Niko Tinbergen

R. W. Burkhardt, Jr., University of Illinois at Urbana-Champaign, Urbana, IL, USA

Life and Scientific Career

Nikolaas (Niko) Tinbergen, the third of five children of two Dutch schoolteachers, was born in The Hague on 15 April 1907. Remarkably, two of the family's four sons were eventually awarded Nobel Prizes. Niko's elder brother Jan received the Nobel Prize in Economics in 1969; Niko received the Nobel Prize in Physiology or Medicine in 1973. When reporters asked Niko how it was that his family had produced two Nobel Prize winners, he attributed this not to innate abilities but rather to the supportive conditions in which he and his siblings were raised. The Tinbergen parents allowed their children to follow their own interests. For Niko, this meant outdoor activities – sports, nature rambles, camping out, and eventually a career as a field biologist (**Figure 1**).

Nature studies flourished in Holland in the early twentieth century. Tinbergen joined the Dutch Youth Association for Nature Study (the Nederlandse Jeugdbond voor Natuurstudie or NJN) and took great pleasure in learning about the native flora and fauna, and in particular, watching and photographing animals. However, while living nature inspired him, traditional academic botany and zoology, with their emphasis on taxonomy and anatomy, left him as cold. It was only after a 3-month stay in 1925 at the Rossitten bird station on the Baltic Sea, where he watched the autumn bird migration, that he decided to become a professional biologist.

Tinbergen enrolled as a zoology student at Leiden University in January 1926. Although he found most of the zoological and botanical instruction there to be just as boring as he had feared, there were a few notable exceptions. Jan Verwey, a young field biologist, encouraged Tinbergen to pursue field studies of behavior. Later, Tinbergen's Ph.D. advisor, Hildebrand Boschma, permitted him to do a field study for his thesis. Tinbergen's topic was the orientation behavior of the bee wolf, *Philanthus triangulum*. The experiments he conducted for it were modeled in part on the work of Karl von Frisch. As events transpired, Tinbergen was allowed to submit a dissertation that was exceptionally short – only 31 pages in print – so that he could receive his degree and participate in a Dutch expedition to Greenland. In the spring of 1932, he was awarded his doctorate, he got married (to Elisabeth Rutten), and the young couple set off for East Greenland. Tinbergen had constructed a scientific justification for the trip – a study of the territorial behavior of the snow bunting in spring – but his primary goal was to live in the Arctic among the Inuit and witness the stark, natural beauties of the area.

After 15 months in Greenland, the Tinbergens returned in the fall of 1933 to Holland. Tinbergen took up again an assistantship in the Leiden Department of Zoology (a position to which he had been originally appointed in 1931). In this capacity, he developed a program of research and teaching involving field and laboratory studies of animal behavior. He established in the spring of 1935 a special, 6 week, laboratory 'practical' for third-year undergraduates. In this course, he and his students researched the reproductive behavior of fish, most notably the three-spined stickleback. In summers, he took students to a field camp in the Dutch dunes to study the behavior of insects and birds.

Tinbergen was thus already launched on his career when he met the Austrian zoologist Konrad Lorenz at a small conference on instinct held in Leiden in November 1936. Tinbergen at this time was just 29; Lorenz was 33. The more senior animal psychologists attending the conference were interested in understanding instinct in terms of the animal's subjective experience, whereas Tinbergen and Lorenz were interested in creating a new, objectivistic, science of animal behavior that was biologically rather than psychologically oriented. The two men quickly bonded with each other. Tinbergen was greatly impressed by the way Lorenz was uniting a vast array of disparate information in a single, coherent, theoretical system. Lorenz, for his part, was particularly impressed by Tinbergen's talents as an experimenter. Tinbergen was able to report on the stickleback experiments that he and his student, Joost ter Pelkwijk, had recently conducted. Using 'dummies' to elicit the fish's instinctive reactions, they had investigated the different sign stimuli to which three-spined sticklebacks respond in fighting, courting, spawning, and the like. Lorenz, whose new theoretical system featured releasers, innate releasing mechanisms, and innate motor patterns, regarded Tinbergen's experimental results as just what his new science needed.

