PREFACE

The Phenomenon of Dual Sexuality

Who among us has not fantasized, at one time or another, about becoming a member of the opposite sex? If you are a man, what would it feel like to be a woman, if only for a day, a week, or a year? And if you are a woman, what would it feel like to be a man? For most people, such fantasies are idle because our genes and hormones normally dictate that each of us remains of one sex from conception to death. However, for individuals in several hundred species of fish, as well as for those that comprise numerous species of plants and invertebrate animals, experiencing life both as a male and as a female is the reproductive norm. Such dual-sex organisms are hermaphrodites.

Among the vertebrates (animals with backbones), approximately 99% of all species consist of separate-sex individuals, meaning that each individual is either male or female. Most of the other 1% of vertebrate species are hermaphroditic,[1] and essentially all of these are fishes. In some hermaphroditic fish species, an individual may begin its life as a functional male and then later switch to become a functional female, whereas in other species most individuals begin life as females before perhaps later transforming into functional males. In a few fish species, particular individuals switch back and forth repeatedly between male and female. And in still other fish species,

[1]A few species among the "other 1%" consist solely of females who reproduce asexually, or clonally (i.e., by parthenogenesis or related reproductive modes). These all-female species are the subject of a companion book to which interested readers are referred: *Clonality: The Genetics, Ecology, and Evolution of Sexual Abstinence in Vertebrate Animals* (Avise 2008).

an individual can be both a functional male and a female at the same time. In some of these simultaneous hermaphrodites, an individual may alternate between male and female behavioral roles during a spawning episode with another hermaphrodite. Finally, in one small taxonomic group of fishes, each hermaphroditic individual normally reproduces by fertilizing itself. When such "selfing"—an intensely incestuous behavior—is repeated generation after generation, the result is a highly inbred lineage, the members of which can become so genetically uniform as to be, in effect, clonally identical to one another.

All of these and additional hermaphroditic phenomena in fishes find their near-perfect analogues in many species of plants and invertebrate animals that also display various forms of dual sexuality. For example, approximately 95% of all species of flowering plants (angiosperms) include at least some dual-sex individuals (hermaphrodites), as do more than 50,000 species of invertebrates. In general, the reproductive lifestyles of hermaphroditic organisms can seem outlandish to us humans, who are more accustomed to thinking of the two sexes being housed in separate bodies.

Hermaphroditism in Fiction

Dual sexuality apparently held a special fascination for the ancient Greeks, as gauged by its prominence in their classical mythologies. Indeed, the word *hermaphrodite* derives from the Greek myth of Hermaphroditus, a son of Hermes and Aphrodite, the ancients' gods of male and female sexuality. As a boy, Hermaphroditus was raised by nymphs on sacred Mount Ida, in what now is the country of Turkey. At age 15, while swimming naked in a pool near Halicarnassus (modern Bodrum, Turkey), the handsome young man was admired and soon accosted by a lovely naiad—Salmacis—who embraced him, kissed him, and prayed to the gods that they be united forever. Her wish was granted; their bodies blended and Hermaphroditus thereafter was part male and part female, simultaneously. In Greek paintings, Hermaphroditus is often depicted as a winged youth with mixtures of male attributes (including male genitalia) and female attributes (including hairstyle, breasts, and broad thighs).

Tiresias—the blind prophet-priest of Zeus—was another type of hermaphrodite who in this case switched sequentially between male and female. It all began when Tiresias chanced upon a pair of copulating snakes and beat them with a stick. Hera (the wife of Zeus) was infuriated, and punished Tiresias by transforming him into a woman. Tiresias then married, had children, and according to some accounts became a female prostitute of considerable renown. Seven years later, Tiresias again encountered two mating snakes, but

this time she left the serpents alone. As a reward, Hera permitted Tiresias to regain the male condition. In an interesting footnote to this story, Tiresias became embroiled one day in an argument between Hera and Zeus about who enjoyed sex more: men (as Hera claimed), or women (as Zeus claimed). Having experienced sex both ways, Tiresias was posed the question, and he answered that the female receives ten times more pleasure. Infuriated by this response, Hera struck Tiresias blind. Zeus could not stop this action, but, in partial compensation, he was able to grant Tiresias the gift of foresight, thereby enabling Tiresias to become a seer.

Agdistis was another hermaphrodite in Greek mythology. (S)he was conceived one day when Zeus fell asleep upon the ground and some of his leaked seed (semen) accidentally impregnated Gaia (mother Earth). Agdistis was a superhuman being, simultaneously male and female. However, the gods feared Agdistis and soon castrated it.

In another story from ancient Greece, hermaphroditism was humanity's original state. However, Zeus then decided to split the hermaphrodites, only to find that the now-separate genders spent most of their time in futile efforts to reunite. So, Zeus decided to reconstruct the genitalia such that when men and women embraced, they would fit nicely together and thereby conceive and propagate. And so it has been ever since.

