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Behavioural ecology's ethological roots

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ABSTRACT

Since Krebs and Davies's (1978) landmark publication, it is acknowledged that behavioural ecology owes much to the ethological tradition in the study of animal behaviour. Although this assumption seems to be right—many of the first behavioural ecologists were trained in departments where ethology developed and matured—it still to be properly assessed. In this paper, I undertake to identify the approaches used by ethologists that contributed to behavioural ecology's constitution as a field of inquiry. It is my contention that the current practices in behavioural biology owe ethology something much subtler than the simple transposition of Tinbergen's Four Problems for heuristic purposes. Demonstrating what ethology inherited from the long naturalist tradition shows the tensions that strained the field and that later led to the loss of both its unity and its specificity. It also allows for a precise delineating of what behavioural ecology picked up from the ethological practice, and it helps to cast some light on the introduction of economical thinking in behavioural sciences.

1. Introduction

Amongst biologists studying animal behaviour, there is a general consensus on the foundational role of ethology. Behavioural ecologists (Alcock, 1973; Cézilly, 2008; Krebs & Davies, 1978) explicitly recognise the pioneering work of classical figures such as the three recipients of the 1973 Medicine Nobel Prize: Karl von Frisch (1886–1982), Konrad Z. Lorenz (1903–1989) and Nikolaas Tinbergen (1907–1988). Owing to the diversity of his work (Kruuk, 2003), to a non controversial career in comparison to Lorenz's (Kalikow, 1983; Krebs & Sjölander, 1992; Deichmann, 1996, pp. 179–204), and to its critical involvement in the development of ethology in the Anglo–American world, Tinbergen seems to hold the central position of this pantheon. This has certainly been helped by the fact that his "Four Problems", following the distinction made earlier by Ernst Mayr (1961), have become a genuine tool to introduce and teach behavioural sciences, and behavioural ecology more specifically. Given its important epistemological value, it is no surprise if the framework outlined by the Four Problems is considered as ethology's trademark. This is unfortunate because this salient feature in the historical development of the biology of behaviour offers a poor assessment of ethology's legacy. The current understanding of animal behaviour is not simply based on a better and more balanced understanding of the Problems, using improved technical and conceptual means for instance. Amongst other fields of inquiry, behavioural ecology has both drawn and departed from much subtler elements of the ethological practice.

Narrowing ethology's posterity to the framing of the Four Problems is arguably a simplistic view of the field. But it is one that still make some sense: it allows for the understanding of behavioural ecology as part of a long tradition of scientific inquiries and this, in turn, probably plays an important psychological function for practitioners of such a young scientific discipline (Gross, 1994). Unfortunately, granting too much attention to the Problems brings along some difficulties as well. First, it obscures most of the differences between ethology's and today's understanding of animal behaviour. Overall, ethology taught contemporary behavioural sciences much more than the framing of their problems. But it also defended positions and assumptions that were short lived, and dropped off one by one from the 1950's. In that sense, entertaining a caricatured image of ethology—and leaving aside most critical

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details—tends to bias the analysis of contemporary practices in the field of animal behaviour. Moreover, and although the topic won't be dealt with in what follows, it maintains an important conceptual haze over the current uses of the word ethology as in neuroethology, cognitive ethology and applied ethology.

With the first of these two considerations in mind—that is the analysis of current practices in behavioural sciences—, I undertake to draw a critical appraisal of ethology's contribution to the constitution of behavioural ecology. As it will ultimately be shown, behavioural ecology has inherited two distinct but complementary approaches from ethology, or two inference-building schemes[1]: the comparative and the adaptationist approaches. First, in order to assess ethology's overall contribution, I will draft the context in which ethology arose and initially developed to become a scientific discipline. Since this field of inquiry has been given a brilliant general history (Burkhardt, 2005), as well as numerous accounts bringing forth the more particular histories of its founding fathers (Von Frisch, 1967a; Evans, 1975; Lorenz & Kickert, 1978; Dewsbury, 1989; Röell, 2000; Kruuk, 2003) my description of ethology will be strictly focused on the epistemological elements it was both a concatenation and an expression of. Then, having done so, it will be possible to add to the picture by bringing forth the conception of animal behaviour it implied at that time. It is arguably an ambiguous one: most of the early ethologists seem to have advocated an understanding of animal behaviour that had not completely parted with vitalism. But, and this help explains why circumscribing the scientific field encompassed by the word ethology is a difficult task, this representation of animal behaviour was quickly sharpened and replaced by a strictly mechanistic one. It is this later conception that gave hold to the various economical understandings of animal behaviour, and from which arose and prospered the thoroughly evolutionist stance of behavioural ecology.