The friendship that sprang up between Tinbergen and Lorenz in November 1936 was consolidated the following spring when Tinbergen, with the benefit of a research leave from his department, traveled to Austria to work for 3 1/2 months with Lorenz at Lorenz's home in Altenberg. There the two naturalists conducted their classic study of the egg-rolling behavior of the gray lag goose. There too they experimented on how young birds react to simulated predators. Tinbergen also continued a series of

Figure 1 Niko Tinbergen. Photo by Lary Shaffer. Courtesy of Lary Shaffer.

experiments he had begun in Leiden with his student, D. J. Kuenen, on the gaping response in young blackbirds and thrushes.

Years later, Tinbergen and Lorenz would look back wistfully to their months of being together at Altenberg in the spring of 1937. The Second World War put them on opposite sides politically. After Germany invaded Holland in May 1940, they continued to exchange letters on scientific matters, but this ceased in 1942, when Tinbergen was incarcerated in a prisoner of war camp after resisting the occupiers' attempt to Nazify Leiden University. Lorenz took part in an effort to have Tinbergen released, but Tinbergen would have no part of it. He remained a prisoner for 2 years. After the war, his experiences during the occupation made him unwilling to resume relations with German scientists right away. With regard to Lorenz, Tinbergen's thoughts were especially ambivalent. He was aware that the man whom he had regarded both as a friend and as the pioneer of animal behavior studies had been somewhat 'Nazi-infected.' He was saddened, nonetheless, when the news arrived that Lorenz was missing in action and presumed dead.

It turned out that Lorenz was not dead after all but had been captured by the Russians. However, Lorenz had no prospects of being released soon. Tinbergen concluded that he had to take charge of the postwar reconstruction of ethology himself. One of his key efforts in this regard was the founding of the journal *Behaviour*, the first issue of which appeared in 1947. He also lectured abroad: in Switzerland, Britain, and the United States. The special series of lectures he gave early in 1947 in New York became the basis of his book, *The Study of Instinct*, which, when it finally appeared in 1951, was ethology's first general text. 1947 was also the year Tinbergen was promoted to a chair of experimental biology that been created especially for him at the University of Leiden. Two years later, when he gave up his post to take up a lecturer's position at Oxford, many of his Dutch colleagues were angry with him. The explanation he offered them was that he felt the need to serve as a missionary for ethology in the English-speaking world.

Tinbergen moved to Oxford in the fall of 1949. There he made his new home with his wife and five children. He would remain at Oxford for the rest of his life, establishing a strong program of behavior studies that attracted many talented PhD and postdoctoral students. He and Lorenz would continue to be the leading figures of the discipline through the 1950s and 1960s, playing conspicuous roles at the international congresses that helped shape ethology's identity. Tinbergen was also a successful popularizer of ethology, most notably with his books, *The Herring Gull's World* (1953), *Curious Naturalists* (1958), and the Time-Life volume, *Animal Behavior* (1965), and with films.

Tinbergen was promoted to a professorship at Oxford in 1966. In addition to the honors he received for his scientific research (which included his election as a Fellow of the Royal Society and his receipt of the Nobel Prize), he was recognized for his achievements as a filmmaker, receiving with Hugh Falkus in 1969 the Italia Prize for their film, *Signals for Survival*. In the 1970s, he joined his wife in a study of child autism. Tinbergen died in Oxford on 21 December 1988.

Practices and Concepts

First at Leiden and then again at Oxford, Tinbergen established a program of researches that featured investigations in both the field and the laboratory. The patient watching of sea gull colonies and field and lab experiments on selected species of insects, fish, and birds characterized his work. In early experiments on the reproductive behavior of sticklebacks and on the gaping behavior of young blackbirds, he used 'dummies' to test the stimuli eliciting the animals' instinctive reactions. His results seemed to correlate nicely with Lorenz's new theorizing about the interrelations of external stimuli, innate releasing mechanisms, and instinctive behavior patterns, and Tinbergen proceeded to employ these concepts in his new work, including the studies he conducted with Lorenz in Austria in the spring of 1937.

In their collaborative experiment on the egg-rolling behavior of the graylag goose, Tinbergen and Lorenz distinguished between two components in the motor sequence by which the goose returns an egg to her nest: an instinctive behavior pattern on the one hand and an orienting response or 'taxis' on the other. In the experiments they conducted on the response of young, hand-reared fowl to simulated predators, their primary interest was the correspondence between external stimuli and innate releasing mechanisms.

