CHAPTER 1

Introduction

I spent my earliest days as a professional biologist happily tramping through the forests of southern Canada recording the survival, reproduction, and movement patterns of tiny mice that make their living among the detritus of the forest floor. My study subjects were the big-eared, dark-eyed deer mice that so often plague country cabins, apparently preferring the security and constant availability of food in human habitations to the perils of life in the wild. The official motivation for my study was to determine what causes the numbers of mice in a given population to fluctuate over time, and this, in turn, was motivated by the general question of what determines the numbers of individuals in any animal species. This was (and remains) a laudable goal, and I set forth on the study with full confidence in its scholarly legitimacy. Nevertheless, like most field biologists, I had chosen this type of research partly because it allowed me to spend much of my time out in the natural world rather than standing at a laboratory bench or hunched over a microscope. I had always been fascinated with the lives of wild creatures, and spending my time in the woods discovering how mice get through life seemed like just the ticket.

I captured my subjects in small metal boxes that my assistants and I placed strategically along mouse highways or close to mouse burrows. To entice the mice to enter our boxes, each was packed with a handful of nutritious seeds, a large dab of peanut butter, and a generous wad of cotton batting that the occupant invariably fluffed into a warm nest. The boxes were fitted with trap doors that closed when a mouse entered, and so we were able to catch the mice alive and release them again unharmed. The first time we caught a given mouse we would put a numbered, metal tag in its ear (much like a personalized ear stud) so that we could identify it when we caught it again. Our boxes were mouse magnets, and we caught hundreds of individuals, following many through most of their lives. To find out more about their individual personalities, I also brought each mouse into the laboratory for several nights (these are nocturnal mice) and ran it through a series of behavioral tests before taking it back to its capture site in the wild. Through all of this I got to know many of my mice quite well, and I was always delighted when old "friends" jumped out of their trap boxes in the cool of a morning. Once a mouse had finally disappeared from my study area, I would go back through my trapping records and reconstruct its life history. I could see where it had probably been born, where it traveled during its life, and how long it lived. If the mouse was a female I could tell when she was ready to mate, when and how often she had been pregnant and gave birth, and for how long she nursed her litters. My reproductive information was sketchier for males, but I could at least tell when they were ready and eager to mate.

Although my study was ostensibly designed to predict population numbers, as I got to know my mice I became increasingly absorbed by the obvious differences among them—and particularly by the different ways that males and females functioned in the population. For example, my females faced many hazards associated with pregnancy and lactation, and many died or lost their litters due to cold, rainy weather or lack of food. In contrast, my males ignored their offspring and spent the reproductive season searching for receptive females and interacting aggressively with other males. Their greatest hazard seemed to be displacement by more aggressive rivals. Although the numbers of both sexes showed similar seasonal fluctuations, it became clear to me that this demographic similarity masked profound and fascinating differences between the sexes. As it turns out, this revelation set the course for much of my future research and ultimately provided the motivation for this book.[1]

I've come a long way since my deer mouse days. I now ask questions about the evolution and adaptive significance of animal characteristics rather than about population sizes and demography, and several years as a fisheries biologist followed by several decades studying various insects and spiders have expanded my animal horizons beyond the familiar world of temperate mammals. Nevertheless, the differences between males and females that emerged so strongly in my studies of deer mice have remained a persistent theme. Time and again I have discovered how different life is for males and females in the natural world. The sex of animals affects their morphology, life history, behavior, and ecology, and this is true throughout the animal kingdom. The modest differences I observed in deer mice are trumped many times over by much more sexually dimorphic species in many different animal lineages. In some of these species the sexes differ so much that they would never be recognized as belonging to the same species had they not been observed actually mating or emerging from the same batch of eggs. In this book I ask why sexual differences are such a pervasive and significant part of the fabric of animal variation and, in particular, why males and females have come to differ to truly extraordinary degrees in some animal lineages.

I answer these questions by looking at sexual differences across the animal kingdom with emphasis on species where the differences are at the extremes of the distribution. These extraordinary species are particularly apt examples because they so clearly illustrate the division of reproductive function between the sexes and the extremes to which each sex can go to perfect its role. At one extreme are species in which males are large, muscular despots defending harems of much smaller females against constant challenges from rival males, whereas at the other extreme are species in which the females are solitary, large, and fierce, while their mates are minuscule sexual parasites capable of little more than producing sperm. My aim is to reveal what life is like for males and females at both ends of this continuum and to explain why such extreme differences have evolved.

