

FOUR MORE REASONS WHY ETHOLOGY MATTERS TINBERGEN AND THE HUMAN SCIENCES

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ABSTRACT

Tinbergen's paper on aims and methods in ethology is, quite rightly, a citation classic. Here, we would like to emphasize that, 50 years after its initial publication, it continues to offer fresh insights into study of ethology and human ethology in particular as well as offering a valuable historical perspective on the biology of behavior more generally. Everyone, we think, can benefit from (re)reading Tinbergen (1963).

Key words: human ethology, behavior, psychology

INTRODUCTION

Like most people trained in behavioral biology "Tinbergen's four whys" were central to our understanding of how to study behavior: we were required to memorize the four kinds of "why" question, and explain what these entailed. Indeed, we can still recite in our sleep the different levels of explanation that characterize the major problems of biology, and earnestly describe how these should not be confused or conflated, and that each level should provide a self-contained explanation that nonetheless is consistent with the others. The one thing we weren't required to do, however, was actually read "On Aims and Methods in Ethology", the paper that Tinbergen published in 1963, and whose 50th anniversary this essay celebrates.

Reflecting on this now, it seems a bit of a shocker. Surely we should have been given it as a reading? Surely we should have been asked to absorb these insights from the man himself, and not a textbook? To sound less whiny, self-serving and useless: surely we should have taken it upon ourselves to search out and read the paper, given its importance and degree of influence on the field? (This is especially so for the Dutch half of this pairing, given that he was educated and now works at a University that has a "Niko Tinbergen chair in Behavioral Biology", and where Tinbergen's nephew himself carries on the ethological tradition). The thing is, of course, that the truths contained in Tinbergen's paper (1963) were, by the time we received our behavioral training (especially the more youthful Dutch half), taken to be self-evident: there were a multitude of studies in animal behavior, ethology and behavioral ecology that bore out

Tinbergen's ideas and suggestions quite convincingly. The 'promise of a biology of behavior' that Tinbergen hoped for in 1963 had, in many ways, been fulfilled: why bother to consult an early road-map that laid out the nature of the journey when the destination had been reached? Why not just revel in the accumulation of elegant behavioral studies and the insights they provided?

Having since rectified this gap in our education, we'd like to tell you why we think it's still worth the effort. First, (re)reading Tinbergen (1963) is a useful means to gain some historical perspective: it is slightly disorienting to realize that areas of research so familiar to us today, like behavioral ecology and evolutionary developmental biology, were, in 1963, no more than prescient twinkles in Tinbergen's eye. A second reason to make the effort is simply because it is a very good read, one that gives you a sense of Tinbergen the person, as well as Tinbergen the scientist or the Tinbergen the Nobel Prize Winner: he doesn't hesitate to reveal his admiration for Konrad Lorenz, admit his own ideas might seem unsophisticated, and never hides the fact that many of the issues he discusses are personal bees in his bonnet. The final and most important reason is that Tinbergen's paper continues to offer us a number of other, equally valuable, and relevant insights into the biology of behavior, in addition to the classic 'four questions', especially for those of us who study humans.

"An Admittedly Vague Question"

After a preamble establishing ethology as a branch of biology, and paying tribute to Konrad Lorenz (heralded as 'the father of Ethology'), Tinbergen begins his paper by tackling the issue of observation and description. Here, he describes how the earliest ethologists felt the need for a return to 'an inductive start', taking naturalistic observation seriously and asking the 'admittedly vague question' of 'why do these animals behave as they do?' In this, he notes, they were reacting against the behaviorist turn in American comparative psychology, where almost all studies of behavior were devoted to the experimental study of a small number of species (basically, pigeons and rats) under highly artificial conditions. The clear antipathy toward behaviorism expressed by Tinbergen no doubt reflects his (and Lorenz's) view that this approach placed too much emphasis on learning (i.e., electively treating behavior as an entirely psychological phenomenon), so neglecting hereditary influences and processes occurring inside the animal (i.e., treating behavior as a biological phenomenon); a view expressed, most notoriously perhaps, in their earlier theory of 'instinct', which was given a rather severe pummeling by Lehrman (1953) (although it's clear that Tinbergen had taken these criticisms on board by the time of writing the 1963 paper).

