

PREFACE

Because humans are mammals that reproduce sexually, people are familiar with the concept of pregnancy (i.e., with the otherwise outlandish notion that one individual carries a genetically different individual inside its body for an extended period of time before expelling the latter through an orifice). If you are a man, you might feel relieved that this weighty reproductive imposition has been delegated to females in *Homo sapiens*, and if you are a woman, the thought of becoming pregnant might elicit any of a gamut of feelings from joy and contentedness to fear or even loathing. Such powerful emotional responses within and between the sexes are understandable given the profound impact that pregnancy can have not only on one's mortal life but also on one's genetic legacy. In short, pregnancy is a huge deal both personally and evolutionarily.

However, the standard mammalian perspective on pregnancy is much too parochial for this book. Instead, I explore the fascinating diversity of pregnancy-like phenomena in the many animal species that provide extensive gestational services for their offspring. Such evolutionary diversity is impressive in several regards. With respect to duration, a pregnancy may last just a few days or several years, depending on the species. With respect to the number of embryos, a pregnant parent may brood just one offspring at a time or many thousands (as in some fishes and invertebrates). With respect to a parent's energetic investment in offspring, pregnancy in various species can range from a rather minor inconvenience to one of life's greatest physiological challenges. With respect to gender of the gestating parent, anything goes, as evidenced by the fact that males become pregnant in more than 200 fish species, females do so in many others, and even some hermaphroditic

(dual-sex) and parthenogenetic (asexual) individuals carry their offspring internally. Finally, with respect to the site of incubation, a "pregnant" parent in various species might house embryos in its ovary, uterus, stomach, mouth, vocal sac, or gill chamber; inside or outside a ventral epithelial pouch; cemented to its back or tail or legs; hooked to its forehead; or cased within either hard or soft eggs that might be shed immediately, retained and hatched internally, or perhaps deposited in special external hatcheries that one or both parents may have constructed or adopted.

Via the strong selection pressures that pregnancy motivates, the phenomenon in any species can have powerful feedback effects not only on the evolution of alternative gestational modes but also on many temporal reproductive processes ranging from prezygotic and postzygotic sexual selection to perigestational natural selection to extended postpartum parental care. Gestational phenomena in nature can be both fascinating and frustrating: fascinating because they evidence the sheer inventiveness of evolution, yet also frustrating because they can make "pregnancy" difficult to characterize. For example, many animals gestate progeny on their outer body surfaces rather than internally, but is this a key biological distinction, or should we expand the definition of pregnancy to include such organisms? If we do the latter, might we then go one step further by extending what we call pregnancy to encompass taxa in which an adult incubates its embryos in an "external phenotype" (such as a nest) that may be adjacent to but physically separate from the parent? These are just a few of the unorthodox questions about the ontogeny and phylogeny of pregnancy that this book explores. For now, my point is simply that pregnancy-like phenomena in nature offer a tantalizing smorgasbord for comparative evolutionary analyses.

Overall, pregnancy by almost any definition occupies a key node in the nexus of biological factors that can influence an individual's genetic fitness via both natural selection and sexual selection. Furthermore, many of the selective pressures related to pregnancy presumably have operated throughout the relevant phylogenetic history of a specified lineage, so we might expect each mode of pregnancy to have left decipherable genetic signatures on many of the reproductive structures, physiologies, and innate sexual behaviors of extant species. This book explores the many biological ramifications of pregnancy from novel evolutionary vantages. The perspectives developed here should intrigue almost anyone, but they should be especially illuminating for readers who might be unaccustomed to thinking in a comparative evolutionary vein.

This is the third in the author's trilogy of books on the evolution of alternative reproductive systems in nature.* Like its two predecessor books, which

* The author's other two books in this trilogy are *Clonality: The Genetics, Ecology, and Evolution of Sexual Abstinence in Vertebrate Animals* (Oxford: Oxford University Press, 2008) and *Hermaphroditism: A Primer on the Biology, Ecology, and Evolution of Dual Sexuality* (New York: Columbia University Press, 2011).

dealt with clonality (asexuality) and hermaphroditism (dual sexuality), the current treatment is at once broadly comparative, entertaining, and educational and as such intended for a wide audience. More specifically, this book is intended for college students, teachers, natural historians, interested laypersons, scientists in other fields, and anyone else who might appreciate a sweeping introduction to the biological ramifications of heavy parental investment in offspring. To my knowledge, no other book occupies the current niche: a biology-rich overview of the phylogeny, ecology, ontogeny, and natural history of pregnancy from diverse and oft-unorthodox evolutionary vantages. As in all of my writings on natural history and evolution, my overarching goals are to inform a broad readership about the wonders of nature and our planet's marvelous biodiversity.

This book is divided into two sections: Part I (Distribution and Diversity of Pregnancy) is largely pattern based, whereas part II (Evolutionary Ramifications of Pregnancy) is more process oriented. The five chapters in part I set the biological stage. Chapter 1 asks what characterizes pregnancy in various taxa, addresses the role of pregnancy in the broader scheme of procreation, and introduces several reproductive arenas in which selection pressures associated with pregnancy have been important during evolution. The next four chapters in part I then canvass the scope of pregnancy in nature, beginning with viviparity in vertebrate animals (chapter 2) and continuing with alternative manifestations of pregnancy in other vertebrates (chapter 3) and invertebrate brooders (chapter 4) before concluding with a brief introduction to human pregnancy in both fact and fiction (chapter 5). Chapters in part II then shift more of the focus toward evolutionary processes by emphasizing how viability-based natural selection in mammals (chapter 6) and fertility-based sexual selection in fishes (chapter 7) relate to alternative modes of pregnancy and brooding. Chapter 8 then summarizes all of these topics from a comparative vantage and emphasizes the possible interconnections between animal mating behaviors and different gestational modes. Thus, all of the chapters contribute to the book's two overarching themes: that pregnancy-like phenomena are fascinating in their own right and that evolutionary perspectives on pregnancy offer a powerful conceptual framework for examining one of life's most awesome occurrences.