Although the latter experiments were never written up in detail, they can serve as a good illustration of the kind of experiments Tinbergen used in his studies of behavioral causation. In this case, he and Lorenz tested the reactions of various species hand-reared fowl to simulated flying predators (cardboard dummies of different shapes, pulled along a rope above the turkeys). The naturalists found that for young turkeys (though not the other barnyard fowl), the shape of the dummies made a difference. Dummies with 'short necks' elicited the young turkeys' alarm calls much more readily than did dummies with 'long necks.' The most striking results involved a single, relatively crude dummy constructed with the 'wings' located off center so as to make one end of the body relatively short and the other end relatively long. Which end appeared to be the neck and which end appeared to be the tail depended simply on the direction in which the dummy was moving. The young turkeys displayed more alarm when the dummy crossed above them with its short end first than with its long end first (**Figure 2**). The appeal of the case was that it appeared to show how well innate releasing mechanisms were tuned to the stimulus situations that triggered them. Though experiments 20 years later would suggest that the young turkeys' behavior was best explained in terms of habituation, Tinbergen and Lorenz interpreted the young turkeys' reaction to the short-end-forward shape as an innate response', forged by natural selection, to an environmental cue signaling 'predator.' The short-necked version, they explained, corresponded to the shape of a hawk, while the long-necked version corresponded to the shape of a goose.

Tinbergen had already found in experiments with male sticklebacks that the optimal stimulus eliciting their fighting response was not just any red fish model but instead a model that was red underneath. Young thrushes likewise directed their gaping responses toward certain models more than others, depending on how the models' 'heads' were presented in relation to the rest of the body. Tinbergen concluded that the behavior of the young turkeys was similar in that they were not responding to the shape of the 'hawk-goose' model per se, but they were responding to the particular configurational stimulus produced when the model moved slowly above them short end first (like a hawk). In the decades that followed, later investigators found it difficult to replicate

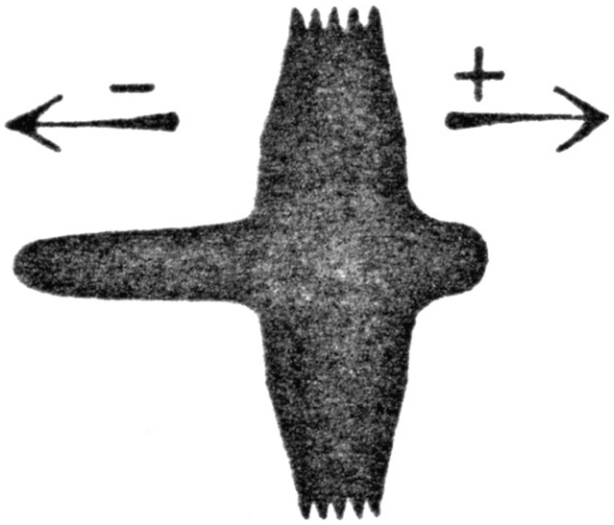

Figure 2 Tinbergen's illustration of a 'card-board dummy that releases escape reactions when sailed to the right ('hawk') but is ineffective when sailed to the left ('goose').' Reproduced from Tinbergen N (1948) Social releasers and the experimental method required for their study. *The Wilson Bulletin* 60: 6–51, 34.

these early experiments on innate releasing mechanisms. Be that as it may, these experiments played an important role, early on, in establishing ethology's credentials as a new science.

