EVOLUTION OF SOCIALITY AND COOPERATION IN TROPICAL ANIMALS

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Contents

Summary

In this chapter we broadly review the conceptual framework for cooperative and social behavior, illustrating these concepts with examples from the tropics. We provide a brief historical perspective concerning the interest that cooperative behavior has generated in the past, linking this with the development of hypotheses and ideas in the psychology domain. We present a brief list of costs and benefits linked with sociality, and discuss important concepts such as group vs. individual selection, reciprocal altruism, by-product mutualism, kin selection, Hamilton's Rule, and inclusive fitness. After this introduction to the theory underlying the evolution of cooperation, we provide examples of animals that have developed cooperative breeding within two distinct vertebrate taxa, birds and mammals. After introducing the definitions available for cooperative breeding

in these two groups of animals, we highlight systems for which there are long-term studies available. For birds, these include cooperative systems of the Seychelles warbler, ostriches, acorn woodpeckers and guira cuckoos. The three latter species exhibit cooperative breeding using joint nests and shared reproduction, whereas in the case of the Seychelles warbler, the primary reproductive pair is assisted by adult offspring of the pair that remain in the natal territory. We then conclude by describing some aspects of cooperative breeding found in the Order Primates. Within this order, the best examples of cooperative breeding are found in the Neotropical marmosets of the subfamily Callitrichinae (Family Cebidae).

1. Introduction

The theory of **psychological hedonism** suggests that the only two ultimate goals that motivate people are avoiding pain and obtaining pleasure, and that everything else is subjugated to these two main motives. This is a more specific interpretation of the theory known as **psychological egoism**, which considers that an individual's main objectives in life are to benefit him- or herself. This interpretation of life views all human actions, even those that benefit others, as ultimately related to bringing benefits to the self. In fact, this view of life is quite pervasive, and most people are not very surprised when faced with behavior that ultimately results in benefits to the individual carrying out the behavior, but may be very surprised when observed behaviors apparently carry no attached benefits to the individual, but may even benefit others. The field that attempts to understand the psychological framework of humans that involves behaviors and motivations associated with selfishness versus altruism lies within the realm of psychology. However, Charles Darwin's theory of **natural selection** clearly is one fundamental piece of the puzzle that has to be considered, especially if we allow that the evolution of behavioral traits observed in humans had its origin in pre-human animal lineages.

There obviously is a link between our concepts of **altruism** and goodness. Evolutionary biologists have been interested in the concept of goodness and its evolution at least as far back as Darwin. The evidence of "goodness", or altruism, represented a problem for Darwin's theory of natural selection. Darwin observed altruistic behaviors, not only among humans, but among several other animal species, especially the **eusocial insects**. How could the altruistic suicidal behavior of a honeybee protecting its hive be explained through natural selection? Or the helping behavior exercised by a sterile cast of ants in favor of the reproducing queen?

The basic premise of natural selection, as defined by Darwin, is that all traits evolve because they somehow benefit the individual with those traits, helping it to survive and, ultimately, to reproduce, thus passing on the trait and spreading it within the population. Thus, natural selection would tend to eliminate altruistic behaviors, given that individuals that behaved in a manner that favored others would not maximize their own reproduction, and the altruistic trait would not be replicated as efficiently as more selfish traits. Consequently, it appears that altruistic behaviors would be weeded out through natural selection. But Darwin was so baffled by his observations of altruistic behaviors in nature that he considered altruism as "one special difficulty, which at first appeared to me to be insuperable, and actually fatal to my whole theory." However,

Darwin himself proposed that natural selection could sometimes act on groups, thus invoking **group selection** as a principle that could promote the survival of some groups at a cost to other groups. He used this principle to explain the evolution of human traits such as patriotism, fidelity, obedience, courage and sympathy, among others. Darwin used the principle of natural selection acting on groups very sparingly, and he usually did so with the family as the unit of selection. He recognized that kinship could be a factor underpinning the evolution of cooperative behavior, thus brilliantly anticipating the principles of **kin selection** one century before William D. Hamilton's papers on the evolution of sociality based on kinship, published in 1964.

The puzzle concerning the origin and evolution of altruistic traits continued to fascinate biologists and psychologists, primarily, but also appealed broadly to scientists from many different areas. The modern foundations for the understanding of cooperative behavior in animals and humans can be traced to George C. William's book, *Adaptation and Natural Selection* in 1966, Richard Dawkins classic, *The Selfish Gene* published in 1976, E. O. Wilson's revolutionary contribution, *Sociobiology*, published in 1975, and Richard Alexander's work on human behavior in 1979. However, there are two historical allusions that are important when discussing the evolution of cooperation. The first refers to the thinking of Prince Peter (Pyotr) Alexeyevich Kropotkin, a Russian anarchist born in the mid-1800s. He advocated a social model wherein society would be free from a central government. In addition to his writings on the workings of society, he also was a geologist and naturalist. In his frequent trips around the world he made observations concerning cooperation among animals and humans and published these as essays which later became a book (*Mutual Aid: A Factor of Evolution*). He concluded that cooperation and mutual aid were important mechanisms in the evolution of species. A second noteworthy mention concerns Dr. W. C. Allee, a leading twentieth century ecologist, and one of the founders of the "Chicago School of Animal Behavior". He developed a great interest in behavioral patterns that influence aggregation and made many observations concerning the benefits of sociality in animals. Among these, as described by Lee Dugatkin in his book *Principles of Animal Behavior*, some of the more interesting are the following examples: (1) goldfish and *Daphnia* survive in toxic environments for longer time periods when living in larger groups; (2) survival of flatworms under ultraviolet light is a function of group size, similar to the per capita growth rate of bacteria; (3) goldfish grow more rapidly when living in groups; (4) amphibians regenerate their tails more rapidly when in groups.

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Biographical Sketches

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