To digress just a little, it is somewhat ironic that the ethologists considered the behaviorist position too extreme given that Watson, in particular, emphasized environmental influences precisely to restore a balance he felt was lacking in American thought at the time, with its overt emphasis on innateness and simplistic ideas about instinct (see Malone 2009 for a discussion). Indeed, Watson's actual writings on this issue are much more reasonable than we're often led to believe (Malone 2009). Given that Watson studied the behavior of terns in the Florida Keys, he could even be seen as a 'proto-ethologist', as Dewsbury (1994) suggests. In later years, Lorenz at least came to realize that many of the differences between the European ethological view and that of the behaviorists were really more apparent than real. In a letter to Dewsbury, written in

1982, Lorenz says "I begin with the confession that I am quite aware of having done some injustice to the behaviorists in general and to John Watson in particular", although, rather less generously, he continued "I feel that having done some real ethological work on terns he is more reprehensible for having held his later views" (Dewsbury 1994, p. 178).

Tinbergen's (1963) mention of behaviorist psychology is, however, used to make the broader point that psychology as a whole "skipped the preliminary descriptive stage that other natural sciences have gone through, and so was soon losing touch with the natural phenomena" (Tinbergen 1963, p.411; a point developed more fully by Malone 2009). This lack of a descriptive phase can still be felt in certain areas of contemporary human psychology, as well as continuing to affect certain areas of comparative psychology (Barrett & Stulp 2013). This is particularly true of human evolutionary psychology, where experimental studies (that often rely on some form of self-report) dominate the discipline to the exclusion of descriptions of people's actual behavior. In some ways, then, the anniversary of Tinbergen's paper could be used to prompt a similar "return to nature" and "an inductive start" in our studies of humans; we should place greater emphasis on ethology as a fully integral part of human psychology, and not just an allied discipline. This would be particularly elective and useful in the context of industrialized societies where there is still a paucity of naturalistic, observational studies. Indeed, the ethnographic literature on small-scale societies, as well as the early cross-cultural literature in human ethology, provides us with a much more comprehensive understanding of natural patterns of human behavior, but does so in the context of societies that are very different from those in which most contemporary psychological research is conducted (a point we return to below).

Pushing for an ethological turn not only means supporting efforts to observe behavior in its natural social settings, but perhaps it also requires us to be a little more skeptical of findings from self-report pen-and-paper tests, which record only what people say and leave unanswered the question of what they actually do (unless, of course, one is interested in the study of self-report itself; although this is not usually the goal of such research). The great emphasis on preferences in studies of human mating behavior, for example, may need some reconsideration, as recent studies have demonstrated that expressed preferences show only a moderate relationship to actual pairing in contemporary societies (Courtiol et al. 2010 ; Stulp et al. 2013a). Moreover, mutual mate choice processes can sometimes result in compromises that fail to satisfy the preferences of either sex (Stulp et al. 2013b). Although discovering that "you can't always

¹ Another interesting thing about Tinbergen's observation regarding the necessity of observational studies is that, even as early as 1963, he was worried that the descriptive phase was coming to a "premature end" and that this would be to the detriment of the discipline as a whole. As he notes "already there are journals which demand a reduction of descriptive material to the absolute minimum required for an understanding of the experiments reported on (or even to less than this minimum)" (p.412). Any contemporary academic can tell you that this was a trend that has continued more or less unimpeded; indeed, one can only imagine how Tinbergen would view modern academic publishing where all the details of the study are increasingly to be found in online "supplementary material" and not in the body of the paper itself. More to the point, it is also the case that any descriptive or correlational study of human or non-human behaviour is usually prefaced by the adverb "merely" as though it cannot tell us anything much of interest.

get what you want should come as no surprise to scientists and laypersons alike, the continued scientific focus on preferences alone, with relatively few attempts to relate these preferences to actual behavior, is rather surprising. This is especially so given the way in which preference studies are placed in an evolutionary context, and are often suggested to represent psychological adaptations. Without measuring how these preferences relate to current behavior, however, few conclusions can be drawn about the meaning of such preferences, and even less about their potential adaptive value, whether in the past or the present day.

