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Tribute to Tinbergen: Putting Niko Tinbergen's 'Four Questions' in Historical Context

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(Invited Review)

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Abstract

Niko Tinbergen's (Zeit. Tier. 20, 1963, 410) paper 'On aims and methods of ethology' is appropriately remembered as the paper in which Tinbergen characterized ethology as 'the biological study of behavior' and went on to explain that to study behavior biologically is to ask four distinct questions about it: (1) How is it caused physiologically? (2) What is its survival value? (3) How has it evolved? and (4) How does it develop in the individual? Here, we consider Tinbergen's paper in its historical context by looking at it from three different perspectives: (1) a comparison of Tinbergen's formulation of 'ethology's four questions' with similar, but different formulations of biology's basic problems offered by Julian Huxley, Konrad Lorenz, and Ernst Mayr; (2) a survey of the roles that the four questions played in Tinbergen's own work over the course of his career; and (3) a consideration of the two explicit goals of Tinbergen's (Zeit. Tier., 20, 1963, 410) paper, namely (a.) to honor Tinbergen's friend and colleague Konrad Lorenz (as part of a Festschrift for Lorenz on the occasion of his sixtieth birthday) and (b.) to provide a sketch of ethology's scope and an evaluation of the ways the field needed to develop in the future. We suggest that just as the work of Tinbergen's Oxford research team revealed how the behavior of gulls reflected compromises worked out in the face of the diverse selective pressures of particular environments, we can identify certain conflicts that arose for Tinbergen in trying to write something that his friend Lorenz would like while also assessing ethology's current state and future prospects. That said, however, Tinbergen's enduring concern was to do all he could to ensure that ethology thrive as a field and develop a scientific understanding of animal (and human) behavior. For this to happen, he insisted, the four questions of ethology needed to be pursued in a balanced, comprehensive, and integrated fashion.

Introduction

In October 1962, Niko Tinbergen wrote to the German zoologist Otto Koehler to propose that a *Festschrift* be organized to honor Konrad Lorenz on the occasion of Lorenz's sixtieth birthday. Tinbergen had not yet decided what the subject of his own contribution should be, but by February 1963, he was able to tell Koehler that he had made up his mind: 'I want to write something for Konrad that he likes a lot. I am now writing some thoughts down about (don't panic) 'What is ethology?'' (Burkhardt 2005, p. 426.)

Over the course of the next 5 wk, Tinbergen completed his paper, which he entitled 'On aims and methods of ethology' and sent it off to the *Zeitschrift für Tierpsychologie*, where it was received on March 16, 1963. It was published later the same year in the *ZfT*'s October issue (the first of five straight issues devoted to papers dedicated to Lorenz). For the half century since, Tinbergen's paper has stood out as one of the

classic papers of the field. It is routinely cited whenever an ethologist wants to identify what ethology is all about. What has stuck in the discipline's collective memory is that it was here that Tinbergen characterized ethology as 'the biological study of behavior' and then went on to explain that to study behavior biologically is to ask four distinct questions about it: (1) How is it caused physiologically? (2) What is its survival value? (3) How has it evolved? And 4.) How does it develop in the individual (i.e., what is its ontogeny)?

Today, these four questions are commonly referred to as 'ethology's four whys' – or even as 'Tinbergen's four whys.' At least to some extent, they have also taken on a certain air of timelessness as their original historical context has correspondingly faded from view. The aim of this paper is to recall certain features of that original context. To aid in this enterprise – and to complement and mirror Tinbergen's insistence on the necessity of asking different kinds of questions in ethology – we will borrow three of the tropes of ethology – comparative behavior study, ontogeny, and function – to see what heuristic value they might have when applied to the historical project of making sense of Tinbergen's paper in its own day. (At the same time, we urge readers of the present paper to go back to read Tinbergen's original paper, for this paper does not pretend to offer a thorough review of all that is to be found there.)