Hermaphroditic or androgynous beings are similarly embedded in the religious traditions or mythologies of several other cultures around the world. For example, in one interpretation of Genesis in the Bible, Adam's body was hermaphroditic originally, but later it was cleaved or partitioned into male and female (Eve) as a part of the fall from grace in the Garden of Eden. In the tribal stories of some native North Americans, a mythological Trickster is mostly male but dresses as a female and gives birth to children. He carries his penis in a box, which he sends to women for purposes of intercourse. In the Dogon peoples of the Mali region in West Africa, a newborn baby who touches male and female outlines—drawn in the sand by a mythical figure—becomes possessed by two souls and may remain androgynous, without a strong proclivity to procreate.

India is especially rich in mythologies entailing dual sexuality. The great Hindu deity Shiva is often portrayed as partially fused with his female alter ego, Parvati. In Buddhism, a male Bodhisattva (a person who has attained Enlightenment) named Avalokitesvara later became a female, Guan Yin. There are East Indian legends in which ancient hermaphrodites are replaced by twins; of individuals who switch month to month between king and queen; of men who were made woman-like by a god's curse; and of males bearing children. A central feature of Tantrism is the desirability of activating both the male and female components of a person's inner self, thereby bringing greater wholeness to the life experience. Sequential hermaphroditism can

even be intergenerational. For example, a central idea in Hinduism is that souls transmigrate such that an individual is reborn time and again, often in opposite sex to that of the previous life.

Hermaphroditism also recurs as a theme in modern fiction. In *Star Wars*, Hutts are hermaphrodites, as are Hermats in the series *Star Trek: New Frontier*. In the novel *Raptor* by Gary Jennings (1993), the main character is a hermaphrodite, and so too is the protagonist in the book *Middlesex* by Calliope Stephanides (2002). In the novel *The Left Hand of Darkness* by Ursula Le Guin (1966), a planet is populated by sequential androgynes. For 24 days each month, these people are sexually inactive, but for the ensuing two days they become either male or female as determined by appropriate negotiation with an interested sex partner.

Hermaphroditism in the Real World

As intriguing as such mythological dual-sex characters may be, they hardly outmatch the marvelous hermaphroditic plants and animals that actually do populate our planet, and that are the subject of this book.

In this book I provide an introductory overview of real-life hermaphroditic organisms. I pay special attention to ecological and evolutionary explanations for the remarkable reproductive behaviors and lifestyles of these dual-sex creatures, which in some respects seem to have achieved a best-of-two-worlds outcome by combining male and female functions within each individual. The book will convey two central themes: hermaphroditic species can be highly successful ecologically and evolutionarily; and their successes (and failures) offer fresh perspectives on the adaptive significance of alternative sexual systems.

Beyond conveying these basic biological messages, this book is meant to be entertaining as well as educational for a wide audience. It is intended for college students, teachers, natural historians, and others who would appreciate a nontechnical introduction to the biology of dual-sex organisms. Hermaphroditism has been addressed in many previous works, but typically either from a mostly theoretical perspective (e.g., Charnov 1982) or as a small and specialized component of much broader topics such as sexual allocation, sperm competition, or sexual selection (Birkhead and Møller 1998). To my knowledge, no other book occupies the current niche: a biology-rich overview of the natural history, ecology, and evolution of the phenomenon of dual sexuality.

Chapter 1 sets the general biological stage by asking what defines maleness versus femaleness in diverse organisms. It contrasts hermaphroditism with the standard separate-sex condition (termed *gonochorism* in animals and *dioecy* in plants), and outlines the many ecological and evolutionary

topics for which the issue of hermaphroditism is highly germane. The remainder of the book canvases the vast scope of hermaphroditism in the biological world, beginning with plants (chapter 2) and invertebrate animals (chapter 3), and then building on these observations and concepts to describe various hermaphroditic phenomena in fishes (chapter 4). All of the chapters contribute to the broader thesis that hermaphroditism is not only fascinating in its own right but also provides a unique biological vantage for reexamining the ecological and evolutionary significance of familiar separate-sex reproduction.

Trudy Nicholson provided the line drawings of animals and plants that grace this book (figs. 2.4–2.9, 3.1, 3.2, 3.4–3.9, 3.12, 3.14–3.16, 4.2–4.9, 4.16–4.22, and the frontispiece). She has illustrated several of my books on natural history, and it is always a joy for me to work with this gifted and conscientious artist. Judith Mank kindly provided unpublished information, from her earlier dissertation research, on the taxonomic distribution of hermaphroditism in fishes. Thanks also go to Joan Avise for several forms of assistance, and to Felipe Barreto, Rosemary Byrne, Diane Campbell, Jinxian Liu, Ann Sakai, Andrei Tatarenkov, Steve Weller, and several anonymous reviewers for helpful comments on various drafts of the manuscript.