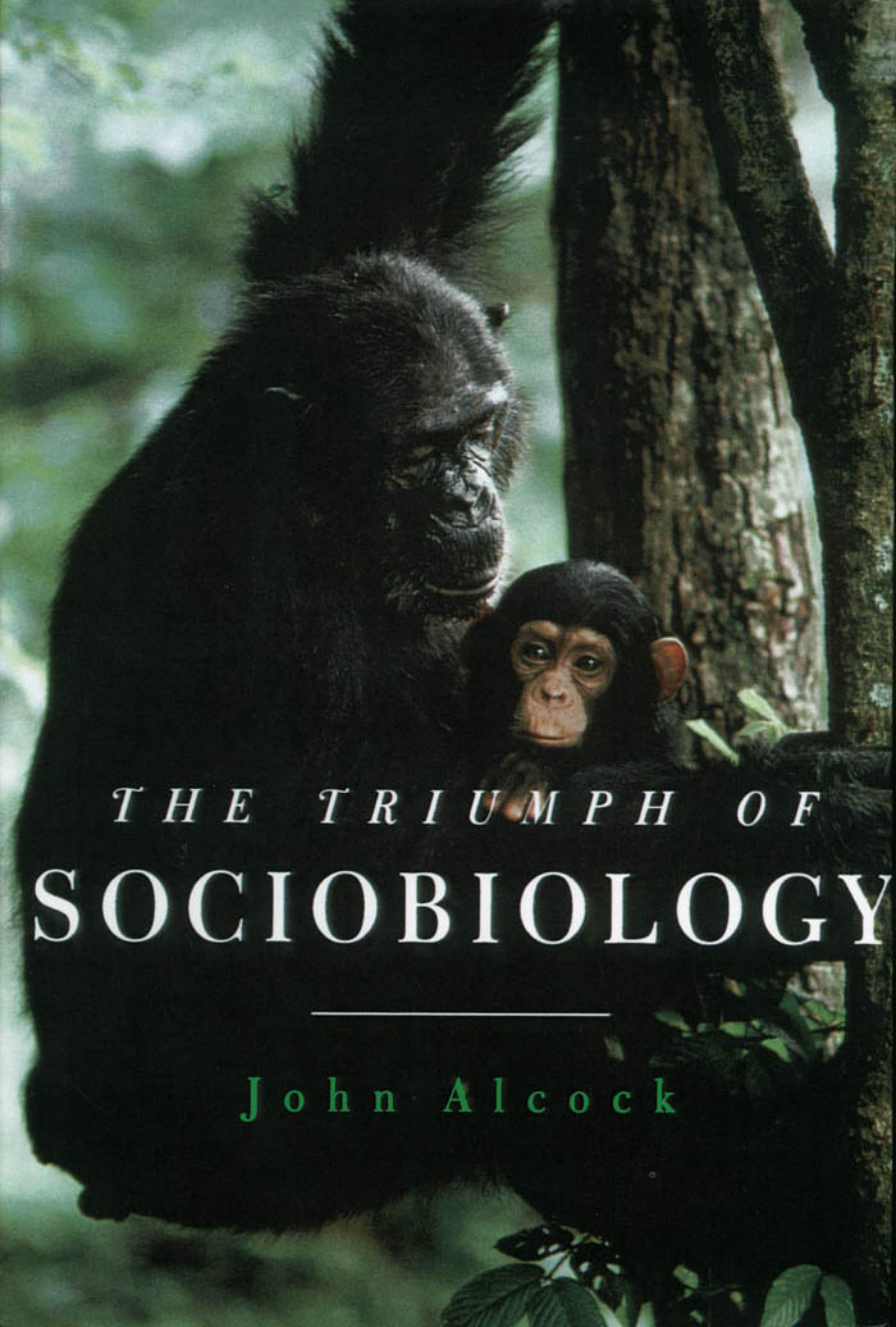

THE TRIUMPH OF SOCIOBIOLOGY

John Alcock

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Acknowledgments

Fortunately, my academic career in animal behavior began shortly before sociobiology was introduced to the public, and thus I have been associated with the discipline since its inception. The foundation for my long and happy association with sociobiology began in 1964, when my undergraduate adviser, Lincoln Brower, alerted me to *Adaptation and Natural Selection*, by George C. Williams, the first modern sociobiologist. Later, in graduate school at Harvard, I took a course in animal behavior taught by Edward O. Wilson. My doctoral thesis was supervised by Ernst Mayr, one of the architects of the modern synthesis of genetics and evolutionary theory. By virtue of this pedigree, I was able (barely) to get my first job at the University of Washington, where two colleagues, Robert Lockard and Gordon Orians, did their best to educate me further on the relation between natural selection and behavior. I began teaching animal behavior as a coinstructor with Orians to classes who accurately viewed me as a callow interloper who deprived them of lecture time with the charismatic half of the teaching team. I too would have preferred listening to Orians!