Comparative Behavior Study

'Comparative behavior study' – vergleichende Verhaltensforschung – was the phrase Konrad Lorenz preferred to use in identifying his approach and his field. He maintained that one could use instinctive behavior patterns (just as one could use morphological structures) in the zoologist's task of reconstructing phylogenies. In our effort to put Niko Tinbergen's 'four questions' paper into historical context, we too will use comparisons. We will set Tinbergen's formulation of ethology's four questions side by side with three similar but different formulations of biology's basic questions offered, respectively, by Julian Huxley, Konrad Lorenz, and Ernst Mayr. These biologists were all contemporaries of Tinbergen (and friends of Tinbergen as well). Our purpose is not to offer a judgment about intellectual homologies or convergences but instead to underscore two simple yet important historical points: (1) Tinbergen's formulation of the basic questions of biology was not the only such offering in his day; and (2) in each of the cases under consideration, the act of identifying biology's basic questions amounted to more than simply a logical partitioning of biology's domain. In each instance, the identification of biology's basic questions served the function of supporting a particular vision of how the study of biology (or animal behavior) needed restructuring or readjusting.

Julian Huxley

When Tinbergen presented his 1963 formulation of the major problems of biology, he took Julian Huxley as his point of departure. Huxley, Tinbergen allowed, liked to speak of three basic kinds of biological questions, namely, those of causation, survival value, and evolution. Tinbergen cited offered no reference here, but he could have had in mind Huxley's *Evolution: the Modern Synthesis,* where Huxley identified 'the three aspects of biological fact' and allowed: 'every biological fact can be considered under three rather distinct aspects. First, there is the mechanistic-physiological aspect, how is the organ constructed, how does the process take place? Secondly, there is the adaptive-functional aspect: what is the functional use of the organ or process, what is its biological meaning or value to the organism or the species? And in the third place, there is the historical aspect: what is the temporal history of the organ or process, what has been its evolutionary course?' (Huxley 1942, p. 40.) Significantly, Huxley did not offer this as a simple taxonomy of what biologists do. He offered it instead in the context of claiming that to understand evolution, one needed to employ more than a single biological approach. While paleontology, for example, could speak to the course of evolution, it could not speak to its mechanisms. To illuminate evolution's mechanisms, its biological meaning, and its historical course, Huxley called for a synthesis that brought together data from a host of different branches of biology. (Behavioral biologists of the present who study the role of behavior in evolution may be interested to note that Huxley, notwithstanding his own pioneering studies of behavior, did not try to incorporate animal behavior studies in the synthesis.)

Konrad Lorenz

Konrad Lorenz provides us another example of a biologist who set forth a set of biological questions in the service or transforming a field. Late in 1936, the young Austrian zoologist arranged to give a special lecture to an audience including members of the newly founded German Society for Animal Psychology (*Deutsche Gesellschaft für Tierpsychologie*). Keen to

have an influence on the development of this new scientific society, Lorenz chose as his topic the importance of asking biological questions in animal psychology. He began his lecture with the observation that while biology, like physics and chemistry, necessarily had the question of causation as part of its purview, it also involved three *additional* sorts of questions that were special to it – and essential to the understanding of animal behavior. These three additional questions, which could and should be asked of any behavior pattern, were: (1) What is its purpose or survival value? (2) How does it relate to the whole pattern, or *Gestalt*, of the animal's natural activities? (3) How has the behavior evolved? (Lorenz 1937).

The question of relating smaller parts to a larger whole, which Lorenz discussed under the heading '*biologische Ganzheitzbetrachtung*,' represented an attempt on his part to find common cause with the German *Gestalt* psychologists who had taken an interest in animal behavior. He may have especially hoped that his comments would find favor with the zoologist Otto Koehler, a leading figure in the new society for animal psychology who had written at some length on the topic of *Ganzheitsbiologie* (Koehler 1932). Nonetheless, what Lorenz wanted to promote most of all to the animal psychologists was 'the comparative evolutionary viewpoint.' This, he believed, was where animal psychology was most deficient – and also where he was an authority. In January 1937, as he prepared a major address on this subject that he would give at the German Society for Animal Psychology's first annual meeting, he told his mentor Oskar Heinroth, 'our way of formulating problems *could* seize command of the new society, if we did it skillfully' (Burkhardt 2005, p. 186). As it was, Lorenz was already well on his way to assuming a commanding position in the new society. When the first issue of the society's new journal, the *Zeitschrift für Tierpsychologie*, appeared in 1937, Lorenz's article on biological questions was in it and his name was on the masthead as one of the journal's three co-editors.

