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Tribute to Tinbergen: The Place of Animal Behavior in Biology

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COMMENTARY

The place of animal behavior in biology: Tinbergen's ethological legacy

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Abstract. Tinbergen is famous for emphasizing behavioral fieldwork and experimentation under natural circumstances, for founding the field of ethology, for getting a Nobel Prize, and for mentoring Richard Dawkins. He is known for dividing behavior studies into physiology, development, natural selection, and evolutionary history. In the decades since Tinbergen was active, some of the best research in animal behavior fuses Tinbergen's questions, connecting genes to behavioral phenotypes, for example. Behavior is the most synthetic of the life sciences, because observing the actions of an organism can tell us what all those physical and physiological traits are for. Insights from behavior tell us how traits in one individual impact those in another in ways that challenge our definition of an organism. Behavioral conflict and cooperation among animals has led to theory that explains within-organism conflict and cooperation and human malfunctions of many kinds. Darwin certainly began the evolutionary study of behavior, but Tinbergen brought it forward to the heart of biology. The challenge for the future is

to apply concepts from animal behavior across biology with tools that would have amazed Tinbergen.

Why is it so hard to say where exactly the study of behavior fits as a research category? Is it because behavior is what all of the social sciences are about, so people view it as a human field first? Is it because behavioral acts seem so variable that systematic study is impossible? Is it because behavior is either seen as the end product of nervous system functioning or as the first product of evolution? Is it because actions often cannot be broken into smaller pieces for analysis? Is it because of the way social interactions intertwine the fitnesses of different actors? We have been searching for a general theory of behavior before and after Richard Alexander thoughtfully posed the question (Alexander 1975).

Ethology was important because it brought behavior to biology and earned the only Nobel prize so far for behavior or evolution

The Nobel Prize has been given once for animal behavior, to Tinbergen, von Frisch, and Lorenz. The research that the Nobel Committee recognized is famous because it placed behavior firmly within biology as a testable science. The laureates called this new field ethology. Its central tenets involved careful observations of individually marked animals in their natural habitats. Its key finding was that under these conditions, behavioral actions were predictable and understandable as evolved traits that benefited their bearers and had physiological and genetic underpinnings.

Specifically, the prize was for discovering the "origin and elicitation of individual and social behavior patterns" (Nobelprize.org 1973). In his speech granting the prize, Börje Cronholm talks about failed approaches to behavior as being either too focused on learning or too vitalist, so not subject to analysis (Cronholm 1973). He lauds the ethology trio for treating behavior as something that could be studied as any other biological trait in an evolutionary framework, with some actions being genetically determined. Cronholm cited von Frisch for discovering honeybee dance communication, Lorenz as the discoverer of fixed action patterns, imprinting, development, and observation, and Tinbergen for experimentation and the discovery of extra-normal stimuli that released cascades of actions. Thus the Nobel committee was most impressed with the innateness of behavior. It was a victory for Lorenz's view that behavior should be treated like an organ, with the same evolutionary and mechanistic possibilities and constraints.

Of course, Darwin had very clearly and convincingly begun the evolutionary study of behavior long before the ethologists. He definitely viewed behavior as subject to natural selection. Darwin's thoughtful approach to behavior might be said to have languished before the ethologists (Burkhardt 2005).

The problem with ethology

Though the Nobel Prize was for bringing behavior into biology by emphasizing its innateness, the specific theories of the ethologists (fixed action patterns, releasers, and the hydraulic model of behavior, for example) have not endured as central concepts to behavior. In fact, they have hardly endured at all. At

best they were curiosities that sometimes described particular acts. At worst they emphasized behavior as innate and invariant sequences rather than as an evolved expression of adaptive actions, as plastic and subject to learning as is favored for the specific circumstances of their bearer. What we mean today by ethology shares little with the early work. The modern view owes most to Tinbergen and von Frisch and emphasizes both careful observation and judicious experiments in natural settings.

By 1963 Tinbergen had moved on from ethology's concern with innateness, in part because of the fierce attacks on ethology from across the Atlantic. These criticisms are summarized in a famous paper by Daniel Lehrman (Lehrman 1953). What Lehrman argued was that it was impossible to demonstrate how genetic an action was by simply observing it in a naïve animal. After all, how can we rule out the very earliest experience, as a chick might have during development, for example? If one cannot say what is truly innate and not learned at any time during development, what can one really say about instinct? However, Lehrman took it too far, claiming that if we cannot tell what is learned and what is acquired, then we have a blank slate where learning is everything.

Lehrman's descriptions of deprivation experiments make for horrifying reading. They also make it clear that organisms cannnot play out their natural histories in isolation from their environment, so learning and instinct cannot be disentangled. Perhaps this was not so hard for Tinbergen to believe, because his emphasis was on animal behavior under natural circumstances. Tinbergen also accepted that leaving the innate vs. learned dichotomy unsolved still left plenty of

interesting questions and approaches, in particular how organisms evolve to express optimal traits in natural environments. Tinbergen befriended Lehrman, but there were still differences.

It is interesting that the fight for behavior between the European biological ethologists and the American psychological behaviorists had a surprising ending. It turns out that behavior belongs to biology. But then so does psychology. But this does not mean that all actions are genetically based, or that learning and experience are not part of the story. The weakness of the ethologists was that while they had the biggest picture correct, that behavior is part of biology, they lacked a general theory for behavior. In later work, Tinbergen did not solve this problem but instead turned his attentions to how we study animal behavior. This was particularly advantageous for a Festschrift honoring Konrad Lorenz who clung more fiercely to innateness.

