Patterns of Behavior: Konrad Lorenz, Niko Tinbergen, and the founding of Ethology
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Ethology’s Ecologies
We all know that history matters, but sometimes it is helpful to be reminded why. Richard W. Burkhardt Jr., Professor Emeritus of History at the University of Illinois, provides such a reminder towards the conclusion of his absorbing, meticulously researched account of the origins of ethology. As suggested by Burkhardt (pp. 472-3), research into the works and lives of our scientific predecessors, whatever our fields of study, can:

• lend our own work authority and context, as we come to understand, appreciate, and reference earlier instantiations of concepts of interest;
• provide “inspiration in the efforts of kindred spirits”, as we learn for example how our predecessors overcame operational and conceptual challenges;
• highlight concepts that have subsequently fallen by the wayside, now free for discovery and reinterpretation (concept mining); and, most importantly,
• enrich our ability to reflect critically on the meaning of our own scientific activities, particularly as it relates to our individual times, places, and circles of colleagues.

The attentive reader of Burkhardt’s volume will find much to contemplate and value along these lines, with regard to our own discipline of behavioral ecology.

The organizing principle of Patterns of Behavior is that the ebb and flow of scientific inquiry and achievement depends not just on the world of ideas — for example the core concepts of an emerging discipline — but also, and perhaps more so, on the world of people and personalities that produces, disseminates, and defends those ideas. This principle is now familiar, in part because of the influence of the philosopher of science David Hull (e.g., Hull 1988), although this was not the case when Burkhardt began his research. Burkhardt proves to be an engaging and authoritative guide to “Ethology’s Ecologies”, as he phrases it. Above and beyond a vast published literature, Burkhardt draws upon a significant body of unpublished work, including excerpts from his own interviews with Lorenz and Tinbergen, and a wealth of correspondence among Lorenz, Tinbergen, and an all-star cast of 20th century behavioral scientists including Wallace Craig, Oskar Heinroth, Margaret Morse Nice, Julian Huxley, William Thorpe, Erwin Stresemann, David Lack, and, especially, Ernst Mayr, who had also advised Burkhardt’s doctoral studies. Patterns of Behavior thus offers readers a front-row seat to the development of ethology, as it unfolded against a fascinating political backdrop of global tensions, world war, subsequent reconstruction, and the interplay of British, American, and Continental European scientific personalities and traditions.

Patterns of Behavior focuses, naturally, on Konrad Lorenz and Niko Tinbergen, the two central architects of ethology. The careers of these men were complementary and intertwined to a degree that some readers may not have realized. What set Lorenz and Tinbergen apart, we learn, was not only their intellectual talents but also their persistence and skill in galvanizing institutional support for their research programs, and their ability to win over colleagues, both junior and senior. Burkhardt suggests that ethology could have presumably found a “viable niche” (pg. 158) earlier on, via Charles Otis Whitman, Craig, or Huxley, all of whom had crafted pioneering research programs, and had mulled the potential fit of behavioral studies within (and among) the more traditional realms of biology, psychology, and philosophy. Yet all three were, in the end, derailed. The (pigeon-centric) research programs of Whitman and Craig in the United States were severely stunted by financial woes. To wit, Craig at one time lamented to a colleague that he “must keep hens; while I watch their behavior we can eat their eggs, and later we can put the specimens themselves in the pot. I must keep large pigeons as well as doves; we can eat the squabs” (pg. 47). The scramble for resources, as well as a lack of self-confidence and feelings of intellectual isolation on the part of Craig (p. 175), left little time for synthesis and institution-building, and the early American ethological perspective was soon overshadowed by the emerging field of comparative psychology. Huxley in Britain might also have jump-started the study of animal behavior, on the heels of his influential 1914
paper about mating rituals in great-crested grebes. A skilled spokesman for his work, Huxley was a “master of organization, synthesis, and presentation” (p. 124). Yet the ambitious Huxley believed he could make stronger impacts in other arenas, particularly evolutionary biology, and in the end his most important publication (1942) made little attempt to integrate animal behavior into the broader topics of ecology and evolution.

Burkhardt paints a detailed picture of how Lorenz and Tinbergen emerged as major players and then imagined, first independently and then jointly, possibilities for animal behavior as a formal discipline. Both men enjoyed, early in their careers, the support of sympathetic families and colleagues. Lorenz, a son of privilege, grew up on a family estate with woods, ponds, and facilities in which he could tend and watch animals. In medical school at the University of Vienna, Lorenz found an encouraging mentor in the comparative anatomist Ferdinand Hochstetter, under whose guidance he pursued the idea that patterns of behavior can be useful in reconstructing phylogenetic relationships among species. Tinbergen grew up within a rising Dutch naturalist tradition, manifest in popular books, school nature clubs, and, of particular relevance for Tinbergen, the newly founded Dutch Youth Association for Nature Study. Tinbergen soon discovered that he preferred to be outside than to be in school, and was transformed when he visited a German field station and learned that field research could be pursued as a vocation. Within a few short years, both scientists had become leading researchers in their respective countries. Lorenz’ first publications, on the behavior of hand-reared jackdaws, drew the favor of the leading German ornithologists Stresemann and Heinroth. Under Heinroth, who Lorenz came to regard as his most influential mentor, Lorenz began to articulate a distinction between innate and learned behavioral patterns, as illustrated in his influential 1932 Triebhandlungen and 1935 Der Kumpan manuscripts. Tinbergen, meanwhile, enjoyed the mentorship of a number of talented naturalists including Jan Verwey, Fritz Portielje, and C.J. van der Klauw, and shortly thereafter began to pursue his famous doctoral studies on homing behavior in digger wasps. Tinbergen came to be known for his emphasis on observations of animals in natural habitats, and for using simple, precise experimental approaches to test questions about behavioral mechanism and function.