Ernst Mayr

The evolutionary biologist Ernst Mayr affords another example of a Tinbergen contemporary who offered an important categorization of biology's basic questions. In 1961, in his paper 'Cause and Effect in Biology,' Mayr stressed the importance of distinguishing between proximate causes (the domain of the functional biologist) and ultimate causes (the domain of the evolutionary biologist). Functional biologists, he explained, are interested with structural elements and functions. Like physicists and chemists, their chief technique is the experiment. They are always asking the question 'How?' In contrast, evolutionary biologists ask the question 'Why?' This, Mayr elaborated, could either refer to the historical question – 'How come?' – or to the more 'finalistic' question – 'What for?' (Mayr 1961).

Mayr did not claim to have originated the distinction, but he felt he was expressing the distinction more clearly and forcefully than anyone had carried out before him (for earlier discussions, see Baker 1938; Lack 1954). As the philosopher of biology John Beatty has indicated, Mayr's discussion of biological causation helped establish the subfield of the philosophy of biology. For our purposes, however, what is most instructive are Beatty's observations on how intimately Mayr's interest in the proximate/ultimate distinction was tied to Mayr's experience as an evolutionary theorist faced with the rapid expansion of molecular biology. By Beatty's account, 'Mayr returned to the proximate/ultimate distinction to defend the importance of systematics and evolutionary biology at a time when molecular biology was casting an ever greater shadow over the natural historical sciences' (Beatty 1994, p. 347).

Niko Tinbergen

Tinbergen's enumeration of the four questions of ethology resembles Huxley's three questions of biology, Lorenz's slightly different enumeration of biology's questions, and Mayr's distinction between proximate and ultimate causes, not just because it overlapped with them in content, but also because it had a similar function. Each author was motivated by a desire to redress a contemporary imbalance. Huxley argued that no single biological field held the key to understanding evolution. Lorenz sought to reshape animal psychology by adding to it the evolutionary perspectives that it lacked. Mayr sought to maintain intellectual and material support for evolutionary biology in the face of the powerful juggernaut that was molecular biology. Tinbergen, for his part, felt, as we shall see, that ethology in the early 1960s was much too asymmetrical, with studies of causation greatly outweighing other questions, in particular the question of biological function.

Tinbergen's Ontogeny

Tinbergen's development as a scientist has been treated at length elsewhere (see for example Tinbergen

1985; Hinde 1990; Roëll 2002; Kruuk 2003; Burkhardt 2005). Here, we offer a summary sketch of the chronology of Tinbergen's career considered with an eye to the topics of physiological causation, evolution, survival value, and development – and to his strong commitment to biological field studies.

Tinbergen chose to become a professional biologist only after he was persuaded that it was possible to pursue a biological career in which fieldwork played a central part. From the beginning, his attraction to biology was part and parcel of his abiding love for being out in nature watching, photographing, and matching wits with wildlife, a love he developed early on as a member of the Dutch Youth Association for Nature Study (the Nederlandse Jeugdbond voor Natuurstudie). This disposition survived his undergraduate years at Leiden, where he disliked most of his formal instruction but relished the hours he was able to spend outdoors on his own watching the behavior of colonies of gulls. Later, when it came time to write his doctoral dissertation, he successfully lobbied to have his research be a field study – on the homing behavior of the bee wolf, *Philanthus triangulum*. Subsequently, as a junior faculty member in the University of Leiden's zoology department, he was able to include field studies as well as laboratory studies in his teaching and research.