2. Ethology as a novelty

Basically, ethology can be said to be an offshoot of the long and determining tradition of Natural History. Although it is not the place to draw a precise account of this important tradition, it is useful to highlight some of the tensions that have repeatedly challenged its boundaries: these allow us to appreciate the very intellectual fabric from which ethology arose. Importantly, the tensions I am concerned with are intertwined, but for the sake of simplicity it is useful to separate them. Thus, in this section, I consider Natural History's determining impact on ethology according to the three following contrasts: the one between empiricist and rationalist grasps of nature, the one between vitalism and mechanism, and the one between field and cabinet practices.

Since antiquity, accounts on animal whereabouts are torn between two opposed epistemological currents. On the one hand, there is the tendency to investigate individual organisms for themselves, and to draw and compile observations judged relevant about them. On the other hand, there is an important movement to design philosophical systems that could possibly account, and ideally explain, the ever broadening collection of facts about the natural world. The *Histoire naturelle, générale et particulière* (1749–1788) of Georges-Louis Leclerc de Buffon (1707–1788), since it aimed to establish a middle ground between the excesses of empiricism and rationalism, allows the appreciation of these two polarized conceptions (Farber, 1975; Llana, 2000). According to Buffon, Natural History is more than the accumulation of elaborated descriptive works such as René Antoine Ferchault de Reaumur's (1683–1757) *Mémoires pour servir à l'histoire des insectes* (1734–1742). Indeed, the compilation of facts must partake in the knowledge of the relations amongst natural objects and, conversely, this knowledge gives its orientations to the observational and descriptive work. Hence, a practice based on abstract and a priori principles, such as the Linnaean taxonomy, is meant to fail to account for important features of the world. This being said, Buffon's own methodology still relies on some important rationalist premises, as Phillip Sloan (1976) demonstrates.

At its foundation, ethological practice arose in the broad range of middle-ground positions opened up by Natural History. Although it pursued Natural History's empiricist tradition of description, it also heavily relied on a taxonomic frame of thought. Given the way 'biological sciences' had developed at that time, this was almost inevitable. Indeed, as nature provided a plethora of phenomena from which regularities could be inferred, interests in animal behaviour at the end of the 19th century were mainly drawn in three broad directions. If one wished to study the diversity, the specific character or even the evolution of behavioural manifestations, rather than their underlying physiological or psychological mechanisms, zoology was the sole perspective available at the time. Whereas Buffon was confronted to an innovative and bold attempt to classify living beings, preethologists such as Charles Otis Whitman (1871–1945) and Oskar Heinroth (1842–1910) were simply trained in the practice of taxonomy and morphology. It is thus no surprise if early ethologists undertook to put their behavioural observations into a taxonomic perspective, defending the idea that some units of behaviour (the later *fixed action patterns*) can be used in the same way morphological characters were at that time (Lorenz & Kickert, 1978, p. 13). As a result, ethologists were at first mostly preoccupied by behavioural traits of a certain type: those relevant to the field of taxonomy.

Secondly, at the time ethology started to acquire its theoretical framework, thus slowly distancing itself from the morphologists' enterprise, it had to posit itself in the mechanistic-vitalist debate. Inherited along with the practice of Natural History—especially along considerations on the directedness of animal conducts, and on the special character governing the organization of living entities (Hein, 1972)—this tension was to critically influence, and restrict, the array of phenomena that initially attracted the attention of ethologists. The first important step toward the adoption of a purely mechanistic framework was the adoption of the 'objectivist' stance (Tinbergen, 1974 [1951]), thus leaving aside all questions relating to animal subjective experiences, and taking a stand against purposive psychology such as William McDougall's (1871–1938). But this epistemic statement about the type of phenomenon that ought to be studied by ethology did not completely expunge all traces of vitalism. Indeed, the theoretical foundation laid down by Lorenz was constructed around the convenient but highly ambiguous concept of drive. Nevertheless, the units that were actually observed by ethologists, the 'fixed action patterns', were considered first and foremost to be specific mechanical expressions of some complex underlying neural organization. This materialist hypothesis had many consequences for the later development of the discipline. Firstly, being in line with most of the biological work of the time, it restored some sort of respectability to the observation of animal in the wild. Secondly, the hypothesis was perfectly coherent with the task of comparing units of behaviour between related species for taxonomic purposes: as discrete expressions of a neuro-physiological constitution, the fixed action patterns were thus considered essential characteristics of the species.

[1] By inferences-building scheme, I have in mind a pattern that allows the drawing of a specific type of material inferences (as opposed to formal inferences). This is an important epistemological claim that requires an independent treatment. On the topic of material inference, see Norton, 2003 and Brigandt, 2010.