Consistent with Burkhardt’s thesis, we learn that both Lorenz and Tinbergen possessed key personality traits and talents — “youthful energy, programmatic brashness, and conceptual promise” (p. 103) — that enabled them to build upon their early successes. Lorenz had, above all, the “gift of gab”, as we used to say in New York — he could fill a room and charm an audience. His skills and enthusiasm as a lecturer and raconteur helped pave the way for favorable reception of his written work, especially for his 1935 Der Kumpan manuscript which came to earn rave reviews from the likes of Huxley, Nice and Craig. Tinbergen was markedly, and famously, more low-key than Lorenz — he played, in effect, Ego to Lorenz’ Id — but he was no less effective in spreading his message. Perhaps most notably, Tinbergen developed, at the University of Leiden, a training program called the “block practical” which, in contrast to more traditional training approaches, provided students with hands-on guidance in the myriad challenges of field study. Tinbergen thus directed a rising, expanding cohort of continental field biologists towards an ethological perspective. Lorenz and Tinbergen finally met, at the Leiden “Instinct” symposium in 1936, Lorenz later noting that he had been surprised to find that Tinbergen was so young (only 29) given all that he had already achieved. The connection forged between Lorenz and Tinbergen at this symposium, and the following year at Lorenz’ private research station in Altenberg, proved central to the founding of ethology. At Altenberg, in addition to conducting joint studies on instinctive behavior (egg-rolling in greylag geese, innate responses to aerial predators), the two men observed how their approaches — Lorenz the farmer, Tinbergen the hunter, as they thought of it — were complementary, and how in synergy could define a research program for a new discipline of ethology. Central to ethology, both agreed, would be the objective and experimental study of behavior in natural settings, an approach that was largely absent from both American and European research programs. Both men later claimed their time at Altenberg as the happiest in their lives. Tinbergen visited America in 1938, where he received, due in large measure to Nice’s advocacy of Lorenz’ work, a warm reception from psychologists, biologists, and naturalists, keen to learn more about the ethological program and what it had to offer.

A Hollywood script writer would be hard-pressed to conceive a more intriguing turn of events when, with the onset of World War II, Lorenz rose in stature within the National Socialist regime, whereas Tinbergen, who had resigned from the University of Leiden in protest of the German occupation, was held as a prisoner of war. As Burkhardt notes, significant attention has been paid in recent years to the nature of
Lorenz’ ties to National Socialism (e.g., Klopfer 1994, Schleidt 2001). Burkhardt devotes a full chapter to exploring these ties and making sense of Lorenz’s behavior in the complex terrain of Third Reich biology. We learn that Lorenz was pleased when the Nazis came to power in Austria in 1938, above all because he believed it would enhance his career possibilities. When he joined the Nazi Party a few months later, Lorenz imagined this would help him secure a regular scientific position (which, incredibly enough, he still did not have at this time). He promoted his animal behavior studies with the claim that in studying the breakdown of instinctive behavior patterns in domesticated animals, one could recognize comparable dangers of genetic deterioration in civilized, human societies. Without becoming a strident ideologue (Burkhardt notes, for example, that Lorenz never published derogatory statements about Jews), Lorenz signaled to those in power his willingness to be an actor on the stage of Third Reich biology. Eventually he did receive a professorship, at the University of Königsberg, although he served in that capacity only briefly before being called up for military service. It thus seems, as we follow Burkhardt’s account, that Lorenz’s wartime efforts to warn about genetic decay in civilized society were most closely catalyzed by his own concerns for career advancement. Years later, when pressed on the subject, he would allow that he had been “naive” about the intentions of the Nazis. However, as Burkhardt puts it, Lorenz was never willing to contemplate the idea that “in promoting ideas of racial hygiene and using a language of ‘elimination,’ he had possibly made an indirect or inadvertent contribution to a program that resulted in genocide.” (p. 278). Post-war “exposure” of Lorenz’ Nazi-era writings came to foster mistrust of Lorenzian ethology, particularly in America. Burkhardt notes, to illustrate that the comparative psychologist T.C. Schneirla was active on the political left and was “not disposed to regard Lorenz’s career in the Third Reich as easily forgettable” (p. 368). Schneirla would convince his student Daniel Lehrman to write the now-classic critique of Lorenzian ethology (Lehrman 1953).