Although he endorsed Lorenz's basic system of releasing stimuli, innate releasing mechanisms, and innate motor patterns, Tinbergen's developing thoughts on behavioral causation were not an exact mirror of Lorenz's. In Lorenz's model of instinctive action, instincts were treated as basically independent of each other, at least in the sense that each was fed by its own 'action-specific energy.' Tinbergen, to the contrary, came by the early 1940s to think of instincts as being hierarchically related. Tinbergen' doctoral student Gerard Baerends in this period interpreted the behavior of a digger wasp of the genus *Ammophila* in terms of hierarchically arranged internal states or 'moods.' Hierarchical thinking about instincts also appeared in the thinking of the Dutch animal psychologist, Adriaan Kortlandt. Tinbergen proceeded to describe the instincts of sticklebacks in much the same terms that Baerends used. Stickleback males, by Tinbergen's account, are brought into the reproductive 'mood' through internal, hormonal changes and perceiving an appropriate territory. Once they have reached this general state, they are capable of a number of different activities, notably fighting other males, building a nest, and courting females. Whether a male comes into a fighting, building, or courting 'submood' depends on which stimuli it receives. If the appearance of an opponent brings it into a fighting submood, how the opponent then acts will determine how the male reacts: by fighting, chasing, threatening, biting, etc. (**Figure 3**).

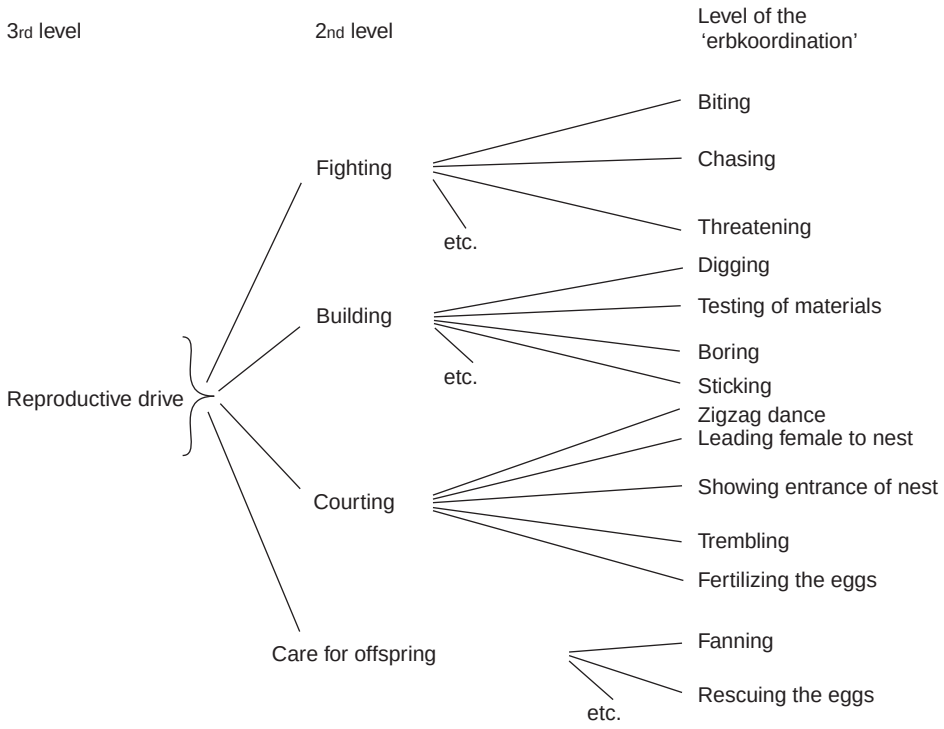

Figure 3 Tinbergen's representation of the hierarchical arrangement of drives. Reproduced from Tinbergen N (1942) An objectivistic study of the innate behaviour of animals. *Bibliotheca Biotheoretica* 1: 39–98, 57.

Tinbergen's work on behavioral causation also involved the identification and explanation of what Tinbergen called 'substitute activities' (later 'displacement activities'). These are stereotypic movements that appear as 'irrelevant' acts, such as birds stopping to feed or preen or collect nest materials while in the midst of fighting or courting. He interpreted these activities as outlets for a strongly activated drive (or two conflicting drives, such as fighting and fleeing) when it is prevented from being normally discharged. He also noted that displacement activities can serve as signals, becoming increasingly distinctive and 'ritualized' in this capacity over the course of evolution.

When Tinbergen moved to Oxford in 1949, he recognized the need to widen the scope of his researches beyond studies of causation. Lorenz had stressed the value of doing comparative studies and had illustrated this with a long, comparative study of the reproductive behavior of ducks. Tinbergen decided to do some comparative work of his own. Having already developed a detailed knowledge of the behavior patterns of the three-spined stickleback and the herring gull, he decided to set his new graduate students to work studying additional species of sticklebacks and gulls. However, he did not want simply to use new species to replicate Lorenz's work. Instead, he wanted to understand how behavior had evolved in particular ecological settings.