As an evolutionary biologist I take an overtly Darwinian approach to understanding sexual differences. The basic assumption of this approach is that sexual differences are adaptations that increase the success of males and females in their respective reproductive roles. The currency of evolutionary adaptation is Darwinian fitness, which in this context means the number of descendants produced or, alternatively, the number of genes passed on to future generations. Thus, when I ask why male and female animals differ, I am really asking how the Darwinian fitness of males and females is enhanced by these sexual differences. Survival, particularly survival to reproductive maturity, is an important component of fitness in both sexes, but it is not the only determinant of success in leaving descendants. The number and quality of eggs or offspring produced are key components of fitness for females, and the number and quality of eggs fertilized or offspring sired are analogous components for males. These major fitness components can be further subdivided to measure more specific aspects such as survival through a particularly difficult part of the life cycle, escape from particular predators, or success in capturing certain types of prey. By definition, if traits are adaptive, they must enhance at least some of these aspects of fitness. This is the signal that the trait or at least certain values of the trait are being favored by natural selection.[2] The implication of relevance here is that we expect the traits typical of males to enhance male fitness, whereas those typical of females should enhance female fitness. In other words we expect the trait distributions typical of each sex to be adaptive for that sex.

In studies of sexual differences one type of selection has received particular attention, and that is selection that acts through differential success in acquiring mates. Darwin coined the term sexual selection for this type of selection, and he described its importance in the evolution of secondary sexual traits, particularly in males.[3,4] He presented copious evidence that males in many species are adapted for success in competition for mating opportunities and that many exaggerated male traits such as elaborate plumage, robust horns and antlers, and courtship songs and behaviors can be understood as consequences of sexual selection. Conversely, he argued that sexual selection was likely to be much less important in females, although he speculated that mate choice by males may have influenced the evolution of secondary sexual traits in human females.

Over the more than 140 years since Darwin published his extensive discussion of the evolution of sexual differences in *The Descent of Man and Selection in Relation to Sex,* legions of behavioral ecologists and evolutionary biologists have added to his evidence and confirmed the importance of sex-specific patterns of selection in producing sexual differences. The concept of sexual selection has now been extended to include competition among males for fertilization success during and after mating (for example, through courtship during copulation, competition among the sperm of different males in the female's reproductive tract, and preferential use of sperm by females). There is also increasing evidence that sexual selection on females is more significant than Darwin supposed.[5] However, these extensions are merely embellishments of Darwin's initial insights. His thesis that sexual differences are adaptive and caused by selection for different suites of traits in males and females is now solidly supported by volumes of theoretical and empirical studies,[6] and it forms the underlying theme of my explorations in the following chapters.

With this Darwinian perspective, I ask why male and female animals so often differ in morphological traits such as body size, shape, and color; in behavioral traits such as aggressiveness and patterns of migration or dispersal; in ecological traits such as what they eat and where they spend their time; and in life history traits such as the age at which they mature and the number of mates they acquire. In the next chapter I answer this question in a general sense by describing the fundamentals of male and female reproductive roles across the animal kingdom. This overview sets the context for chapters 3 through 10, which examine the lives of males and females in species with truly extreme sexual differences. My examples range from elephant seals and shell-carrying cichlid fish, where large and aggressive males defend harems of much smaller females, to deep-sea anglerfishes (called seadevils), in which females are large, fierce predators, and males live as tiny parasites permanently attached to the bellies of their mates. I describe orb-web spiders in which tiny males die spontaneously while *in copula* with their giant mates and open-ocean octopuses in which minuscule males ride on floating jellies as they search for females 40,000 times their size. My most extreme examples are species of marine tubeworms and burrowing barnacles in which adult females live sedentary lives firmly attached to a substrate while harems of dwarf males live permanently in or on their bodies. In each chapter I ask why the sexes are so disparate and how such gulfs between male and female function can possibly be beneficial. In chapter 11, I take a broader view and examine patterns of sexual differences across the entire animal kingdom. I ask why these patterns exist. For example, why can we almost always distinguish males and females by differences in size and shape? Why are females usually the larger sex, and why are species with giant females and dwarf males so much more common than the reverse? Why are color differences restricted to relatively few animal groups and why, when they do occur, are males likely to be brightly colored while females are dull or camouflaged? In all of these chapters my focus extends beyond sexual selection, animal sex, and why males so often have ornaments and weapons not found in females (although all of these themes are certainly included). Through my descriptions of extraordinary species and my survey of variation across the animal kingdom, I explore what it means to be male or female in the broadest sense and illustrate, as vividly as possible, the impact that this division of reproductive function can have on virtually all aspects of an animal's life.

