Ethological principles in the study of animal behaviour

Today, the study of animal behaviour is as far reaching as it was for our hominin ancestors who must have had some sense of understanding of animal behaviour while navigating through ancestral African environments. The effects of behavioural research on contemporary civilizations contributes to many aspects of human social and medical research, as well as impacts topics in conservation, habitat/resource sustainability, food production, and population dynamics. Over the last half century, animal behaviour has taken on several different forms. The aim of this of this essay is to explore the scientific study of modern animal behaviour known as ethology: Look at the historic approach to animal behaviour; review the central concepts of ethology, expanding upon Tinbergen's (1963) four questions of causation, ontogeny, function, and evolution; illustrate the benefits of using ethological methodology in the study of behavioural phenomenon and discuss the potential impact of ethology on future behavioural research. I examine these questions in the light of comparative research on human and nonhuman primates.

Animal Behaviour: A Brief Introduction

The study of animal behaviour spans across many disciplines, each field asking specific questions and offering different levels of explanation. Behaviour can be described in terms of underlying hormonal/physiological mechanisms, developmental mechanisms, adaptive function, and in terms of evolutionary pathways of behaviour (McFarland, 1993). Before the advent of ethology, most behavioural disciplines attempted to answers only one or two of these questions at a time.

For example, investigating how and when behaviours evolved confront behavioural scientists with a daunting task. Evolutionary biologists are equipped to answer these types of questions by using a phylogenetic approach. Phylogenetic trees allow scientist to investigate correlated evolutionary change and reconstruct ancestral states, making it possible to identify evolutionary relationships between homologous behaviours in closely related species (Nunn and Barton, 2001). This comparative method is useful if you are interested in understanding when a specific behaviour emerged in a species' evolutionary history. Often, this line of inquiry leads researchers to generate addition questions: What environmental changes would have selected for this type of behaviour? Is this behaviour adaptive? How would this behaviour increase fitness and persists over time? Comparing similar behaviours between closely related species, occupying a similar niche, and evolutionary histories, provide a solid framework to begin generating testable hypotheses to these aforementioned questions.

In the early 20th century, psychology comprised its own unique set of methods and experimental techniques that usually consisted of running controlled experiments in a laboratory setting while investigating behaviour (Bateson and Klopfer, 1989). Psychologists were concerned with designing experiments that tested proximate causations of behaviours. For example, a psychologist might investigate the developmental factors that affect the acquisition of learning and imprinting (Martin and Bateson, 2007). Investigating causal relationships to behaviour provide insight into whether behaviour is innate or if it is learned in the context of an individual's environment.

On the other hand, behavioural neuroscience aimed to understand causal physiological mechanisms and corresponding neural controls that are modulated by environmental stimuli (Carlson, 2006). This field is concerned with identifying how an animal's physiology interacts and is influenced by environment factors, and how this interaction elicits a behavioural response.

In the mid 20th century, the behavioural sciences operated independently of one another, as if each discipline's research was a mutually exclusive approach. At that time the competing schools of thought failed to recognize the significant relationships between causation, development, function, evolution, or how each of the corresponding fields actually were complementary to each level of explanation. The scientific study of animal behaviour was in dire need of a complete synthesis that would incorporate proximate and ultimate classes of behaviour into a complementary, integrative framework.

The Birth of Ethology

The modern study of ethology filled this gap, and sought to piece together the fragmented behavioural scientific approaches. This new field aimed to explain all four classes of behavioural determinants, providing a full account of the phenomenon under study (Bateson and Klopfer, 1982). In the remaining section, I will define ethological principles, highlight the pitfalls of focusing on either proximate or ultimate levels of explanation, and present the case of modern ethology as the more systematic approach to the study of animal behaviour.