When Tinbergen and Konrad Lorenz first met at a conference on instinct, held in Leiden in November 1936, Lorenz had just turned thirty-three years old and Tinbergen was twenty-nine. Lorenz was especially excited by Tinbergen's reports of his laboratory work. From Lorenz's perspective, the 'dummy' experiments that Tinbergen and his student Joost ter Pelkwijk had conducted on the sign stimuli triggering instinctive reactions in the three-spined stickleback were just what Lorenz's new science of animal behavior needed. Tinbergen for his part was struck by Lorenz's gifts as a theory-builder. This apparent division of talents between Lorenz the theorist and Tinbergen the experimenter was displayed in the famous study the two zoologists conducted the following year on the egg-rolling behavior of the gray-lag goose (Lorenz & Tinbergen 1938), where Lorenz provided the theoretical structure and Tinbergen provided the experimental setup. One must not be content with this theorist vs. experimenter schema, however, for it does not suffice to characterize the differences between the two men. Lorenz was indeed a highly creative theorist, and he provided the greater part of ethology's early conceptual foundations, but over time Tinbergen proved to be the more critical analytical thinker of the two. Furthermore, Tinbergen's practices as a field naturalist led him to insights that were unlikely to arise via Lorenz's practices as an animal raiser.

When they joined forces in the late 1930s, Tinbergen and Lorenz saw their major competitors in the study of animal behavior to be subjectivist animal psychologists like the Dutch scientist J. A. Bierens de Haan. In contrast to the subjectivists, Tinbergen and Lorenz saw themselves as developing a distinctively objectivist approach. Tinbergen in 1942 described this approach as 'applying physiological methods to the objects of animal Psychology' (Tinbergen 1942, p. 40). The causal analysis of the physiological mechanisms of behavior would continue to be the primary focus of Tinbergen's behavioral studies up into the early 1950s. When in 1951, he finally published *The Study of Instinct* (this, the first book to offer an overview of the whole field of ethology, was virtually complete in 1949 when Tinbergen left Leiden for Oxford), the physiological causation of behavior took center stage.

It bears mentioning that *The Study of Instinct* can leave a reader confused about exactly how many major problems of biology or ethology Tinbergen thought there were. At one point in the book, he explicitly identified 'three major problems' of biology, namely causation, adaptiveness, and evolution (Tinbergen 1951, p. 185). In the book's introduction, however, he mentioned *four* problems (the three identified previously, plus ontogeny), all of which he said had to be considered when asking 'why does the animal behave as it does?' (Tinbergen 1951; pp. 1–2). Elsewhere in the book, in discussing the adaptiveness of behavior, he introduced the distinction between 'ultimate' and 'proximate' causes, crediting this important distinction to [John R.] Baker, but botching the reference (he gave the wrong date for Baker's work and then failed to reference it in his bibliography) (Tinbergen 1951, p. 152; see Baker 1938). But even if the *Study of Instinct* left some doubt about how to characterize biology's major problems, Tinbergen left no doubt that the book's primary concern was the mechanics of behavior. He devoted four chapters to behavioral causation and only one chapter each to behavioral development, adaptiveness, and evolution. He expressed embarrassment about the unevenness of these last three chapters, but he allowed that his inclusion of 'these more or less neglected fields of our science' was a motivated by 'the hope that by doing so I could contribute toward a more harmonious development of ethology as a whole' (Tinbergen 1951, p. xiii).

After he moved to Oxford, and partly as the result of Lorenz's urgings, Tinbergen decided to take up comparative studies as a way of illuminating the

course of evolution. Previously, his species of choice had been the herring gull and the three-spined stickleback. He now set about comparing different gull species and different species of sticklebacks. The gull work in particular proved to be more than just a replication, with new species, of the studies Lorenz had performed previously with ducks. This was because Tinbergen's work had an ecological dimension that Lorenz's work had lacked. Especially instructive in this regard were the field researches on the kittiwake conducted by Tinbergen's student, Esther Cullen (Cullen 1957). Cullen showed how the kittiwake was distinguished from other gulls by a whole series of behavioral peculiarities, all of which were correlated with the kittiwake's cliff-nesting habit. Among these were specific releasers, special fighting movements, and distinctive features of nest construction. These findings led Tinbergen to think more and more about entire adaptive systems and the way that 'selection pressures must often be in competition with each other,' which in turn led to different sorts of 'compromises' (Tinbergen 1959, p. 326).