Although Orians refused to give my lectures, he encouraged me to begin writing a textbook in animal behavior that would cover the many new developments in the study of behavioral adaptations. In 1975, the same year E. O. Wilson's *Sociobiology* was published, my textbook *Animal Behavior: An Evolutionary Approach* appeared, albeit to considerably less fanfare and no controversy. The need to revise this textbook from time to time has given me ample motivation to follow behavioral research over the years. *The Triumph of Sociobiology* reports a few of the achievements of the ever-growing band of accomplished sociobiologists and behavioral ecologists who have taught us all a great deal about behavior and evolution since 1975.

In writing this book, I have received generous assistance from many people. I am of course very grateful to Kirk Jensen and his colleagues at Oxford University Press for their willingness to publish the book. Several persons have offered useful criticisms and suggestions (some of which I have even accepted), including Helen Hsu, Doris Kretschmer, Lynn Margulis, Dorion Sagan, Paul Sherman, Robert Triv-

ers, David S. Wilson, Edward O. Wilson, and several anonymous reviewers. Many colleagues, and any number of publishers, have supplied research papers and have given permission to use certain figures that have appeared in their work. Full credit for copyrighted material appears on p. 247. The numbers in brackets that appear in the text of the book refer to references that are listed alphabetically and numerically beginning on p. 231.

The Life Sciences Visualization Group at Arizona State University (Charles Kazilek, Barbara Backes, Laural Calser, and Anne Rowsey) provided expert assistance in preparing many illustrations for the book. In addition, Peter Farley and Andrew Sinauer at Sinauer Associates were very helpful in supplying some other figures. Barbara Terkanian graciously agreed to produce an original drawing for me. Finally, I thank my colleagues in the Department of Biology at Arizona State University and my wife, Sue, and sons, Nick and Joe, for their fine company over the years. Both departmental life and family interactions have provided me with innumerable opportunities to observe sociobiology in action. I would be delighted if my book does for others what my family experiences and faculty meetings have done for me, which is to recognize that evolutionary thinking is both illuminating and entertaining.

The Triumph of Sociobiology

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Introduction

On 15 February 1978, a young woman carefully poured a pitcher of ice water onto the head of Edward O. Wilson while he sat waiting to address an audience at the annual meeting of the American Association for the Advancement of Science. A band of accomplices joined their pitcher-pouring confederate on stage to wave placards and chant, "Wilson, you're all wet." After repeating this modest witticism for a few minutes, Wilson's assailants left the field to their victim, who dried himself as best he could with a paper towel and then delivered his talk without further interruption [345].

In a world characterized by much more exciting and dramatic violence, this brief aquatic and acoustical assault was nevertheless moderately newsworthy because of its setting—a scientific get-together—and its target—a Harvard professor. Academics are a contentious group and academic arguments can get loud and nasty on occasion, but physical confrontations are rare. Even if fights were fairly common in scientific meetings, Wilson would hardly interest anyone fond of hand-to-hand combat. He is a world authority on ants and the other social insects, a tall, thin person with a passion for entomology, not fisticuffs. By his own account, he was utterly surprised to have achieved the kind of notoriety that evidently inspired his band of youthful opponents [345].

But Wilson is also known as the "inventor" of sociobiology, having published a book of coffee table dimensions in 1975 entitled *Sociobiology: The New Synthesis* [343]. In the interval between the book's appearance and the AAAS meeting, a group of Wilson's colleagues at Harvard University did some publishing of their own. Richard Lewontin, a leading geneticist, and Stephen Jay Gould, just beginning his own rise to fame and fortune as a writer on matters evolutionary, were among the authors of a manifesto printed in the *New York Review of Books* [16]. They did not send their critique to Wilson prior to its publication but instead let him, a member of their own department, learn about it indirectly—not the most collegial of actions. In their broadsheet, Lewontin, Gould, and fellow co-signers declared that Wilson had produced a theory that could be used to justify the political status quo and

existing social inequalities. Worse, according to them, sociobiology was founded on the same kind of pseudoscience that was used as a foundation "for the eugenics policies which led to the establishment of gas chambers in Nazi Germany." Clearly, academics have the capacity to play rough.

Although Wilson soon responded in print to these unnerving charges [344], the vehemence of the opposition to sociobiology and the personal nature of the initial attack and follow-ups colored the general view of Wilson and his apparent creation. The average person is cautious toward a subject that is associated with intense controversy, and in this case Wilson's accusers included individuals with impeccable scientific credentials. As a result, to this day many persons, academics and nonacademics alike, have the sense that sociobiology may be slightly or substantially tainted, all the more so because Gould has continued over the years to cast aspersions on the discipline and its practitioners [146, 151–152]. In this he has found allies in various academic camps [76, 269], with some feminists and social scientists especially eager to dismiss sociobiology as misguided at best and socially pernicious at worst [304].