More focused observational ethological studies that characterize exactly what people do in different kinds of social and ecological settings, with detailed descriptions of how they engage in particular kinds of behavior, would thus lend balance and insight to contemporary psychological research on humans. The pioneering work of Eibl-Eibesfeldt (1970) and his students aimed at exactly that, of course, and indeed beat Wilson's (1975) *Sociobiology* to the punch with its evolutionarily informed view of human social behavior: *Ethology: the Study of Behavior* was published in 1970 and *Love and Hate: the Natural History of Behavioral Patterns* was published in 1971. Ethological work on human courtship behavior, for example, provides the clear and obvious link between preferences and choice processes, and can help generate a more well-rounded view of human mate choice (e.g., Grammer 1990, 1998). Ethological work has also shown itself to be particularly valuable when placed in cross-cultural perspective as in, for example, the classic work on behavioral expressions and signals like the *eyebrow flash* (Grammer et al. 1988). Indeed, the identification and observation of similar behavioral patterns across cultures can provide useful information about the likely evolutionary history of a trait, perhaps even more so than any pen-and-paper test on a Western sample. This is why we would argue that descriptive, naturalistic studies of behavior should be an integral part of any evolutionarily informed human psychology, and it would be wonderful if we had more studies taking place in modern industrial society. It is clear, then, that Tinbergen's words still hold true today, when he says: "Our science will always need naturalists and observers as well as experimenters and we should certainly not discourage the man with a gift for observation. Instead, we should attract such men for they are rare." (Tinbergen 1963, p. 413; indeed, some may even be women). Such sentiments were recently echoed by Wulf Schiefelshvel, President of ISHE, when he stated that while "ISHE embraces laboratory, survey, or theoretical approaches, our distinct identity lies in the pursuit of direct observation in natural environments and that approach, so essential to good science, must be particularly encouraged" (quoted in Fisher 2013; see also Bateson & Laland 2013).

"The Godwit Walks Differently From the Lapwing"

Obviously, we wholeheartedly share these sentiments regarding observational studies, which makes it interesting to note again how much work in contemporary evolutionary psychology and, to a lesser extent, human behavioral ecology, doesn't seem to draw on the ethological literature as heavily as it might. The same is true of the (under appreciated) work of Roger Barker in the US (e.g., Barker 1978; Barker and Wright 1951, 1955). His work in *eco-behavioral science*, which was strongly ethological in approach, was prompted by his recognition that he had no means of placing his experimental results on children's development in context, thanks to a complete lack of any description

of how children went about their daily business (He% 2001). His subsequent work demonstrated that children's behavior was more accurately predicted by the nature of the "behavioral setting" than by any immediate stimulus a person received, with the result that the behavior across people within a given setting was more similar than any given individual's behavior across settings. To put this in concrete terms: his studies showed that children in a playground all behaved very similarly to each other, whereas the behavior of any given child in a playground setting versus that of, say, a church, was very different. His work helped reveal how the different environments we encounter, which includes the people in them, both generates and constrains certain possibilities for action, demonstrating how it is possible to locate meaning in the shared public environment, in the form of the practices shown by people engaging with each other in a physical space structured and created by their own activities. In so doing, he moved away from the classic Cartesian notion that all meaning is both created and located solely in the private, individual mind (see He% 2001 for an excellent review of Barker's work).