Thus, by the late 1950s, Tinbergen was devoting increasing attention to questions of survival value in addition to questions of evolution and causation. A nice example of his sense of how these questions relating to each other dates from 1958, when Huxley told Tinbergen about a potential source of new funding and Tinbergen responded by identifying some research projects that might prove eligible for it. With respect to the work that his research group had already performed on gulls, Tinbergen stated: 'We would like to continue these studies on as broad a basis as possible, that is: investigating more species, studying the total behavior pattern of each species, and giving equal attention to problems of causation, function, and evolution.' He continued: 'There is an obvious 'interfertility' between all these aspects: studies on motivation of postures helps in discovering their evolutionary origin; comparison between species throws light on ritualization; adaptations in one sphere of behavior may have repercussions on other behavior elements (see Cullen's paper on the Kittiwake which shows the many ramifying effects of cliff breeding), etc.' Tinbergen also mentioned some possible stickleback work to Huxley and then noted that he had another 'urgent' project in mind, a study of 'the ontogeny of behavior by raising birds in isolation, and by interchanging young of two species, preferably Kittiwake and Black-headed Gull.' (Tinbergen, 'Proposed project on the behavior of gulls,' manuscript dated June 1958, J. S. Huxley papers, Rice University. Cited in Burkhardt 2005, p. 422–423.)

Tinbergen's mention of a possible study of behavioral development is instructive. Neither he nor Lorenz had carried out much research on development, aside, that is, from Lorenz's work on imprinting. This apparent lacuna in their work was highlighted in 1953 by the American comparative psychologist, Daniel Lehrman, in his influential 'Critique of Konrad Lorenz's theory of instinctive behavior' (Lehrman 1953; see further Kruuk 2003; Griffiths 2004; Burkhardt 2005; Vicedo 2013). Lehrman complained, among other things, that Lorenz and Tinbergen had been much too uncritical in their assumptions about the *innate* character of various features of animal behavior and had ignored the complexities of development. Lehrman's critique left Lorenz fuming, but Tinbergen was more or less receptive to it, and he came to acknowledge that the ethologists' original assumptions about 'innate' behavior had been too simplistic. In the years that followed, his willingness to appreciate Lehrman's side of this argument caused a strain in Tinbergen's relations with Lorenz.

Tinbergen's rethinking of the question of development did not lead him, however, to make developmental studies a key part of his research program. This may have had something to do with an informal understanding between the Oxford and the Cambridge ethologists regarding how to divide up the field. But it was also due to the fact that Tinbergen's own interests lay elsewhere. While Lehrman and Lorenz continued to clash over the subject of behavioral development, Tinbergen by 1960 was happily engaged overseeing his own research group's experimental field studies of behavioral function, which for Tinbergen meant survival value. Especially appealing to him was his team's study of eggshell removal in the black-headed gull. Tinbergen's group demonstrated that what was safest for the parents was not necessarily safest for the chicks, and likewise what worked for the gulls in defense against one kind of predator did not necessarily work against other kinds of predators (Tinbergen et al. 1962; Tinbergen 1967).

In sum, when we track the development of Tinbergen's research with respect to 'the four questions of ethology,' we find that his emphases shifted over time. From the mid-1930s to the early 1950s, the physiological mechanisms of behavior occupied the greater part of his attention. Then, without giving up this interest in behavioral causation, he began to pay increasing attention to comparative studies and evolution, which led him in the late 1950s and 1960s to new successes with the experimental study of behavioral function. Though he thought hard about

behavioral development, especially after Lehrman's critique motivated him to do so, development never became a primary target of his research efforts.

The Functions of Tinbergen's 'On Aims and Methods of Ethology'

Just as animal structures or behavior patterns can have multiple functions, so too can scientific papers. Tinbergen's 'aims and methods of ethology' had two explicit functions. One was to honor his friend Konrad Lorenz on the occasion of Lorenz's sixtieth birthday. The other was to offer 'an evaluation of the present scope of our science.' The latter was necessary, Tinbergen indicated, because ethology was 'still very far from being a unified science, from having a clear conception of the aims of study, of the methods employed and of the relevance of the methods to the aims.' He considered it crucial for ethology's future development 'to continue our attempts to clarify our thinking, particularly about the nature of the questions we are trying to answer.' Otherwise, he feared, ethology would be 'in danger of splitting up into seemingly unrelated sub-sciences, or of becoming an isolated 'ism'.'