A history of the sociobiology controversy from the perspective of a sociologist has been written by Ullica Segerstråle [278]. Here I employ the perspective of a sociobiologist to argue that Wilson and his fellow researchers have essentially won the debate with Gould and his loose confederation of academic allies. The more or less neutral readers to whom I address this book may have a vague feeling that sociobiology is still controversial, a discipline born in dispute and raised in uncertainty. I wish to counter this impression, but not by claiming that the field deserves complete immunity from criticism. Research papers and books produced by sociobiologists, like the published work of other scientists, are rarely perfect and, indeed, can be seriously flawed. Sociobiologists themselves often disagree with elements of each other's approaches and conclusions (see, e.g., [170, 302, 323]). Progress in science sometimes occurs as a result of these kinds of disputes. However, many of the most prominent and frequently employed criticisms of the field broadcast by nonsociobiologists are based on avoidable misconceptions and assorted confusions. By dealing with the key misunderstandings, I hope to demonstrate that the discipline employs a basic research approach that deserves our interest, respect, and even admiration as a potential source of improved understanding about ourselves and all other social species, from ants to antelopes.

I am far from the first person to make this claim. Indeed, sociobiology was ably defended at the outset by Wilson and then by many others, including an important early effort in 1979 by the Canadian philosopher of science Michael Ruse [271]. Richard Dawkins has beautifully explained the principles of sociobiology to a wide audience, albeit only occasionally labeling the research he describes as sociobiological [93, 96]. Many more recent books have also attempted to put some of the criticisms of sociobiology to rest (e.g., [57, 254]). For a particularly evenhanded and

complete examination of the misunderstandings surrounding sociobiology, I recommend a paper by the legal scholar Owen Jones [178]. But the criticisms and misconceptions continue, requiring an up-to-date review and response, which I have attempted to supply. It is simply incorrect to assert that

(1) sociobiology is a novel and idiosyncratic theory of E. O. Wilson (chap. 1),

(2) sociobiology is primarily concerned with human behavior (chaps. 1, 6),

(3) sociobiology deals with the evolution of traits that benefit the species (chap. 2),

(4) sociobiology is a reductionist discipline based on the proposition that some behavioral traits are genetically determined (chap. 3),

(5) sociobiology makes use of capricious and selective comparisons between human behavior and that of other animals (chap. 4),

(6) sociobiology is a purely speculative endeavor, specializing in the production of untested, and untestable, just-so stories (chaps. 4–5),

(7) sociobiology cannot account for learned behavior or human cultural traditions, only rigid instincts (chaps. 7–8), and

(8) sociobiology is a discipline that, by labeling certain actions "natural" or "evolved," makes it possible to justify all manner of unpleasant human behavior (chap. 9).

The list of misunderstandings and erroneous claims is long because many people realize, perhaps intuitively, that the sociobiological approach, if valid, would require them to modify some of their own strongly held opinions about human behavior. Almost everyone considers himself or herself an expert on human behavior. Because we care so deeply about the subject and spend much of our lives analyzing the immediate motives or intentions of others, we are better able to plan our own actions. Sociobiology brings another dimension to this analysis, the evolutionary dimension, one that is unfamiliar and even threatening to many, judging from the vehemence with which the discipline has been attacked. These attacks, past and present, have deterred some from appreciating the beauty and productivity of the approach championed by Wilson. This is unfortunate because sociobiological research conducted by hundreds of behavioral biologists since 1975 has explained much that is puzzling and wonderful about the social lives of all animals, ourselves included. The research record assembled by these scientists constitutes a great success. My book is an effort to put this record forward, freed from the misconceptions attached to it by others, so that my readers can understand the triumph of sociobiology.

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1

What Is Sociobiology?

Defining the Discipline

This spring morning I climbed to the top of Usery Mountain, which, happily for me, is only a twenty-minute walk up a steep hill in the Sonoran Desert of central Arizona. Once I reached the undulating ridgeline and regained my breath, I walked along the hilltop checking the palo verde trees, creosote bushes, and jojobas to see which plants were occupied by males of a locally common tarantula hawk wasp, *Hemipepsis ustulata* (fig. 1.1). Males of this large, black-bodied, red-winged species dedicate themselves to a life of ritualistic combat over control of entire trees or shrubs, which the males use as lookouts to scan for approaching virgin females of their species.