The comparative gull studies paid off handsomely for Tinbergen's research team, with the black-headed gull and the kittiwake proving especially instructive. Working on the kittiwake, Esther Cullen, one of Tinbergen's students, identified a whole range of species-specific behaviors that were corollaries of the bird's habit of breeding on the narrow ledges of steep cliffs. These behaviors included particular releasers, specialized fighting movements, distinctive nest-building behavior, and the nonremoval of eggshells from the nest site.

Tinbergen was greatly impressed by Cullen's findings. He was pleased to note how the kittiwake's adaptive characters fit together in a coherent system. From this, he drew two conclusions. One was that a species would often be subject to conflicting selection pressures, from which 'compromises' of various sorts would result. The other was that characters that looked by themselves like the product of random change could prove upon close examination to be the indirect results of selection on the whole adaptive system. To Tinbergen, this constituted a validation of field biology. Field biologists were in a better position than museum taxonomists – or observers of animals in captivity – when it came to observing the effects of selection.

Tinbergen indeed felt that this new research established something that Lorenz had not anticipated. Lorenz had insisted that releasers are especially valuable for taxonomic purposes because they are not closely linked to a species' ecology and thus not subject to convergence. He represented them as arbitrary, historical conventions

developed over the course of evolution. Tinbergen concluded to the contrary that the kittiwake's special displays were not arbitrary conventions but were instead intimately linked to the species' cliff-dwelling habit. More generally, he went on to argue that one could expect to find convergence in the threat displays of very different species, because there are only a limited number of postures a bird can adopt in signaling its likelihood of attacking or withdrawing.

In 1957, at the International Ethological Congress in Freiburg, Tinbergen reported that he was feeling with respect to his work like a butterfly emerging from a chrysalis. Although he was not very explicit what he meant by this, the context of his remark seems clear. The previous several years had been a complex time for ethology. A number of its original concepts had come under fire. Within ethology, a new generation of students had identified problems with Lorenz's psycho-hydraulic model and Tinbergen's hierarchical model of instinctive action. From the American comparative psychologist Daniel Lehrman came in 1953 a scathing critique of Lorenzian ethology, claiming, among other things, that Lorenz's notion of 'innate' behavior was hindering the study of behavioral development. Tinbergen saw the value of establishing a dialog with Lehrman, and he indeed came to agree with some of what Lehrman was saying. But after this period of engaging with critics and trying to decide which of ethology's original concepts were still viable and which were not, Tinbergen wanted to get on with new work. His comparative gull studies were leading him to new studies of behavioral function, that is, how behavior patterns contribute to an animal's survival. In the late 1950s and early 1960, as he engaged in experimental field studies of behavioral function, he concluded that this type of work appealed to him more than any other. This was the basis for his sense of metamorphosis.

Studying the function of eggshell removal in the black-headed gull revealed to Tinbergen and his students how complex and how beautifully adapted the bird's behavior was. What was safest for the parents was not necessarily what was safest for the brood. Likewise, what helped protect against one kind of predator, such as carrion crows, did not necessarily work against other kinds of predators, such as foxes. The timing of removing eggshells from the nest area was itself a kind of compromise: while predation by herring gulls and crows constituted a selection pressure favoring the rapid removal of eggshells, leaving newly hatched chicks briefly unprotected exposed them to being eaten by neighboring black-headed gulls. Through his experimental field studies of selection pressures and adaptations, Tinbergen helped stimulate the development of modern behavioral ecology (**Figure 4**).

Fittingly enough, when Tinbergen in the early 1960s took an opportunity to comment on how his research program had developed at Oxford, he described the choices he had made in setting up his program in much the same terms that he used when describing adaptive radiation in gulls. His choices in building his program, he said, were influenced not only by general considerations about where ethology should be heading, but also by local conditions. He had been keen to connect with Oxford's strong traditions in ecology and evolutionary biology. At the same time, he knew that he had to be economical with the limited budget at his disposal. By his account, the character of the Oxford program ultimately reflected a compromise between breadth of approach and close attention to specific subjects.

