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Sex, Size & Gender Roles

Evolutionary Studies of Sexual Size Dimorphism

Daphne J. Fairbairn, Wolf U. Blanckenhorn and Tamás Székely

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EDITED BY

Daphne J. Fairbairn
University of California, Riverside, USA

Wolf U. Blanckenhorn
Universität Zürich-Irchel, Switzerland

Tamás Székely
University of Bath, UK

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Acknowledgments

The chapters in this volume are derived from an international workshop on the evolution of sexual dimorphism held at Ascona, Switzerland, in August of 2005. The three editors jointly conceived and organized this workshop in response to the burgeoning literature on sexual size dimorphism, and in the hope of providing a forum for the exchange of ideas across traditional disciplinary and taxonomic boundaries. The 42 participants in the workshop (Figure i.1) engaged in 5 days of intense discussion and exchange, and the breadth and excitement of these exchanges is evident in the resulting chapter essays. The editors are very grateful to all of the participants, and particularly to the chapter authors whose excellent contributions form the substance of the book. We are also grateful to the staff of the Centro Stefano Franscini and the Hotel Monte Verità for their excellent infrastructure and competent organization, and to Rosemarie Keller and Yves Choffat (Zoological Museum, Zurich) for administrative and technical assistance. We also thank the following organisations for providing financial and/or organizational support for the workshop: the Association for the Study of Animal Behaviour, Centro Stefano Franscini, Ethologische Gesellschaft e.V., Kontaktgruppe für Forschungsfragen (KGF Basel, Switzerland, including Novartis, Roche, Serono, and Syngenta), Swiss National Fund's SCOPES programme, Swiss Academy of Natural Sciences (SCNAT), Swiss Zoological Society, and Zoological Museum, University of Zurich.

Figure i.1 Participants in the international workshop on the evolution of sexual size dimorphism held in Ascona, Switzerland, August 21–26, 2005. The photo is taken on the lawn in front of the Hotel Monté Verita, overlooking Lake Maggiore. From left to right, front row: Alex Kupfer, Ellen Kalmbach, Derek Roff, Lynda Delph, Isabella Capellini, Tiit Teder, Henry John-Alder, Wolf Blanckenhorn, Evgeny Roitberg, Lee Ann Galindo, Daphne Fairbairn, Doug Emlen, Jacob Gonzales-Solis, and Antigoni Kaliontzopoulou. Middle row: Alois Honek, Martin Schäfer, Toomas Tammaru, Robert Cox, Virginia Salaver-Andres, Jordi Figuerola, Vojtěch Jarošík, Stéfanie Bedhomme, Jordi Moya-Laraño, Marguarita Ramos. Back row: Daniel Frynta, Martin-Alejandro Serrano-Meneses, David Carrier, Lukáš Kratochvíl, Subhash Rajpurohit, Toomas Esperk, Tamás Székely, Craig Stillwell, Matthias Foellmer, Terje Lislevand, Maria Martinez Benito, Turk Rhen, Patrik Lindenfors. Missing from the photo: Marguerite Butler, Michael Cherry, Krzysztof Koscinski, Sergiusz Pietraszewskj, and Abdul Jamil Urfi.

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Contributors

Stéphanie Bedhomme, Department of Biology, Queens University, Kingston, Ontario, Canada K7L 3N6

Maria M. Benito, Departament de Biologia Animal (Vertebrates), Universitat de Barcelona, Av. Diagonal 645, 08028 Barcelona, Spain

Wolf U. Blanckenhorn, Zoologisches Museum, Universität Zürich-Irchel, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

Russell Bonduriansky, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia

Marguerite A. Butler, University of Hawaii, Department of Zoology, Honolulu, HI 96822, USA

Isabella Capellini, Evolutionary Anthropology Research Group, Department of Anthropology, University of Durham, Durham, DH1 3HN UK

Adam K. Chippindale, Department of Biology, Queens University, Kingston, Ontario, Canada K7L 3N6

Robert M. Cox, Department of Evolution, Ecology and Organismal Biology, The Ohio State University, Columbus, OH 43210, USA

Lynda Delph, Department of Biology, 1001 East Third Street, Indiana University, Bloomington, IN 47405, USA

Daphne J. Fairbairn, Department of Biology, University of California, Riverside, CA 92521, USA

Jordi Figuerola, Department of Applied Biology, Estacion Biologica de Donana, CSIC, Avenida Maria Luisa s/n, E-41013 Seville, Spain

Matthias W. Foellmer, Department of Biology, Adelphi University, 1 South Avenue, Garden City, New York 11530, USA

Charles W. Fox, Department of Entomology, University of Kentucky, Lexington, KY 40546-0091, USA

Daniel Frynta, Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-128 44 Praha 2, Czech Republic

John L. Gittleman, Institute of Ecology, University of Georgia, Athens, GA 30602, USA

Alois Honek, Research Institute of Crop Production, Prague, Czech Republic

Vojtěch Jarošík, Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-128 44 Praha 2, Czech Republic