This morning many familiar males that I had daubed with Liquid Paper or dots of acrylic paint launched themselves from their territorial stations in pursuit of intruding males, and one even had the special pleasure of responding to a receptive female that flew toward his territorial shrub. This male, marked with yellow dots on his thorax and right wing as a result of an earlier encounter with me and my paints, dashed out after the flying female to grasp her in midair. They fell heavily to the ground and mated without preliminaries. As the female walked a short distance forward, the coupled male toppled over, lying on his back with his wings spread on the gravelly soil. A second male, which had reached the female a few seconds after "yellow dots," attempted without success to mate with the already fully engaged female. After a minute passed, the mating pair separated and yellow dots returned to his perch while his rival continued to probe the female to no good effect until he too flew back to his territorial perch nearby. The female then left to cruise downslope. As I write, she is doubtless out tracking down tarantulas and other large spiders, which she will sting into paralysis before depositing her victims in underground burrows where they will be slowly consumed by the wasp's larval offspring.

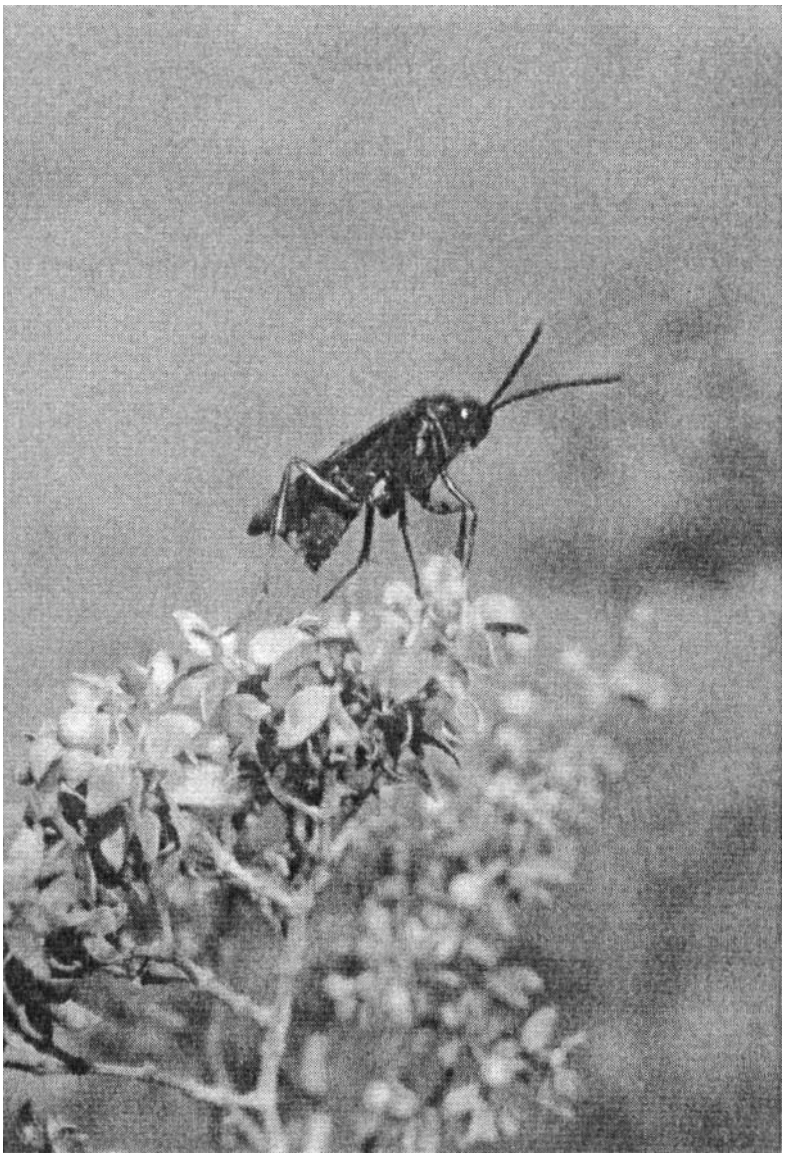


Figure 1.1. A male of the tarantula hunting wasp *Hemipepsis ustulata* scanning for rival males and receptive females from his perch territory on top of a peak in central Arizona.

Although the hunting behavior of female tarantula hawks is fascinating, the main goal of my project has been to understand the evolution of the species' unusual system for getting females together with males [6]. Why should this be the only tarantula hawk wasp of several local species in which males defend hilltop trees and shrubs in order to have a chance to mate? Why do receptive females of this species choose to visit hilltops and why do they accept the first male that grasps them in midair? Why do males employ a distinctive method of competing for possession of certain palo verdes and other plants, flying up with a rival high into the sky and then diving back down to the site that they both desire, only to repeat the upward flight again and again until one of the two gives up? The tarantula hawk wasp, like many other animal species, experiences episodes of sex and aggression, activities that require at least two participants and thus can be considered social. Studying the possible evolutionary causes of these social acts makes me a sociobiologist, according to Edward O. Wilson, who was first to define sociobiology "as the systematic study of the biological basis of all social behavior" [343].