Tinbergen did a masterful job pursuing these two aims simultaneously. While his generosity of spirit in praising Lorenz was evident, so too was his deep concern for the future of the discipline that he had helped Lorenz found. But Tinbergen's task was not a simple one. His friendship with Lorenz had begun nearly twenty-seven years earlier. He knew as well as anyone that his friend Lorenz loved to be the center of attention but was not inclined to take criticism very well. Mirroring the way that Tinbergen found in his gull studies that different selective pressures could work at cross-purposes with each other and produce behavioral compromises, we can identify places in Tinbergen's paper where he pulled his punches and failed to dwell on the way that certain of Lorenz's ideas, after helping establish ethology in the first place, subsequently served to hinder further development. When Tinbergen asserted that he could 'honor Konrad Lorenz in no better way' than by engaging in a 'kind of 'soul-searching'' about ethology's current issues and needs, he did so recognizing that this would not necessarily amount to writing something 'that [Konrad] likes a lot.'

The essence of Tinbergen's tribute to Lorenz was to explain why Lorenz deserved to be called 'the father of modern Ethology.' The answer he provided was that Lorenz was the man who 'made us look at behavior through the eyes of biologists.' This, Tinbergen insisted – and not the great mass of novel facts that Lorenz had discovered – had been Lorenz's greatest contribution to the study of animal behavior.

With respect to the physiological causation of behavior, the case for identifying Lorenz as the founder of ethology was straightforward. As Tinbergen explained, Lorenz's treatment of instinctive behavior patterns as complex, mechanical phenomena had been path breaking. It had enabled ethology to escape (at least for the most part) from the pitfalls of subjectivism. Tinbergen acknowledged that Lorenz's psychohydraulic model of instincts had been oversimplified – as had his own sketch of the hierarchical organization of instincts. Nevertheless, he said, the analytical approach initiated by Lorenz continued to reap benefits, and the gap between ethology and neurophysiology was progressively narrowing.

As for the question of survival value, Tinbergen happily observed that Lorenz, in thinking of animal behavior patterns as organs, had always been interested not just in 'How does this work?' but also 'What is this good for?' A prime example of this, Tinbergen allowed, was Lorenz's concept of the 'releaser,' that is, 'an organ adapted to the function of sending out stimuli to which other individuals respond appropriately, that is, in such a way that survival is promoted' (Tinbergen 1963, p. 417). Tinbergen was also able to identify a particular way in which Lorenz's practice of observing hand-reared animals living freely under partly artificial conditions led to the identification of behavior patterns with special functions. When a behavior pattern conspicuously 'misfired' under circumstances that were clearly inappropriate for it, that inspired the investigator to ask what it was good for in its proper context. But that was Tinbergen's chief concern at this point anyway. His primary goal in this section of his paper was to argue that behavioral function could be studied in its proper context, that is, out in the field in the animals' natural surroundings. Devoting more pages of his paper to this topic than to any of the other three, he discussed lucidly and at length the possibilities, difficulties, and importance of conducting field studies on the 'underworked' problem of survival value. He stressed the importance of making long-term observations on a species, noting how such observations could lead to new 'hunches' about survival value that could be tested experimentally. (Needless to say, Tinbergen did not mention here that when Lorenz wrote about survival value, he tended to do so in a much more intuitive, uncritical fashion, talking about 'the good of the species' and never suggesting how the alleged function might be tested.)