Along with the work in (a slightly different kind of) ecological psychology by James Gibson (e.g., Gibson 1966, 1979), Barker's research highlighted the deep significance of the natural environment for psychology and behavior, and close study of this work makes clear why a satisfactory psychology can be achieved only once the environment is recognized as constitutive of human cognitive systems, and not just the stage on which the products of wholly internal cognitive systems play out (see Barre& 2011 for a review of these ideas in relation to non-human animals as well as humans). In other words, this perspective is one that embraces the classic Darwinian view of the mutual dependence of organism and environment (organisms shape their environments as much as they are shaped by them) but takes this further, arguing that organism and environment do not only exist in causal relation to each other, but that each forms a constituent part of the other. The cognitive system of an animal is not contained within the organism's "skin and skull" but incorporates environmental structures as well, and as such should be considered more of a process than as a "thing".

This view resonates with those of us who would like to escape the structures imposed by the dominant representational and computational theories of mind with its strongly anthropocentric undertones (Barre& 2011). Indeed, work in the field of "distributed cognitive ethologies" (e.g., Barnier 2008; Su&on et al. 2010) is beginning to make some headway here, where ethological and ethnographic forms of data collection are incorporated into studies of classic psychological constructs, like memory, which are usually investigated purely experimentally. This fundamental shift in philosophical perspective opens up the way to ethological study as part and parcel of "traditional psychology". To transfer part of Tinbergen's (1963) survival value argument to a new context, this approach involves an attentiveness to seemingly trivial details of behavior, like the difference in the way a godwit walks compared to a lapwing that, on closer inspection, turn out to be crucial to our understanding of how "flexible, adaptive behavior is brought about. This more holistic approach may thus be crucial in providing

² Ö..yet Klomp (1954) showed that these differences are adaptive: godwits lift and fold their feet much more than do lapwings and thus avoid getting their toes caught in the tall grass in which they breed. Lapwings avoid habitats with tall vegetation.Ö Tinbergen (1963, p. 421).

us with a well-rounded assessment of the ways that evolution acts to produce behaviorally "exible and psychologically sophisticated animals.

"A Human Being Has to Learn to Stop When the Traffic Lights Turn Red"

To develop this theme further, one of the aspects of human life that points to our immense behavioral "exibility is, of course, the sheer diversity of human cultural practices, and the learning mechanisms that support these, both during ontogeny and throughout adult life. As Tinbergen puts it, "[a] newly-hatched herring gull pecks selectively at red objects...but a human being has to learn to stop when the traffic light turns red...It is the contrast between man and animals in the ways they acquire either "knowledge" or "skill" which arouses in most of us an interest in the ontogeny of behavior" (p.423), where ontogeny here refers not only to early development but overlaps with the "causation of cyclical or recurring behavior in the adult." (p.427). It is therefore somewhat disturbing, as Henrich et al. (2010) have recently pointed out, that our knowledge of human psychology, and hence our means of understanding how such practices are acquired and transmitted throughout life, is disproportionately reliant on results from WEIRD people (i.e., those who are "Western, Educated, Industrialized, Rich and Democratic"; see also Burman 1994 for a discussion of this same problem in relation to developmental psychology).

On the one hand, this is acceptable if we recognize the limits of such an approach, and understand we are simply demonstrating something about the psychological processes that take place in a laboratory setting; that is, as Mook (1983) pointed out, external invalidity is not necessarily a problem if our results are not designed to generalize to "real life", but are instead aimed at demonstrating the kinds of responses that are possible given a particular set of conditions. On the other hand, given that most psychological studies are conducted precisely because their authors wish to explain our real-world behavior, the use of WEIRD populations is, indeed, problematic. This is especially the case when such research adopts an explicitly evolutionary perspective, with the results being generalized not only to the population from which a sample is drawn, but to the human species as a whole.