This is not a narrow definition. Social species come in all sizes and shapes. The members of these species do all sorts of things to one another, inspiring an equally great range of questions about sociality. And here we come to the first of the misconceptions that surround the discipline of sociobiology: the belief that sociobiology concerns itself exclusively or even primarily with human social behavior. The chapter on humans in Wilson's *Sociobiology* constitutes a mere 5 percent of his book, and the very large majority of today's sociobiologists conduct their research on species other than humans.

Let me emphasize this point with reference to an issue of the technical journal *Behavioral Ecology and Sociobiology*, which just happens to be on my desk as I write this chapter. "Behavioral ecology" is the study of the evolutionary relationship between an animal's behavior and its environment; sociobiology can be viewed as that component of behavioral ecology that explores the effects of the *social* environment on behavioral evolution. My copy of *Behavioral Ecology and Sociobiology* has articles on the social behavior of a damselfish, a katydid, whirligig beetles, assorted primates, a planarian flatworm, and the honey bee. Humans as sociobiological subjects are nowhere to be seen in this issue, although the journal sometimes accepts papers on *Homo sapiens*. The somewhat intimidating titles on the cover of this issue include "Sperm Exchange in a Simultaneous Hermaphrodite" and "Decentralized Control of Drone Comb Construction in Honey Bee Colonies." The various reports contain information on such topics as how female flies may (unconsciously) select which sperm get to fertilize their eggs by somehow choosing among the ejaculates of several different partners, and why whirligig beetles assemble in groups on the surface of the streams and lakes they inhabit. Sociobiology is a remarkably wide-ranging discipline in which the complete spectrum of social activities across the animal kingdom is fair game for analysis.

Refining the Definition

Although sociobiology ranges widely across topics and species, it is tightly constrained in terms of its theoretical orientation. Wilson's one-sentence definition of the discipline may suggest that any scientist working on any biological aspect of social behavior qualifies as a sociobiologist. But in reality persons who call themselves sociobiologists, or at least those who tolerate this label, invariably use evolutionary theory as the primary analytical tool for their work. These individuals usually ask and try to answer one basic question: What role did natural selection play in shaping the evolution of this society or that social behavior? Put another way, sociobiologists want to know the evolved function or purpose of whatever aspect of social behavior they are studying.

For example, returning to *Behavioral Ecology and Sociobiology*, I see that Penelope Watt and Rosalind Chapman wished to understand why whirligig beetles form aggregations of up to thousands of beetles, all zipping back and forth on the water's surface [330]. For the purpose of their study, Watt and Chapman assumed that the beetles' sociality (*fig.* 1.2) is the product of an evolutionary process dominated by natural selection. They proposed that natural selection in the past favored individual beetles that happened to gather in large groups because these beetles were safer from predators than those with a tendency to live alone or in smaller groups.

The two sociobiologists then tested this proposition experimentally by measuring the rate at which assaults on whirligigs occurred in beetle groups of different sizes held in aquaria with predatory fish. They found that, at least under these experimental conditions, the risk to any individual beetle of coming under attack by a fish in a given period decreased with increases in the size of the aggregation to which the beetle belonged. This finding provides support for the hypothesis that whirligig societies form because social individuals gain survival advantages. If this relationship held in the past, as it apparently does in the present, and if individuals differed in their hereditary tendency to seek out the company of others, relatively social whirligigs in the past would have tended to live longer and leave more descendants to carry on their special social attributes than relatively solitary individuals. If so, a process based on differences in reproductive success in the past would then have shaped the social behavior of today's whirligigs, which are subject to yet another round of selection with the potential to change or maintain the current social nature of these animals. Although Watt and Chapman's evolutionary hypothesis can be tested in many other ways, the point for the moment is that they approached the problem of whirligig sociality from a particular perspective, a historical one, in an attempt to identify the reproductive advantage that social tendencies conferred on individual beetles.

But the evolutionary angle is not the only possible biological approach to social behavior. Another kind of biological question about social behavior exists, one that