Henry B. John-Alder, Rutgers University, Department of Animal Sciences, New Brunswick, NJ 08901, USA

Kate E. Jones, Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK

Ellen Kalmbach, Max Planck Institute for Demographic Research, Konrad-Zase-Str. 1, 18057 Rostock, Germany

Lukáš Kratochvíl, Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-128 44 Praha 2, Czech Republic

Alexander Kupfer, Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

Patrik Lindenfors, Department of Zoology, Stockholm University, SE-106 91 Stockholm, Sweden

Terje Lislevand, Department of Biology, University of Bergen, Box 7800, N-5020, Bergen, Norway

Rudolf Meier, Department of Biological Sciences, National University of Singapore, 14 Science Dr 4, Singapore 117543

Jordi Moya-Laraño, Departamento de Ecología Funcional y Evolutiva, Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, 04001-Almería, Spain

Turk Rhen, Department of Biology, University of North Dakota, Grand Forks, ND 58202, USA

Evgeny S. Roitberg, Department of General and Systematic Zoology, Rostock University, Universitätsplatz 2, D-18055 Rostock, Germany

R. Craig Stillwell, Department of Entomology, University of Kentucky, Lexington, KY 40546-0091, USA

Tamás Székely, Department of Biology and Biochemistry, University of Bath, Bath BA2 7AY, UK

Tiit Teder, Institute of Botany and Ecology, University of Tartu, Lai 40, EE-51005 Tartu, Estonia

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CHAPTER 1

Introduction: the enigma of sexual size dimorphism

Daphne J. Fairbairn

1.1 The phenomenon to be explained: patterns and extremes of sexual size dimorphism

In the dry grass of a California meadow, the taut spiral of an orb web catches the early morning sun. A fat, yellow and black spider rests in the middle of the web, a crazy zig-zag of white silk marking the web below her (Figure 1.1). You stop and look more closely. This is a female *Argiope aurantia* and she is waiting for a morning meal. Her body is almost 20 mm long, and she seems gigantic, with a great round abdomen. Curiously, on the same web a much smaller, thinner, less brightly coloured spider seems to be moving cautiously toward the waiting female. This is a mature male *A. aurantia* and he is attempting to court the female and induce her to mate with him. He is only a fraction of her size (less than 6 mm long), and would easily make a meal. However, if he is successful in seducing her, he may fertilize all of the 300–400 eggs in her next egg sac, a worthy prize indeed (Foellmer and Fairbairn 2004). This is a dangerous enterprise for him because even if he escapes being eaten he will surely die in the end, spontaneous death during copulation being the fate of males of this species (Foellmer and Fairbairn 2003, 2004). Even to achieve his position close to the center of the web, he has had to battle with other males waiting for the female to become reproductively mature. In this contest, larger males had the advantage (Foellmer and Fairbairn 2005a) and yet all of the males are much smaller than their potential mate. Why is this? Surely larger males could out-compete other males and would also be less likely to be treated as prey by the waiting females. Why are the males so small?

Not far away, on the coast of central California at Piedras Blancas, another curious mating drama plays out each winter. In late fall, male northern elephant seals (*Mirounga angustirostris*) haul themselves on to the beach and set up breeding territories from which they attempt to exclude all other males. Males battle with each other, striking blows with their sharp teeth, and most bulls have deep scars over their necks and chests. Although fights are common, much of the competition among males takes the more benign form of bellowing, chasing, and rearing up to display size and strength. Females come ashore a little later than males to give birth and nurse their pups, and they only stay ashore for about a month before abruptly abandoning their pups and going back to sea. Mating occurs only during the last 3–5 days of nursing, and a single bull will attempt to monopolize all the females on his territory (Figure 1.2; and see www.elephantseal.org for a detailed description of this colony). Males are much larger than females, weighing an average of 2275 kg, while females average only 700 kg (Bininda-Edmonds and Gittleman 2000). The great size and aggressiveness of males can be a liability for the females, for both they and their pups are at risk of being crushed during mating attempts or male–male interactions (Le Boeuf and Mesnick 1991; Figure 1.2). In spite of this risk, large males sire more offspring than smaller males because of their ability to exclude other males from their mating territories (Alexander *et al.* 1979; Galimberti *et al.* 2002; Lindenfors *et al.* 2002).

Although this may explain why males grow so large, why are females (and their pups) not also larger? Why are the females so much smaller than their mates?