One solution to this problem, applied by Henrich and his co-workers, as well as other evolutionary psychologists, is to conduct studies across different cultures to help establish both the generalisability of results, and their potential universality. This is, of course, the obvious approach to take, but we feel it is also worth mentioning that many of the experimental paradigms (e.g., the ultimatum and dictator games) now being used to examine cultural diversity are pretty WEIRD themselves. That is, these are games devised by Western behavioral economists and, as such, they are anchored firmly to a Western worldview. Assuming that, deep down, all humans are a particular kind of cost-benefit analyst is entirely appropriate as a model at the functional level (after all, this is the fundamental economic approach that forms the basis of evolutionary analyses of behavior, adapting "economic rationality" to "biological rationality"), but we need to ensure this doesn't get confused with the "proximate" causal world-views that fundamentally shape people's lives in different ways in different places (and indeed across different times). Uskul et al. (2008), for example, have shown that farmers and fishermen from the Black Sea show more holistic forms of categorization compared to herders from the same region; work that builds on Nisbett's (2003) classic research showing similar

differences between East Asian people and those from the US. Recent work has also shown cultural variation in perceptual processes, like eye movements during scene perception (Chua et al. 2005) and the ways we look at faces (Blais et al. 2008).

Part of the worry here is that, if we fail to fully appreciate this fact, other societies will end up being characterized solely by their degree of deviation from the pattern found in modern Western society (in much the same way that an anthropocentric view of cognition anchors other animals' cognitive capacities to human cognitive processes: Barrett 2011). That is, while we can and should document both cultural and ecological variation, and using WEIRD games cross-culturally is a cost-effective and efficient research gambit (especially when studies are carried out across populations within a single cultural group as well as across them: Lamba & Mace 2011), we need to recognize that some aspects of this variation will be hard to interpret from a purely behavioral economic or ecological perspective. This is precisely because such variation reflects the influence of culturally-specific historical processes that have shaped the worldviews of people in their particular cultures, and they have done so in ways that often resist an easy translation into the worldviews of the scientists who study them. In this respect, naturalistic ethological studies of our behavior and habits, rather than experimental studies within a 'classic' psychological paradigm, may help shed more light on how we perceive the environment and each other, and the kinds of strategies and tactics we employ to solve our ecological and social problems.

This is not to say that we should abandon these pen-and-paper-WEIRD methods altogether. Rather, our argument is that we should use all means at our disposal to 'triangulate' on the issues of interest, and so generate good answers to our questions. Human society is simply too complicated and too open-ended for any one approach to provide an exhaustive explanation of what it means to be human. As Tinbergen (1963, p. 427) writes, one can distinguish between two sets of processes that occur 'when a man is afraid of a "ying plane" because he sees it' but also because he has been 'bombed' out a child' and that 'each covers part of the total causal chain involved.' In other words, we require multiple overlapping explanations of the same phenomena, and an appreciation that these will both intersect and interact in complex ways. This is, of course, allied to Tinbergen's ideas regarding integration at all levels of analysis, but it adds to it a recognition that this entails an explicitly pluralist approach, where the idiosyncracies and peculiarities of different cultures are not ironed out simply into variants of a single universal pattern. To be sure, this interest in diversity represents part of the motivation behind Henrich et al.'s (2010) paper, but we would argue that ethological studies, as well as more cross-cultural psychological studies, should form a central part of this research strategy.

"...In Its Subtler Forms it is Still Very Much With Us"

For our final point, we need to turn to an earlier Tinbergen paper, in addition to 'On aims and methods'. Specifically, Tinbergen (1951, p.4) was concerned with the dangers of a certain kind of subjective, teleological thinking in animal ethology: 'There has been, and still is, a certain tendency to answer the causal question by merely pointing to the goal, end or purpose of behavior' and that this tendency was 'seriously hampering the progress of ethology'. What he was getting at here was the tendency of many