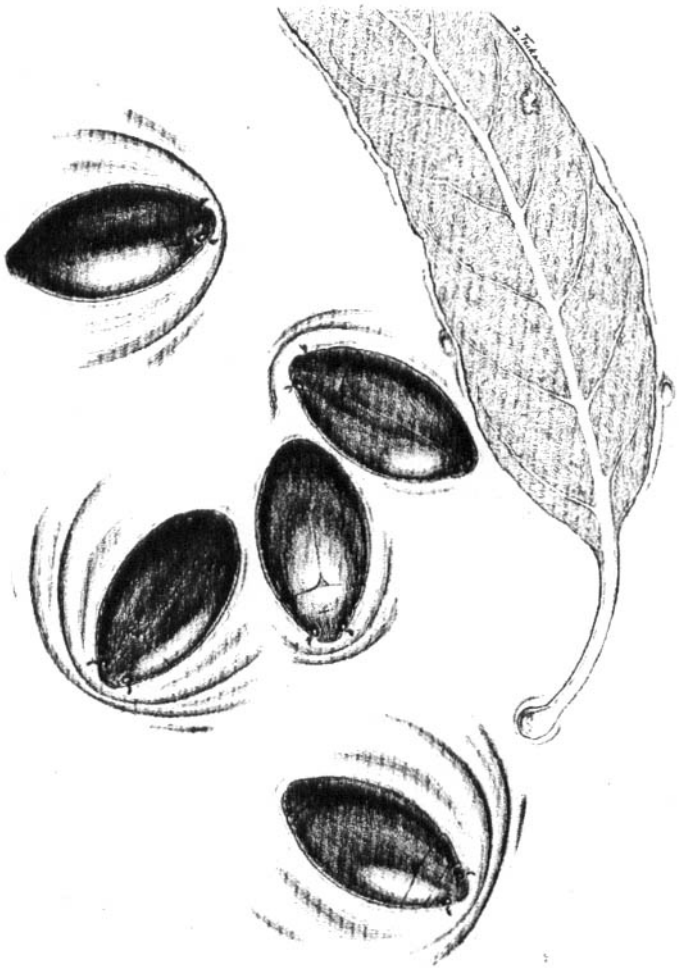


Figure 1.2. An aggregation of whirligig beetles on the surface of a pond. Why do these animals form their simple societies? Drawing by Barbara Terkanian.

does not revolve directly around evolutionary events: How does the internal machinery of life work to produce particular results? Whirligig social behavior is potentially subject to a sort of mechanical explanation. The beetles clearly possess internal mechanisms that enable them to react to their fellow beetles in a particular way and to stay together in groups once they have formed. The mechanisms underlying whirligig social responses include the neurophysiological systems, the wiring, of the insects in question. But Watt and Chapman did *not* attempt to learn how the nervous system of the beetles worked to provide sensory inputs from the environment, which could be used to make neural "decisions" about which batteries of muscles to control in ways that lead whirligigs to gather together. Nor did Watt and Chapman consider how the neural networks of the beetle were assembled as the beetle metamorphosed from a fertilized egg to a functional adult. Solving this problem involves examination of the genetic-developmental mechanisms that result in the growth of the beetle into a complex multicellular organism of a particular design.

Studies focusing exclusively on *how* an animal's internal machinery works are *not* the province of sociobiologists, a point that Wilson made in the first chapter of *Sociobiology* [343]. There he presents a diagram of the relationships between the various biological disciplines that address social behavior (fig. 1.3). Note that according to this diagram the disciplines of sociobiology and behavioral ecology are closely allied; in turn, they are linked with population biology, whose central concern is the description of the genetics of entire populations and the response of gene pools to evolutionary processes, including but not limited to natural selection. These then are the evolutionary disciplines important for an understanding of social behavior. Were Wilson to write an update of *Sociobiology* today, he would also place the newly named field of human evolutionary psychology on the right-hand side of the diagram as a subdiscipline of sociobiology, which in turn would be shown as part of an overarching behavioral ecology. Evolutionary theory is at the heart of all three entities [85].

Evolutionary psychology provides a bridge of sorts to the study of the internal devices that make social behavior possible. On the left-hand side of Wilson's diagram, he placed those disciplines that delve into the operating rules of the machinery of behavior. Integrative neurophysiology examines the interaction between sensory systems and those other internal mechanisms that drive the muscles, which need to be controlled if an animal is to behave. Integrative neurophysiology in turn rests on a foundation of cell biology with its attempt to identify how chemical events within cells regulate the development of the organism, the operation of nerve cells, and the transmission of genes to sperm or eggs, among many other things. In the jargon of biologists, studies of how cellular mechanisms and system-operating rules influence behavior are classified as *proximate* research, which examines the immediate causes of the traits of interest. In contrast, questions about