When Tinbergen came to the question of the ontogeny of behavior, he once again hailed Lorenz's importance for 'insisting on a biological approach' (Tinbergen 1963, p. 426), but this time, he offered no specifics to support his general claim. He rehearsed instead the way that the ethologists, who had emphasized 'the unlearnt character of many aspects of animal behavior' had clashed with the animal psychologists, who had 'explored the ways in which various types of learning might account for behavior ontogeny' (423). Allowing that the debate between the two camps had been 'bedeviled by semantics,' he went on to examine what different sorts of experiments did or did not prove about the innateness of behavior, leading him to the conclusion that it was 'heuristically harmful' to use the word 'innate' in describing behavior characters. But that was as far as he cared to go with the subject. He wrote, 'If I were to elaborate this further I should have to cross swords with my friend Konrad Lorenz himself – both a pleasure and a serious tasks requiring the most thorough preparation' (p.425). The topic of the innateness of behavior already become a bone of contention between Tinbergen and Lorenz, and the end was not in sight (see Burkhardt 2005).

The last of the 'four whys' that Tinbergen addressed in his paper was the question of evolution. Tinbergen gladly acknowledged Lorenz's importance in this domain. There had been precursors in the field, Tinbergen said, but it was nonetheless Lorenz's own emphasis on 'the need for systematic comparative studies' that had initiated 'a concerted attack' on the subject of evolution (p. 427). However, having stated this part of the case, Tinbergen did not dwell on it further. He devoted most of this section of the paper to talking about the influence of selection on the course of evolution. He called attention to the work of Esther Cullen on the kittiwake (as he had performed earlier when discussing survival value), indicating how the species' behavioral traits were 'a pointer to past selection pressures' (p. 428). He diplomatically refrained from pointing out that such work, with its clear demonstration of the importance of ecological context in shaping the kittiwake's signaling behavior, showed Lorenz to have been wrong to insist that the evolution of releasers was virtually impervious to environmental influences and represented essentially an 'internal 'arrangement' within a bird species' (see Lorenz 1935, p. 382).

At the beginning of his paper, Tinbergen allowed of ethology's four questions that it was 'useful both to distinguish between them and to insist that a comprehensive, coherent science of ethology has to give equal attention to each of them and to their integration.' At the end of the paper, on the other hand, he acknowledged that the sketch he had just given of ethology had not been intended to be 'balanced or comprehensive,' rather, he had allowed himself 'to enlarge a little on special issues – on 'bees in my bonnet' – such as the relations between ethology and physiology; the need to spend more effort on studies of survival value and methods to be employed in such studies; problems and methods of behavior ontogeny; and the nature of argument used in the study of evolution.' He then reiterated his historical point that Lorenz's work had inspired ethology via 'his clear recognition that behavior is part and parcel of the adaptive equipment of animals,' along with all that that implied with respect to the questions of causation, survival value, ontogeny, and evolution (Tinbergen 1963, p. 430).

Tinbergen had accomplished what he had set out to do. He had honored his friend Lorenz and he had outlined all that ethology encompassed and where the field stood. At the end, though, there was something still gnawing at him, his sense that the field was unbalanced. In the very last lines of his paper, he observed that whatever one called his field, what mattered most was 'the growing awareness of the fundamental unity of the Biology of Behavior, and the realization that 'Ethology' is more than 'Physiology of Behavior', just as 'Biology' is more than 'Physiology'' (p. 431).

We may well ask, did Lorenz in fact like Tinbergen's paper, as Tinbergen had hoped in setting out to write it? Unfortunately, there is no documentary evidence to tell us whether Lorenz liked it or not. Any letters exchanged between the two men on this score appear not to have been preserved. There can be no doubt that Lorenz was comfortable being hailed as the father of ethology. However, he would not have been so comfortable with Tinbergen's fleeting allusions to the fact that certain of the ideas that had been integral to Lorenz's success in founding ethology had not stood up over time to careful scrutiny (e.g., Lorenz's thoughts on 'innate drives' or his psychohydraulic model of how instincts work).