naturalists to construct arguments of the kind "the animal attacked aggressively because it was angry". Obviously, such reasoning confuses effect (aggressive behavior) with cause, with the additional bonus of using potentially inappropriate anthropomorphic language. The main reason for this way of speaking about animal behavior was, he suggested, because "... introspection leads us to believe that our behavior is controlled, to a certain extent, by "foreknowledge" of ends or goals" (p.4). By the 1963 paper, Tinbergen was able to report "one rarely meets with it in its crudest form ("the animal attacks because it feels angry")" (p.413), but also noted that the problem had not yet gone away, but had simply taken a more subtle form. Ironically perhaps, as Scofield & Phillips et al. (2011) recently pointed out, confusion of the "cruder" form, with function given as proximate cause, still occurs in some areas of human research. Scofield & Phillips et al. (2011) show how, among other examples, the prominent and influential idea of "strong reciprocity" falls prey to this confusion, where "a predisposition to reward others for cooperative, norm-abiding behaviors... [and] a propensity to impose sanctions on others for norm violations" (Fehr & Fischbacher, 2003, p. 785) is offered as a solution to the ultimate problem of why humans cooperate (Scofield & Phillips et al. 2011).

This seems to be a point worth reiterating here because many human evolutionary studies attempt to identify the (proximate) cause of behavior by reference to its function, and do so as a deliberate strategy of "reverse engineering". When we find evidence to support the hypotheses and predictions generated by this process, there is a temptation to assume that we have identified or characterized the mechanism by which the behavior is produced when, really, we have done nothing of the sort. For example, to hypothesize that to avoid incestuous mating, women should reduce contact with their fathers during fertile periods and then, when the evidence suggests this might be the case, to conclude that this can be attributed to a mechanism designed to reduce contact with fathers during fertile periods ("We suspect our data reveal the operation of two different systems: one motivating females to avoid their fathers during periods of high fertility regardless of how close the relationship is" (Lieberman et al. 2010, p.4), is to explain precisely nothing about how the behavior is brought about in terms of a "proximate analysis". In a sense, it is no more than a description of that which a "proximate analysis" could potentially reveal. It therefore seems clear that, even after all this time, we still need to heed Tinbergen's words, and be just as aware of the dangers of "anthropomorphising" our own behavior as we do when dealing with other animals (Kennedy 1992; Barrett & 2011), and just as vigilant about mistakenly treating functions as causes.

CONCLUSION

In essence, by highlighting the need for more ethological work on humans, we are simply advocating for Tinbergen's own approach to research, with its exemplary balance of observation and experiment. Today, with advanced means of collecting phenotypic, genetic and physiological data, in both the field as well as in the laboratory, along with advanced statistical techniques, we are even better placed to be able to conduct the kind of integrative studies he promoted, and so provide more comprehensive answers to all four

of the questions he identified. Moreover, perhaps now is the time to start integrating the answers to the different questions in a more rigorous fashion, which is still rarely achieved (Barrett et al., 2013; Bateson & Laland, in press). Recent technological advances also allow us to collect human data with unprecedented depth and on a vast scale. MIT's Deb Roy, for example, created a "speech home", rigging up microphones and cameras throughout his house to capture and computerize every single utterance made by his infant son, in its natural context, over the first three years of his life. The resulting high-density longitudinal corpus has been used to create new data-driven methods for analyzing human speech acquisition, and testing developmental hypotheses (see e.g., Brandon et al. 2012). Similarly, Sandy Pentland's work on "big data" and "reality mining" uses mobile phone data to uncover the patterns that exist in everyday life, tracking the "digital breadcrumbs" which, when pulled together, offer increasingly comprehensive pictures of both individuals and groups (Lazer et al. 2009). Our ability to tap into the natural social behavior of our fellow humans, particularly in large-scale industrial society, adds another analytical layer to the standard observational and experimental techniques used by ethologists. It will no doubt give us even greater insight into the complex interplay that takes place between individuals and the groups in which they live. By continuing to follow in Tinbergen's footsteps, and integrate these new kinds of data with more traditional approaches, it is clear that exciting times for human ethology lie ahead.

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