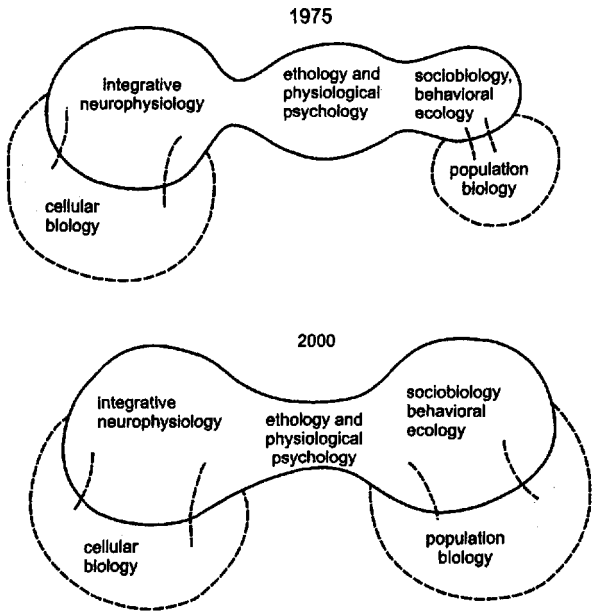
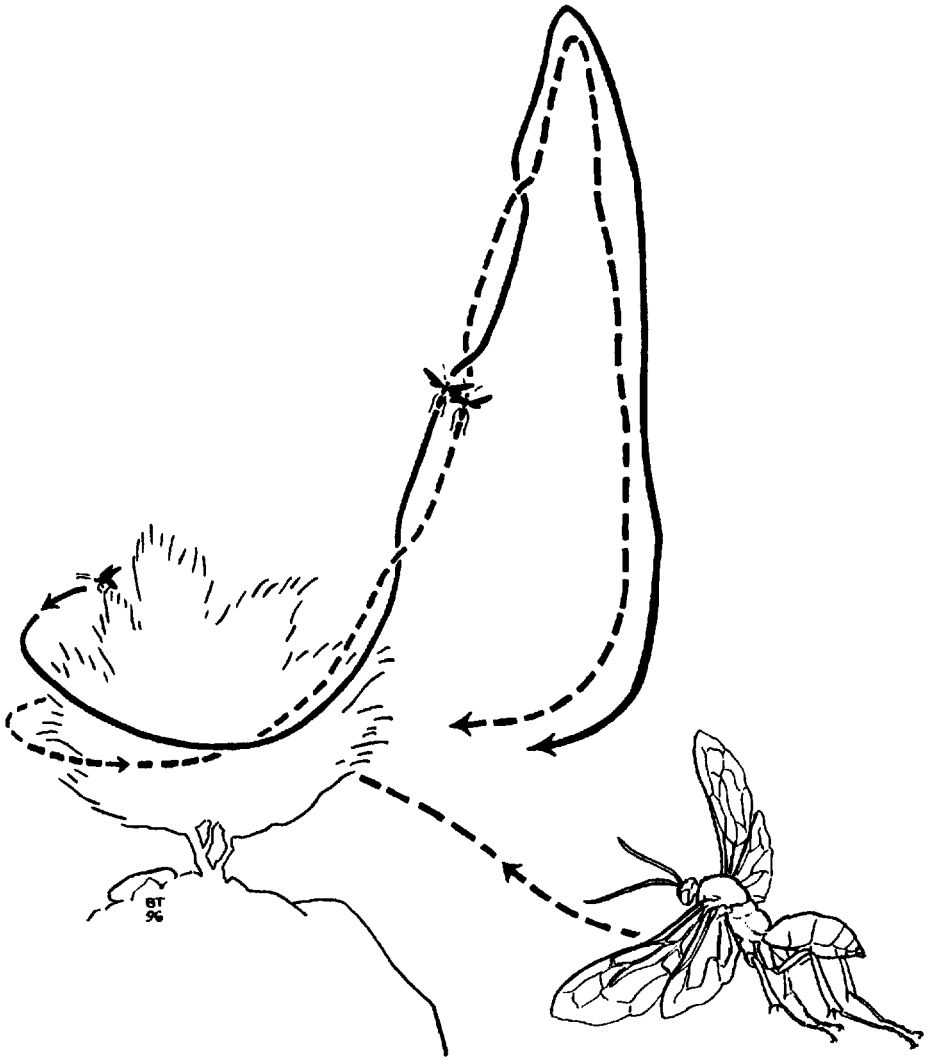


Figure 1.3. The relationship between various biological disciplines and sociobiology, as envisioned by E. O. Wilson in 1975, with his accurate prediction about the development of the different fields between 1975 and 2000. From [343].

the adaptive (reproductive) value of behaviors are labeled *ultimate* questions, not because they are more important than proximate ones but because they are different, dealing with the long-term historical causes of the special abilities of species.

So, for example, I was engaged in proximate, not ultimate, research when I studied what motivated territorial tarantula hawks to fight with intruders, investing time and energy in spiral flights with certain opponents [10]. My colleague Winston Bailey and I knew that territory-holding males of many other species appear to become increasingly motivated to fight with intruders the longer the resident males have held their territories, something that has been labeled the "residency effect" by other researchers studying the same phenomenon in other species. To test whether the residency effect applied to tarantula hawks, we removed territory owners and held them in a cooler until a rival male had established himself on the experimentally vacated territory. We found that, as expected, the longer we let the new male hold his site before releasing the old resident, the more willing the newcomer was to engage the original territory holder in a long series of spiral flights when he returned to reclaim his perch (fig. 1.4). In other words, one of the immediate causes of aggression among male tarantula hawks has to do with the psychological effects of being in control of a territory. The wasps evidently possess internal