Understanding the reason why a particular animal behaves in a certain way requires the right type of questions to be asked. In 1963, Niko Tinbergen, one of the founders of ethology, published the paper, “ On Aims and Methods of Ethology.” In this paper he introduced four distinct and broad questions that he used in trying to answer the question, “ Why does an animal behave like that?” (Shettleworth, 1998). In doing so, he laid the foundation for the study modern ethology. Ethology is the study of animal behaviour which attempts to answer four classes of questions: causation, ontogeny, function, and evolution.

If a researcher wanted to know why baboons groom one another, it would be important to consider the immediate external stimuli which invoke a specific behaviour response in the animal, or otherwise stated you would want to look at proximate causations of behaviour. Researchers would want to develop questions that reveal causal answers: What external environmental stimuli and internal stimuli cause the animal to respond in a particular way? Answers to these questions often rely on the underlying psychological, physiological, and neurological mechanisms regulating an animal’s behaviour (Martin and Bateson, 2007). A possible causal explanation to why baboons groom would be that grooming functions as a as a mechanism to reduce stress (Crockford and et al., 2008).

Moreover, Tinbergen (1963) was interested in investigating how changes in behaviour “ machinery” are affected during development and coined the term ontology to describe this process. What was it about an individual’s development that leads them to behave in a particular manor? Answers to these type of questions require scientists to look at whether a behaviour is

learned or refined through development processes such as imprinting or possibly if it is generated by a genetic predisposition.

In addition to the importance of providing proximate (causal and ontological) levels of explanation, two classes of questions investigate ultimate factors are equally important to investigate. Ultimate questions are interested in understanding how evolution has selected for and produced specific behavioural phenomena. One such questions looks at the adaptive/survival value a given behaviour would confer on an individual. For example, why do primates participate in intergroup aggression? These type of questions are considered functional investigations. As an example, evolutionary based cost-benefit theories would look at the functional/adaptive significance to intergroup aggression. One possible hypothesis to the question of why individuals exhibit intergroup aggression is that the more aggressive primate groups will achieve increased access to reproductive females and increased access to resources (Manson and Wrangham, 1991). Natural selection imposes differential reproductive successes, understanding these functional relationships provide answers to adaptive questions.

The last behavioural problem Tinbergen identified was that of evolutionary history. He explains, “ The fact that behaviour is in many respects species-specific, and yet often similar in related species,...[leads to] the natural conclusion, namely, that behaviour should be studied comparatively just as structures, with the ultimate aim of elucidating behaviour evolution...”(Tinbergen, 1963: 427). Here Tinbergen advocates a phylogenetic approach to analyzing behaviour. Ethology aims to show how natural selection shaped the evolution of behaviour over time while

uncovering possible evolutionary pathways (Tinbergen, 1963 and Barret, et al., 2002). For instance, if researchers were interested understanding why humans breathe the way they do, they would be interested in knowing how we evolved lungs? Farmer (1997) provides an evolutionary account to this question: Human lungs are believed to have evolved from ancestral fish gas bladders. This level of explanation provides clues into when a behaviour may have first arisen and when it diverged between ancestral species. Ethology attempts to reconcile these four levels of explanation into a comprehensive framework for understanding.

One such study illuminates the dangers researchers face when they incorporate only one level of explanation. Power (1975) conducted a study in which he tested whether mountain bluebirds lack altruistic behaviour. He attempted to show this by removing one mate of a pair caring for nestlings to test the claim; if altruism existed, a new mate would instinctually care for the nestlings. The study showed that new mates did not care for the nestlings, therefore the hypotheses, mountain bluebirds are altruistic, was rejected (Power, 1975).

This study was criticized because it failed to account for the fact birds do not usually accept young unless hormonally prepared for them (Emlen, 1976). This process usually entails both mating partners being present during the events leading up to hatching and the presence of nestlings (Emlen, 1976). This physiological knowledge into hormonal cues in mountain bluebirds generated an alternative hypothesis; the new mate did not provide care to the nestlings because it lacked the proper hormonal activation. Therefore, it was concluded that the original hypotheses posed by Power was erroneous

and failed to properly demonstrate if mountain bluebirds were altruistic. This example illustrates how tenuous behavioural studies can appear when they fail to incorporate ethological principles into their research design.