What remains to be said is that Tinbergen could not have paid Lorenz any greater compliment than to say it was Lorenz who 'made us look at behavior through the eyes of biologists' – nor could Tinbergen have made a more self-effacing claim on his own part. Though Lorenz had insisted on the importance of posing biological questions in animal psychology, Tinbergen nonetheless felt – though he would not say this publically – that Lorenz had never quite grasped the

full import of defining ethology as 'the biological study of behavior' (Tinbergen, letters to the author, June 16, 1982 and June 19, 1982, Tinbergen Papers, Oxford). As it was, Tinbergen's 'four questions' paper set the argument out in a way that Lorenz had never carried out. Nearly, two decades later, looking back on his own career, Tinbergen allowed that if there was a contribution for which he himself was known, it was not any particular discovery but instead 'a method of approach, which could be briefly summarized by saying that I have applied to the phenomenon 'behavior' all the questions that are (or ought to be) asked in Biology with reference to other life processes' (Tinbergen, cited in Kruuk, p. 320).

In the 1960s, the work of Tinbergen's research group continued to be highlighted by field experiments on behavioral function. At the International Ornithological Congress held in Oxford in 1966, Tinbergen concluded his paper on the adaptive features of the black-headed gull with a plea for more fieldwork of this kind. 'Field craft,' he lamented, had 'atrophied alarmingly' and was 'in urgent need of redevelopment.' He complained, 'a biological science that gives all its energies to the analysis of causal mechanisms underlying life processes and neglects to study, with equal thoroughness, how these mechanisms allow the animals to maintain themselves, is a deplorably lop-sided Biology' (Tinbergen 1967, p. 57–58).

Tinbergen would repeat this charge in the introduction to the 1969 reprint of *The Study of Instinct*, observing, 'a disproportionally great effort is channeled into questions of causation of behavior,' when 'an equally intense effort ought to be made to understand the *effects* of behavior.' Seeking to explain 'this overemphasis on studies of causation,' he speculated it was related to the way that the knowledge of causes gives humans a power over nature. Unfortunately, he said, when such knowledge was not accompanied by a broader scientific understanding of the human situation, this led to changes in the environment for which humans were behaviorally ill equipped – and thus to behaviors that threatened 'the very existence of our species.' (Tinbergen 1969, pp.x-x.) This had been one of the themes of his inaugural address entitled 'war and peace in animals and man,' which he had given the previous year as the new Professor of Animal Behavior in the Department of Zoology at Oxford. In his lecture, he identified the four problems of ethology and insisted that what characterized ethology was 'the comprehensive, integrated attack on all four problems.' He allowed that when one ignored the questions of survival value and evolution, as 'most psychologists' did, this made it 'impossible to arrive at an understanding of behavioral problems' (Tinbergen 1968, p. 1412).

Not long afterward, the balance of attention given to the different questions of ethology began to shift dramatically. Tinbergen in the 1970s was happy to witness the growth of behavioral ecology, and the increased attention that was given to questions of behavioral function, even if he felt he could no longer fully keep up with the new theorizing in the area. At the same time, he remained committed to the idea that animal behavior studies needed a balanced, integrated, biological approach if they were to thrive (and be useful to society). When the present author wrote to Tinbergen in 1979, asking him if he would entertain an interview about the history of his field, he responded affirmatively, but he took me aback by referring to his science as 'that curious ragbag that is now called 'ethology'' (Burkhardt 2005, p. 5). At the time, I thought Tinbergen's remark was an instance of what others had referred to as Tinbergen's 'pathological modesty.' Later, I came to appreciate that there was much more to it than that, and that the achievement of a fully integrated, biological study of animal behavior, the ideal that Tinbergen had long urged upon his colleagues and his students, remained a goal for the future.

Looking back on Tinbergen's paper, 'on the aims and methods of ethology,' it is clear that Tinbergen was not just surveying a territory when he enunciated the four questions of ethology. Like Julian Huxley, Konrad Lorenz, and Ernst Mayr in their different, respective assessments of the major problems of biology, he was offering perspectives and suggestions regarding how the concepts and problems and practices of the field should be tackled, cultivated, developed, and he was doing so, furthermore, with an eye to certain aspects of the institutional and disciplinary ecologies of his day. The fiftieth anniversary of Tinbergen's paper is certain to inspire a number of modern biologists of behavior to attempt to do something of the same sort, with the added advantage of knowing all that has happened in the years since Tinbergen set forth his vision.

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