The four questions paper of 1963

Tinbergen may have struggled to come up with a contribution to the volume celebrating Konrad Lorenz's 60th birthday in 1963. He used the phrase "crossing swords," as something he did not want to do on the occasion of Lorenz's birthday. Tinbergen's solution was the famous four questions paper. It is more about the process than the product of behavior studies (Tinbergen 1963). In this paper, Tinbergen divides biological research into four categories. His categories are causation, ontogeny, survival value, and evolution. In Tinbergen's words, *Causation* is "physiology of behaviour…all the way down to molecular biology…;" *survival*

value is: “find out, if possible by experimentation how animal behaviour contributes to survival…;”*ontogeny* is “change of behaviour machinery during development;” *evoluti*on is “the elucidation of the course evolution must be assumed to have taken, and the unraveling of its dynamics…”

Tinbergen acknowledges that these categories are not original. In particular Julian Huxley had proposed all but ontogeny (Huxley 1914). Perhaps more seriously, Tinbergen does not credit Ernst Mayr for describing proximate and ultimate questions as the two approaches to biological research two years earlier (Mayr 1961). Mayr calls the two areas functional biology and evolutionary biology, corresponding to how questions and why questions (Laland et al. 2011). Later in his paper, following an example of warbler migratory behavior, Mayr introduces the terms we use most today: *proximate* and *ultimate*. The proximate answer, for example, to the escape of a gazelle from a lion has to do with the physiology of perception and action. The ultimate answer has to do with genes and natural selection: gazelles that escape from lions have more babies than those that do not.

Tinbergen’s four questions paper has resonated with generations of animal behaviorists in important ways. Might Tinbergen not have written it at all except for the need brought about by Lorenz’s birthday? But that Tinbergen was celebrating Lorenz’s birthday with him in 1963 is a greater puzzle.

Konrad Lorenz and the Nazis

Lorenz was an enthusiastic National Socialist who joined the party on 28 June 1938, as soon as he could after the Anschluss (Germany taking over Austria).

Furthermore, Lorenz pointed out in detail how much his work corresponded to the ideals of the Nazis (Deichmann 1999). Lorenz felt that his research on animals was directly applicable to people and that people of the cities, in the south, or of mixed parentage were degenerate and to be eliminated like a cancer (Deichmann 1999; Burkhardt 2005). Additionally, Lorenz did not just leave his ideas as abstract ideologies. He joined the Nazi Office of Race Policy. He went to Posen to participate in the task of sorting mixed Poles and Germans into German-like people that could be rehabilitated and Poles who could not. Neither Deichmann nor Burkhardt indicate exactly what role Lorenz played in this sorting that sent some to concentration camps. Lorenz was certainly not going to help anyone figure out his exact wartime activities. After all, he subsequently even tried to deny joining the Nazi party. Furthermore, he never apologized for his behavior under the National Socialists, or substantially changed his ideas (Burkhardt 2005).

Information as to exactly what Lorenz did during the war was not as easily obtained in the decades after the war as it is now. If it had been, I doubt Tinbergen would have re-established connections with Lorenz, or that the Nobel committee would have recognized Lorenz. The other laureates did not share Lorenz's views on race. Unlike Lorenz, who avoided professional associations with Jews, von Frisch hired and protected a number of Jewish academics and struggled to make it through the war. Tinbergen was active against the Nazis under occupation (Burkhardt 2005). My own family also struggled during those times (Strassmann 2008), something that makes reading through this history particularly difficult.

Yet Tinbergen slowly reestablished contact with Lorenz, in part feeling for him because of Lorenz's years in a Russian prisoner of war camp.

Animal behavior after ethology

Animal behavior advanced a lot in the 50 years since Tinbergen celebrated Lorenz's birthday with the four questions paper. Behavior is clearly part of biology, in all the ways Tinbergen predicted. Social behavior, in particular, has proven to be central (Darwin 1859; Hamilton 1964; Alexander 1974; Trivers 1974; West-Eberhard 1975; Dawkins 1976; Robinson et al. 2008). We now have a Gordon Conference on Genes and Behavior. We can look at the effects on behavior of variation in single genes. We can look at whole sets of genes that impact behavior using modern genomic and transcriptomic methods. In the field we can do many new things, from videotaping to radiotagging.

Tinbergen and his colleagues established that the biological principles that applied to organs could also be applied to behavior. Once the scientific status of behavior was established, the insights could go in the other direction. Findings from behavior could inform other kinds of biology. This is perhaps been most pursued for social behavior where kin selection and mutualism feedbacks in particular have proven to be enormously useful. These theories enlighten our understanding of how life began and elaborated into eukaryotes, multicellular organisms, and nearly organismal groups (Maynard Smith & Szathmáry 1995; Queller 1997). Kin selection tells us about conflicts like those on the battleground

of the placenta (Haig 1993; Crespi 2008; Haig 2008). Animal behavior theories tell us about group movement, including such things as blood flow or cancer metastasis(Deisboeck & Couzin 2009). Understanding many topics essential to human well being may well come from principles of animal behavior, from the study of autism that Tinbergen took on in his later years, to cancer (Crespi & Badcock 2008).

Animal behavior is at the heart of the National Research Council's grand challenges for biology (NRC 2010). All of the challenges have strong behavioral elements, a point made in a recent National Science Foundation white paper(Workshop 2012). The first one involves synthesizing life-like systems. Only with behavior can a system be life-like. A life-like system will have replicating units, will have interactions with other living entities, both cooperative and competitive, and will be likely to transition into more complex forms. The second grand challenge is about understanding the brain, that master controller for behavior. Information is taken into the brain and processed there, and results in behavioral acts. Any harm to the brain will first become evident in changes to behavior. The third grand challenge is to connect phenotype to genotype. Behavior is a key part of the phenotype, perhaps closest to natural selection's blade. The remaining grand challenges involve interactions of organisms and biodiversity, areas where behavior is central. We overstate only a little when we say that at some level all biologists study behavior.

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