Less widely-discussed, but perhaps more important for the future of ethology, were the impacts of World War II on Tinbergen. In addition to having suffered intense psychological damage as a prisoner of war, which may have primed later bouts of depression, we learn that Tinbergen came to be dissatisfied with post-war Dutch society, which he regarded as inappropriately conservative for the time and era. Tinbergen also came to feel overburdened by new administrative and teaching duties at Leiden. These dissatisfactions catalyzed his impending move, in 1949, to Oxford, a change of environment that would significantly broaden his research program and that of the nascent field of ethology.

According to Burkhardt, the original core “Lorenzian” ethological program was perhaps best articulated at the 1949 symposium of the Society of Experimental Biology, “Physiological Mechanisms in Animal Behaviour”. In Burkhardt’s retelling, this symposium stands not just as a landmark event for ethology but also as testament to the post-war resilience and leadership of Tinbergen, who by then had made amends with Lorenz. At the symposium, an animated rift unfolded between Hans Lissman and, in absentia, Erich von Holst, over the relative importance of central and peripheral mechanisms of control (Strangely enough, Lissman translated and presented von Holst’s paper, mocking it in delivery). The symposium also featured Karl Lashley’s classic paper “In Search of the Engram” (Lashley 1950). Most importantly for the future development of ethology, the symposium formally introduced two classical models of behavioral control; Lorenz’ “psycho-hydraulic” model of instinctive action, and Tinbergen’s hierarchical model of the organization of drives. These two models have more in common than this reviewer had realized, particularly in their joint aims to explain the integration of internal states and external stimuli (as suggested in part by von Holst), and in their mutual reliance on Craig’s 1918 paper on appetites and aversions. It is particularly instructive to read Lorenz’ musings, in a letter to Thorpe (p. 323-4), about how the two models might be jointly applied to explain complex behavior.

Burkhardt then walks us through ethology’s subsequent “adaptive radiation” (p. 327), which was guided in particular by Tinbergen’s 1951 book, The Study of Instinct (Tinbergen 1951) and his 1963 paper published in Zeitschrift für Tierpsychologie (Tinbergen 1963). In these works Tinbergen outlined the goals of Lorenzian ethology, but also formally expanded ethology’s reach into the realms of ecology, adaptation, and evolution, consistent with the intellectual environment Tinbergen was experiencing at Oxford, under Alister Hardy and with colleagues such as Charles Elton, E.B. Ford, and David Lack. Interestingly enough, we learn from Burkhardt, Tinbergen was originally hesitant to include chapters on behavioral function in The Study of Instinct, because of concerns that they would draw attention away from questions about “the causes underlying instinctive behavior” (p. 372). Tinbergen’s decision to include these chapters ultimately helped
jump-start the growth of behavioral ecology, imagined earlier by Heinroth (Podos 1994) and later kicked into high gear by the likes of Williams, Hamilton, and Trivers. This indeed might be ethology’s greatest legacy. The negative side of the Tinbergen expansion, however, was that it became increasingly difficult to identify a coherent ethological core, as reflected in Tinbergen’s characterization, in a letter to Burkhardt, of ethology as a “curious ragbag” (p. 5). The diffusion of ethological research in the 1960s and 70s, along with mounting critiques of ethological perspectives on behavioral development, led some observers, perhaps most famously Edward O. Wilson (1975), to question the continued viability of the discipline. Whether or not ethology continues to thrive as a distinct discipline, or alternatively has been subsumed into related offshoot disciplines, is an open question that has occupied behavioral scientists for some time (e.g., Bateson & Klopfer 1989). Burkhardt implicitly provides his opinion on the matter by concluding his history of ethology with the late 1970s.

In the end, irrespective of one’s views on whether ethology persists as a formal discipline, Burkhardt’s account is well worth our while. Of particular relevance to readers of this newsletter, I believe, is the opportunity to resurrect concepts that have since fallen by the wayside (paragraph #1, bulleted point #3). This is by no means an easy task, as our knee-jerk tendency when reading historical accounts such as Burkhardt’s is to dismiss past iterations of concepts and models as being out-of-date, losers since replaced by winners, perhaps not worth our limited time and energy. As we learn more about the people behind the science, however, it becomes increasingly difficult to dismiss their ideas outright – and, if we’re not careful, some new (old) ideas begin to take root in our own minds, like weeds in a well-tended garden.

Towards this end, Burkhardt’s account suggests, at least to me, that we behavioral ecologists must be missing research opportunities in our tendency to overlook the concepts of instincts and drives that were so central in early articulations of ethology (e.g., Craig 1918, Tinbergen 1951). It is convenient to assume that critiques levied at these concepts (e.g. Lehrman 1953) have since rendered them invalid. It is also convenient to ignore concepts such as these that do not fit neatly within our standing conceptual and operational frameworks (but remain, I would argue, preserved within the bar of Wilson’s (1975) dumbbell model). However, just because we have forgotten how to study (or perhaps even talk about) drives and instincts, does not mean they are not worth renewed attention. We have to remember that a main goal of the early ethologists was to observe animals as objectively as possible, even if these scientists were not, as Lorenz had exaggerated, “happily free from even a working hypothesis” (p. 312). For how much longer must we dismiss the ideas and collective intuition of our ethological predecessors?

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References