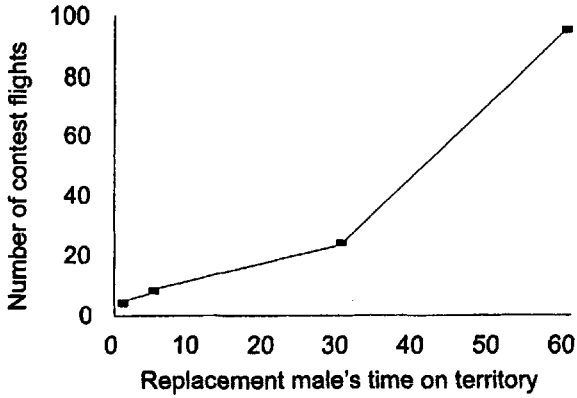


Figure 1.4. The effect of prior residency on the readiness of male tarantula hawk wasps to defend their territory. The longer a replacement male has occupied a territorial perch site (while the previous resident remains in captivity), the more times he is willing to engage in ascending contest flights (see the drawing that precedes the graph) with the returning resident (after that male has been released from captivity). From [10].

mechanisms that record how long they have held a site, and this information somehow influences the neural networks controlling territorial defense. This kind of study falls outside the domain of sociobiology if its *only* goal is to identify the proximate operating rules of physiological systems that generate a behavioral effect.

Proximate research on the residency effect can, however, take on an ultimate character and thus becomes part of sociobiology, when the question changes from *how* does the internal machinery work to *why* does the machinery work that way? Do males experience a reproductive advantage as a result of having proximate mechanisms that enable them to measure how long they have held a territory and that motivate them to defend a desert shrub or tree accordingly? If so, why? Various hypotheses exist on this point, and some have been tested for species other than tarantula hawks but not yet for *Hemipepsis ustulata*. My point here is not to answer the ultimate question about the residency effect but to make the case that one can ask purely proximate and purely ultimate questions, each category dealing with different but complementary aspects of a biological phenomenon.

Let me repeat that: ultimate causes are not somehow superior to proximate ones, or vice versa. In the biological arena, "ultimate" does not mean "the last word" or "truly important" but merely "evolutionary." The existence of the two terms, proximate and ultimate, helps us acknowledge the fundamental difference between the immediate causes for something and the evolutionary causes of that something [11, 286].

Biologists also realize, however, that knowing about the connections between proximate and ultimate causes is as important as understanding the differences

between them. The cellular and physiological mechanisms in today's whirligig beetles and tarantula hawks have persisted to the present because these mechanisms happened to promote reproductive success in the past. Some traits have regularly advanced an individual's chances of getting its genes into the next generation while others have not. The historical differences in the genetic success of individuals with different attributes determined which genes managed to survive to the present. These genes promote the development of particular kinds of neural networks in today's organisms, which provide them with the machinery of behavior. Thus, proximate and ultimate causes of social behavior (and all other biological traits) intertwine across history. The machinery of reproductive success promotes its long-term persistence; in contrast, internal mechanisms that predispose individuals to fail at reproduction wind up in the junk heap of history.

Therefore, to say that proximate and ultimate issues in biology are different does *not* mean that sociobiological approaches cannot be applied to genetic-developmental or physiological-psychological matters. For example, as noted above, the new field of evolutionary psychology analyzes proximate mechanisms of human behavior from an explicitly evolutionary perspective, asking questions about why we possess particular psychological attributes and seeking ultimate answers in terms of the contribution these mechanisms might make or have made to the reproductive success of individuals. No internal proximate mechanism of social behavior exists that cannot be explored in terms of its adaptive value, just as no adaptive behavior occurs whose underlying proximate causes cannot be investigated to good effect.

Sociobiology *before* Wilson

Despite Wilson's explanation of sociobiology as a branch of evolutionary biology, the hoopla and controversy surrounding the publication of *Sociobiology* apparently induced many to accept another misconception about sociobiology, namely, that Wilson produced a idiosyncratically novel, and therefore potentially suspect, theory of social behavior, just one more ivory tower concoction to be added to the pot of competing arguments. However, anyone who sits down with the book will soon realize that it is a massive summary review of the research of other scientists who have employed Darwinian evolutionary theory to make sense of social behavior. Wilson's role was one of synthesis, no mean task since it required (1) an ability to read and digest the vast evolutionary literature on social behavior, (2) a clear and useful organizational scheme, and (3) the readiness to review the major themes in sociality and explain how these made sense in the light of evolutionary theory. Wilson achieved all these things in *Sociobiology*, and so he was fully entitled to give a new, compact, and memorable label to what others at the time were calling "ethology" or "the study of behavioral evolution."

But the theoretical foundation of the book and its approach to explaining social