Figure 4 Tinbergen in the field (in 1972 on Skomer Island, off the coast of Wales). Photo by Lary Shaffer. Courtesy of Lary Shaffer.

The Four Questions of Ethology

Tinbergen is remembered for having defined and promoted ethology as 'the biological study of behavior.' His classic statement of what he meant by this appeared in his 1963 paper, 'On aims and methods of ethology.' There he offered his famous formulation of the 'four questions of ethology.' To understand behavior biologically, he said, one needs to ask of it: (1) What is its physiological causation? (2) What is its function or survival value? (3) How has it evolved over time? (4) How has it developed in the individual? This, he went on to suggest, not only provided the best way to characterize the nature of ethology, but also held the key to ethology's future. For ethology to continue to flourish, he said, it is needed to address all the four of these questions in a balanced and coordinated fashion.

Tinbergen's definition of ethology as of 1963 was a definition that had taken shape in his thinking over the course of some 30 years. Both he and Lorenz back in the 1930s had emphasized that their new approach was bringing biological perspectives to bear on the questions of animal psychology, but what they had actually stressed

at any given time generally depended on the particular audience they were addressing. In 1942, for example, when he was contrasting the objective nature of ethology with the subjectivist approach of his animal psychologist countryman, J. A. Bierens de Haan, Tinbergen maintained that the ethologists' primary interest was behavioral causation, that is, understanding innate behavior in physiological terms. (Lorenz for his part, while equally committed to the study of behavioral causation, was inclined to say that what made ethology most distinctive was its comparative, evolutionary nature.) In 1951, in his book, *The Study of Instinct*, Tinbergen in effect identified ethology's 'four questions,' but without calling them that and certainly without giving them balanced treatment. Tinbergen devoted more than half of the book to the study of behavioral causation. He provided only a scant chapter each on behavioral development, function, and evolution. As it was, when he published his 'Aims and Methods of Ethology' paper in 1963, he did not feel that a balanced approach to the four questions of ethology was anywhere near being achieved. Studies of behavioral causation still far outweighed studies of behavioral function (despite the work that he and his students were doing on the latter topic). Ironically, perhaps, within a decade and a half, the tide would turn dramatically and functional studies would come to enjoy a disproportionate share of the research in ethology.

To view Tinbergen's 1963 paper in historical context is also to consider what it reveals about Tinbergen's ongoing relations with Konrad Lorenz. Tinbergen dedicated the paper to his old friend as part of a *Festschrift* commemorating Lorenz's 60th birthday. Tinbergen's contribution radiated friendship and goodwill, and it gave full credit – indeed in some ways exaggerated credit – to Lorenz's pioneering efforts in the field. Writing the paper required a certain amount of diplomacy on Tinbergen's part, for on the subject of behavioral development in particular, Tinbergen and Lorenz no longer saw entirely eye-to-eye. Lorenz was angry with Tinbergen for having been too accepting of Daniel Lehrman's critique of ethology's early assumptions about 'innate' behavior. Tinbergen acknowledged that he and Lorenz held different opinions with regard to behavior development – Tinbergen had come to believe that applying the word 'innate' to behavioral characters was harmful heuristically – but he did not want to press the issue too hard at that moment. A more subtle critique of Lorenz can be detected in what Tinbergen said in the paper regarding behavioral function. While he lauded Lorenz as one of the first students of behavior to be interested in survival value, he also made it clear that if scientists were to gain a better understanding of how natural selection actually operates, hard fieldwork, including the experimental demonstration of survival value, needed to be done on the subject. In these ways and others, Tinbergen's 'Aims and Methods' paper testified both to the evolution of his own thinking and to his ongoing relations with Lorenz.

Tinbergen's 'four questions' of ethology were simultaneously a vision for the future development of ethology and an affirmation of his life-long commitment to fieldwork. At the end of his career, he felt that if he were to be remembered for anything, it would not be for any particular discovery as much as for his long-term promotion of a fully biological approach to behavior.

See also: Behavioral Ecology and Sociobiology; Ethology in Europe; Future of Animal Behavior: Predicting Trends; Herring Gulls; Integration of Proximate and Ultimate Causes; Neurobiology, Endocrinology and Behavior.

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