot in common with sociobiology, it avoided the exclusive focus on social behavior of the latter. Naming the field behavioral ecology had an unexpected consequence for researchers in non-English-speaking countries. To translate behavioral ecology into French, Spanish, Italian, and other romance languages, the order of the two words has to be inverted (e.g., *écologie comportementale*), which puts the

spotlight on "ecology", not on behavior. As a result, in some universities, the teaching of behavioral ecology was automatically assigned to ecologists with little familiarity with animal behavior. Ecology is critically important to understand the adaptive significance of behavior (Gordon, 2011), but the focus of ethology and behavioral ecology should be the behavior of animals, not their ecology, a point that is often forgotten.

The rise of behavioral ecology was accompanied by a good dose of chauvinism and sporadic separatist attempts by its practitioners, who were generally more interested in differences than in similarities with the work of their predecessors. Wilson (1975) predicted that, by the year 2000, ethology and comparative psychology would be phagocytized by behavioral ecology, a prediction that did not sit well with many ethologists. In 1985, a group of researchers attending the 19th International Ethological Conference in Toulouse lobbied to establish a series of international conferences "dedicated solely to the field of behavioural ecology" that would run every other year, alternating with the International Ethological Conferences. At the first such conference, held in 1986 in Albany, NY, USA, the International Society for Behavioral Ecology (ISBE) was launched (Brown and Choe, 2019).

During the 1980s and 1990s many students on both sides of the Atlantic were attracted to behavioral ecology and became known as behavioral ecologists (Griffiths, 2008b). As Marian Stamp Dawkins explains, students found it much more attractive (and modern) to be a behavioral ecologist applying mathematical models to make testable, quantitative predictions about what animals should do in particular circumstances to maximize their fitness benefits "than an old-fashioned ethologist glumly concluding that the control of behaviour might be highly species-specific and much more complex than it seemed at first" (Dawkins, 2006, p. 350).

In their zeal to promote behavioral ecology, some of its practitioners even declared that studies of adaptive value were more important and deserved more attention than studies of Tinbergen's remaining three aims, that is, of behavioral mechanisms, development, and evolution. In response to this, by the end of the 1980s, many ethologists were complaining that behavioral ecology's parochial approach and narrow focus on the question of function would be detrimental to progress in the field (Bateson and Klopfer, 1989; Dawkins, 1989). In a celebrated metaphor, Marian Stamp Dawkins compared progress in ethology to locomotion in a four-legged animal, with each leg representing one of Tinbergen's aims. By the end of the 1980s ethology had become, in the words of Patrick Colgan, "a one-legged monstrosity" (Colgan, 1990, p. 148).

The imbalance was eventually redressed, at least in part, albeit in a most peculiar way. Behavioral ecologists insisted on the preeminence of functional questions but conceded that knowledge about mechanisms could be useful for the study of function, in order to identify capabilities, costs and constraints, and to allow for more realistic model building (Krebs and Davies, 1997; Birkhead and Monaghan, 2010). Others argued that, in addition to mechanisms, evolution and development should also be considered, but again, only as props for a better understanding of behavioral function (Autumn et al., 2002; West et al., 2003; Cuthill, 2005). Ethologists have long recognized that Tinbergen's four questions are not watertight compartments and that answers to one question can provide insight into the others (e.g., Davies, 1991; Bateson, 2003; Ryan, 2005; Sherry, 2005; Bolhuis, 2009; Ryan and Wilczynski, 2011; Bateson, 2012; Bateson and Laland, 2013; Leca, 2023). Tinbergen often referred to the "interfertility" among the different questions and stressed the need to pursue them in a balanced, comprehensive and integrated fashion (Burkhardt, 2014; Beer, 2020). However, ethology's motto that a true understanding will only come from the cultivation of Tinbergen's four questions, chiseled into the stone and the foundation of our discipline, seems to have been lost on some behavioral ecologists who insist on the superiority of functional questions. A relatively recent behavioral ecology textbook states the following:

"… the great conceptual advance has been the move beyond Tinbergen (1963) four questions. In fact, these four levels of analysis are not on the same footing and it is pointless describing them as alternative approaches. The study of proximate causes cannot in itself suffice to claim any true understanding of kin behaviour." (Cézilly, 2008, p. 25)

Most, if not all, ethologists would agree that the study of proximate causes (mechanisms and development) is insufficient for a true understanding of behavior. However, by the same token, the study of ultimate causes (evolution and function) can, by itself, never suffice for a complete understanding of animal behavior. As Marian Stamp Dawkins (1989) eloquently put it, progress is impossible if ethology rests on only one of its four legs, no matter how hypertrophied the leg. Rather than being alternative, mutually exclusive options to choose from, the four questions address different, equally important, and complementary aspects of animal behavior: answers to any one question cannot be regarded as answers to a different question (Bateson and Laland, 2013; Dawkins, 2014).