Applied Ethological Principles Furthering Insight into Human Behaviour

The more we learn from studying animal behaviour, the more we reveal about ourselves. Because humans are social primates, more ethological attention has focused on the study nonhuman primates as the best model to explain the social behaviour of humans. One such example into the potential benefits of ethological inquiry is articulated by the investigation into the effects of empathy, as one possible emotional mechanism that has evolved to help maintain and reinforce social bonds. Empathy is a complex emotion which has been proposed to exist in humans and nonhuman primates.

Many ethologists have focused on chimpanzee and bonobo social systems, our closest extant ancestors, to better understand potential regulating factors involved in social bonding that could have helped promote and sustain the evolution of cooperation altruism. De Waal (2008) suggests humans as well as nonhuman primates both possess capacity to empathize with others, as a regulating mechanism of directed altruism. Directed altruism is defined as “ helping or comforting behaviour directed at an individual in need of pain, or distress” (De Waal, 2008).

Mounting evidence supports the view; similar cognitive capacities exist in human and nonhuman primates that could facilitate empathetic impulses and be linked to our similar evolutionary histories. Several studies have

shown infants have an innate capacity to be influenced by the welfare of others. “ Infant nonhuman and human primates are known to respond to the distress of others with distress” (Preston and de Waal, 2002). Furthermore, Preston and de Waal consider the hormonal release during suckling in maternal care as a positive promoter that rewards the giver with “ feel good hormones (ie. Oxtocin) to engage in directed altruism (Panksepp, 1998). This hormonal release could play a proximate role in promoting the perceiver to internalize the emotional state of another individual.

Building on the neuroanatomy of empathy research, the central nervous system and the Perception Action Mechanism (PAM) have also been considered as a hard-wired link that controls emotional state matching and motor mimicry in humans and nonhuman primates (Preston and de Waal (2002). Chimpanzee studies reveal an increase in brain temperatures in the right hemisphere when chimpanzees are shown videos of severe aggression compared to neutral or positive videos (Parr and Hopkins, 2000). Negative videos directed a specific physiological reaction in the brain in response to the negative stimuli. These studies identify a potential link between the areas of the brain that are activated when individuals observe and witness emotional states of others (Preston and de Waal 2002). Meaning, the cognitive capacities for the emotional complex of empathy may not be strictly limited to humans, but may also function similarly with closely related nonhuman primates.

The suggestion that nonhuman primate may also posses the capacity for empathy has not come without contention. Many scientists believe humans

are the only species cognitively advanced enough to possess the innate capacity to internalize the emotions of others (eg., Schino, 2007).

If Preston and de Waal's claim is true, then empathetic hard-wiring has an ancient evolutionary lineage that evolved long before modern humans. Theoretically, innate empathetic capacities would help maintain and shape cooperation, reconciliation, and altruism between human and nonhuman primates. The origins of such a complex behaviour may have originated due to stronger selection on maintaining increased group size within ancestral primates. Therefore, it should be no surprises if we discover humans due in fact share the capacity to empathize with other social primates. This study promotes a possible link between the evolution of the complex sociality and empathetic emotional capacities in primates. Investigations like this exemplify the potential ethological methodologies pose when looking into proximate and ultimate roots to complex human and animal behaviour.

Discussion

An ethological approach to animal behaviour derived from early behavioural sciences. Today, modern ethnology places emphasis on different biological aspects to account for the contexts in which animal behaviour occurs using physiological and evolutionary perspectives. Most behavioural phenomena are not satisfactorily explained at the proximate or ultimate levels. Therefore, to understand the behavioural process fully, ethology appropriately focuses on answering Tinbergen's four questions to correctly identify the reciprocal relationship between causal and evolutionary explanations of behaviour.