Chapters 2 and 11 provide important background and context for my exploration of sexual differences, but the heart of the book is the descriptions of the eight species (or in some cases, groups of very closely related species) highlighted in chapters 3 through 10. Each provides a unique and excellent example of widely disparate sex roles, and together they offer a grand overview of extreme sexual differences in animals. However, these few examples are by no means an exhaustive sample. Truly extreme sexual differences, where the two sexes would scarcely be recognized as belonging to the same species, are found in many different species distributed across at least eleven animal phyla.[7] Selecting eight examples from this diverse array of candidates was a daunting task. Although I admit to a modicum of serendipity and even a dash of subjectivity in the selection process (I just found some animals more fascinating than others), I did use a set of objective criteria to narrow the field. My foremost criterion was that the sexes had to show extreme differences in body mass. Because mass is a property of all animals, I could use the ratio of the masses of adult males and females as an objective criterion for comparing the magnitude of sexual dimorphism[8] among species as disparate as elephant seals and octopuses. Mass also correlates strongly with many other aspects of the biology and ecology of animals, including aspects of physiology (metabolic rate, production and dissipation of heat, energetic costs of movement), morphology (robustness of supporting skeletons, relative size of horns and antlers), performance (maximum speed, acceleration), life history (age at maturity, lifespan, clutch or brood size), and ecology (home range size, dispersal distance, population density).[9] Thus, pronounced sexual dimorphism in body mass (sexual size dimorphism) invariably correlates with sexual differences in many other traits.[10] Conversely, marked sexual differences in life history, behavior, ecology, or morphology seldom occur in the absence of sexual size dimorphism. Extreme sexual size dimorphism thus provides an objective, quantitative, and universal indicator of similarly extreme differences between males and females in many, if not most, aspects of their lives.

Having narrowed my choices to species with the greatest magnitude of sexual size dimorphism, I next limited my choices to species in which the ecology, life history, and behavior of both sexes were well described in the scientific literature. Where possible I chose species in which both sexes had been followed from birth to death, so that I could trace the entire life cycle of each sex and relate differences in early developmental trajectories to the disparate adult characteristics.

My final requirement was that the selection of examples should represent as much animal diversity as possible. With room for only eight examples, that was a tall order. Even though fewer than 4 percent of living animal species are vertebrates, we know far more about sexual differences in vertebrate species than in the vast assortment of invertebrates, and I could easily have populated my chapters entirely with vertebrate examples. As it is, I include a mammal, a bird, and two fishes, and the other four example species represent only three of the thirty invertebrate phyla: the mollusks, annelid worms, and arthropods. Given that the latter phylum contains more than 78 percent of living animal species, it seemed appropriate to include examples from two classes: spiders from the class Arachnida and barnacles from the class Maxillopoda. Although these eight examples cannot possibly encompass the full diversity of sexual differences, they do represent the extremes at both ends of the continuum—from a species where males average almost 13 times heavier than females to one where females can be as much as 500,000 times heavier than males.

The book offers much information that will be of interest to biological scholars with expert knowledge of at least some of the concepts and biology described. However, it is my hope that the descriptions of extraordinary animals and summaries of patterns of sexual differences across the animal kingdom will also be read and enjoyed by readers who are not biological scholars but are simply interested in the diversity of animal life or in the biological roots of our own sexual differences. (I discuss sexual differences in humans only briefly at the end of the book, but the principles and overall trends that I describe apply no less to us than to any other animal species.) To serve potential readers with such disparate backgrounds and interests, I provide notes at the back of the book signified by superscripts in the text. These notes contain scientific citations supporting various statements in the text, sources for technical data, and additional explanations, details, or caveats that extend the information in the main text. In deference to nonspecialist readers I have avoided the use of biological jargon as much as possible. The terms that I have used are shown in italics when they first appear and are listed in a glossary at the back of the book for easy reference. To maintain the flow of the narrative and to make the book more enjoyable for nonspecialists, I use common names rather than scientific names for all but the major players in my chapters. The corresponding scientific names can be found in appendix A, listed alphabetically by common name. I also list the major animal lineages (phyla with included classes) in alphabetical order in my tables, rather than clustering them according to their degree of evolutionary relatedness. This allows readers to easily find a given phylum or class, even if they do not know the evolutionary history of that taxon. I offer my apologies to professional colleagues who may be uncomfortable with these breaches of standard scholarly protocol.