History matters

Current opinions on the relationship between ethology and behavioral ecology are divided into two camps. For some, behavioral ecology is a thriving and dynamic ethological subdiscipline that, together with other subdisciplines (e.g., neuroethology, cognitive ethology, applied ethology, etc.) and yet-unnamed areas of ethological enquiry (e.g., the study of the development and evolution of behavior), is part and parcel of modern ethology. According to this view, behavioral ecology is a branch of ethology, which remains the most broadly based approach to the study of behavior (e.g., Dawkins, 1989; Klopfer, 1999; Parker, 2006; Taborsky, 2006b; Taborsky, 2019; Stuhrmann, 2022). Others, however, think that ethology became obsolete shortly after the Nobel Prize award to Lorenz, Tinbergen, and von Frisch, and that its central position in the study of behavior is now occupied by a new discipline known as behavioral ecology (Pulliam, 1979; Giraldeau, 2003; Cuthill, 2005; Greenberg, 2012).

In 1981, Lorenz complained that the field was in danger of losing its identity due to younger ethologists' disregard for the work of their predecessors. He compared ethology to a growing coral colony, noting that younger ethologists were similar to branches

"losing contact with their foundation" and "producing quite a lot of rubble" (Lorenz, 1981, p. xi). Students are often uninterested in the history of their disciplines, but history matters, especially in the field of animal behavior studies (Burkhardt, 2005; Bolduc, 2012; Burghardt, 2012; Stuhrmann, 2022). As Burghardt (2020) rightly points out, "we lose important perspectives if we ignore our predecessors" (p. 241).

Historical analyses reveal a complex picture of the intertwined histories of ethology, sociobiology, behavioral ecology, and, more recently, evolutionary psychology (Griffiths, 2008b; Levallois, 2017; Stuhrmann, 2022). Touting behavioral ecology as a new discipline that has supplanted ethology is misleading and misrepresents both ethology and behavioral ecology. The ethological roots of behavioral ecology are undisputed: behavioral ecology emerged as an offshoot of the ethological tradition (Burkhardt, 2005; Birkhead and Monaghan, 2010; Bolduc, 2012). If, as most behavioral ecologists acknowledge, behavioral ecology focuses on Tinbergen's functional question (Krebs and Davies, 1993; Parker, 2006; Milinski, 2014), or on the ultimate causes of behavior (i.e., function and evolution; Simmons, 2014), then there are no grounds for claiming that behavioral ecology has replaced ethology, as the latter has a much broader scope that includes, among others, the field of study of behavioral ecology. The important differences that undoubtedly exist between the way in which early ethologists studied the problem of function and current behavioral ecology are a reflection of the tremendous progress that has occurred in the discipline, especially in the past 50 years (Gross, 1994; Owens, 2006; Birkhead and Monaghan, 2010; Milinski, 2014; Simmons, 2014). Most of the crucial elements that some find lacking in the early ethologists' approach to the study of behavioral adaptations, such as inclusive fitness, the gene's-eye view of evolution, reciprocal altruism, game theory, and optimization models, were unavailable prior to 1960, a point that is often missed by ethology's critics. The relationship between ethology and behavioral ecology is thus one of descent with modification, not demolition. As Aubrey Manning (2009) put it, "the growth of modern behavioural ecology is a most natural extension of classical ethology" (pp. xii-xiii) and one must wonder, as noted by Dewsbury (2007), if behavioral ecology could have been developed in the absence of classical ethology.

A reaffirmation of ethology

Recently, advocates of the idea that a defunct ethology has been replaced by behavioral ecology have pushed a biased narrative of ethology's history and disciplinary identity. At a recent behavioral ecology meeting, a plenary lecturer matter-of-factly announced that the difference between ethology and behavioral ecology is simply that, whereas the former occupied itself only with matters of mechanisms and development, the latter is devoted to the study of the adaptive value (i.e., fitness consequences in an ecological context) and the evolution of behavior. None of the approximately 300 delegates attending the lecture appeared to object to this assertion. However, this distinction, which unfortunately has found its way to some recent textbooks (e.g., Danchin et al., 2008; Nordell and Valone, 2021), is a clear and unwarranted misrepresentation of the work of ethologists.

In the four aims paper, Tinbergen was as much laying out a research program for a balanced ethology as he was reviewing the work conducted by ethologists prior to 1963. The four questions that he outlined were, and continue to be, part of the goals and scope of ethology, and not of behavioral ecology or some other discipline. Although the emphasis placed on particular questions has seen ups and downs, the early ethologists were certainly interested in the function and evolution of behavior. Two of Lorenz's most celebrated contributions were the promotion of systematic comparative studies of behavior and the recognition that behavior patterns could be used to reconstruct phylogenies. And Tinbergen particularly excelled in the experimental study of stimuli-eliciting behavior and in the study of behavioral function, which he reviewed, together with studies conducted by his students and other researchers, in his 1963 paper. His study on the adaptive significance of eggshell removal by black-headed gulls (Tinbergen et al., 1962) is behavioral ecology at its best.

So, to set the record straight, ethology is concerned with all of the four questions or aims described by Tinbergen. The four aims are considered a defining feature of the discipline, lending coherence to a highly diverse and integrative field of scientific inquiry. In fact, it has been argued that ethology's main contribution to the study of animal behavior was not a theory but "a collection of attitudes, insights, practices, and goals that continued to provide a sense of shape to the field while permitting it at the same time to have considerable flexibility and adaptability" (Burkhardt, 2005, p. 16). Paramount among ethology's goals is the cultivation of the four aims and of their integration (Dawkins, 1989; Huntingford, 2003; Taborsky, 2006a; Bateson and Laland, 2013; Taborsky, 2019; Bolhuis et al., 2022).

Few researchers have the capacity or the ability to address all four whys relating to a particular behavior. Often researchers concentrate on one or two of the four aims, depending on opportunity, tradition, or personal taste. This leads to specialization, as in the case of behavioral ecologists' focus on ultimate questions. However, as Tinbergen warned, "if we do not continue to give thought to the problem of our overall aims, our field will be in danger of splitting up into seemingly unrelated sub-sciences" (1963, p. 410).

My contention is that there is no difference between the work of a behavioral ecologist and that of a contemporary ethologist interested in answering functional questions about behavior. The work of behavioral ecologists is, in essence, still ethology. As Aubrey Manning put it, "we are all ethologists now" Manning (2009), p. xii). The program of the behavioral ecology conference that I alluded to earlier is indistinguishable from the program of similar meetings that cater to a more ethologically inclined audience. Paradoxically, some of the presentations that attracted more attention at that particular meeting were on cognition, not on behavioral function.

But ethologists and at least some behavioral ecologists resist restricting themselves to asking only functional questions. Since the 1980s there have been numerous appeals to integrate the study of mechanisms with the study of function (e.g., Stamps, 1991; Krebs and Davies, 1997; McNamara and Houston, 2009; Bateson and Laland, 2013; Monaghan, 2014). More recently, it has been argued that behavioral ecology should also embrace, in addition to function, evolution, and mechanisms, the study of development

(West et al., 2003), and even animal cognition (Rowe and Healy, 2014; Budaev et al., 2019). Thus, according to some behavioral ecologists, behavioral ecology aspires to provide an integrative framework for the study of behavior, answering both proximate and ultimate questions. But, wait a minute! There already exists such a field, and this of course, is ethology. Perhaps behavioral ecologists are condemned to rediscover ethology and Tinbergen's four questions (Davies, 1991).

Final remarks: what's in a name?

Behavioral ecology? Ethology? Integrative animal behavior? Behavioral biology? We should not become obsessed with names. After all, the aim is clear: we all want to understand animal behavior. Researchers study animal behavior for different reasons and with different goals. They are, of course, free to call their discipline whatever they like, but it would be unfortunate if, along with a new denomination, came a rewriting of the history of our field. To paraphrase the words Bennett Galef (1987) used to describe the status of comparative psychology, neither revisionist histories of nor epitaphs for ethology are needed.

Insofar as researchers continue to be interested in Tinbergen's four aims, ethology has not become obsolete and remains a coherent endeavor, although its disciplinary boundaries are, as they have always been, "porous and permeable" (Grafe and Stuhrmann, 2022, p. 20). As a recently appointed editor of the Adaptation and Evolution section of this new journal, *Frontiers in Ethology*, I am eager to see studies of behavioral function take their proper place next to studies of the mechanisms, development, and evolution of behavior. And as a student of the history of our discipline, I see no reason why we should not call this engaging and fascinating endeavor —the pursuit of Tinbergen's four aims and their integration across levels of biological organization, taxa, methodologies, and interdisciplinary boundaries—what it was already called 50 years ago: ethology.

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