These curious cases are just two examples of differences in the average body sizes of adult males and females in natural populations, a phenomenon known as sexual size dimorphism (SSD). Moderate SSD, in which the sexes differ in size by 10% or less, occurs commonly in both animal and plant lineages whenever reproductive roles are segregated into separate sexes (e.g. Ralls 1976, 1977; Lloyd and Webb 1977; Parker 1992; Andersson 1994; Fairbairn 1997; Geber *et al.* 1999; and chapters in this volume). Dimorphism in our own species, *Homo sapiens,* falls in this range, males being on average about 7% taller than females (Gustafsson and Lindenfors 2004). More extreme examples such as those described above are less common but by no means rare. For example, in the avian order Galliformes (gamebirds) and the mammalian orders Carnivora, Primates, and Pinnipedia (seals, sea lions and walruses), males in some of the larger species typically weigh more than twice as much as females (Greenwood and Adams 1987; Fairbairn 1997; see also Chapters 2 and 3 in this volume). The most extreme male-biased dimorphism among birds and mammals occurs in the southern elephant seal, *Mirounga leonina,* where the 3510-kg males weigh seven times more than females (Greenwood and Adams 1987; Bininda-Edmonds and Gittleman 2000; Lindenfors *et al.* 2002). The record for male-biased SSD, however, belongs to a small shell-spawning cichlid fish in Lake

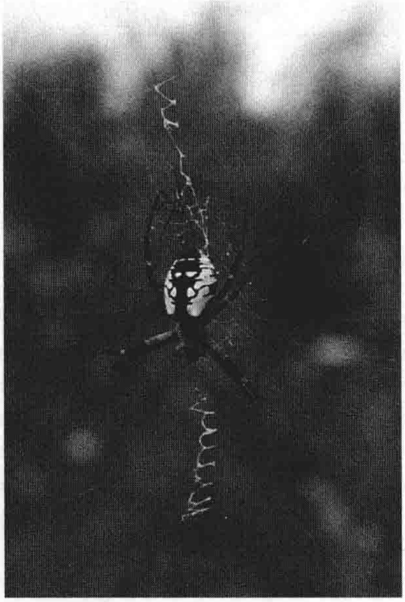

Figure 1.1 Male (above) and female (below) orb-web spiders, *Argiope aurantia*, on a mating web. Photo credit: Matthias Foellmer.

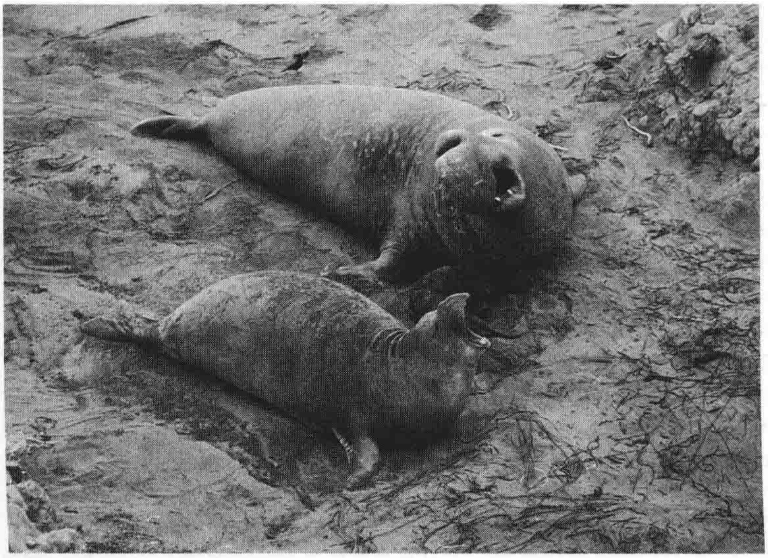

Figure 1.2 Breeding male (top), pup and female (bottom) northern elephant seals, *Mirounga angustirostris*, on the beach at the Piedras Blancas rookery in central California, USA. Photo credit: Daphne Fairbairn.

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Tanganyika (Schütz and Taborsky 2000). Male *Lamprologus callipterus* weigh only 23–33 g but this is more than 12 times the average weight of females. Even though larger females lay more eggs, female size is constrained by the size of the gastropod shells available for spawning because they must enter the shells to spawn. Males, on the other hand, collect the shells and carry them in their mouths to their territories. They have to be large enough to transport the shells, as well as defend their territory, with its harem of females, against other males. The net effect of these selection pressures has been a decrease in female size relative to male size as this breeding system evolved (Schütz and Taborsky 2000).

Although such examples of extreme male-biased SSD are impressive, they pale in comparison to the extremes reached in many taxa where females are the larger sex. Moderate, female-biased SSD is by far the most common pattern in both animals and dioecious flowering plants (Greenwood and Adams 1987; Fairbairn 1997; Geber *et al.* 1999; see also other chapters in this volume). Even among birds and mammals, where male-biased SSD generally predominates, several major lineages are characterized by moderate female-biased SSD (e.g. bats (Chiroptera), rabbits and hares (Lagomorpha, Leporidae), baleen whales (Mysticeti), raptors (Falconiformes), and owls (Strigiformes)), and many other lineages include at least some species in which females are slightly larger than males (Ralls 1976; Fairbairn 1997; see also Chapters 2 and 3 in this volume). Female-biased SSD predominates in most other vertebrate and invertebrate lineages, and in these groups extreme SSD, where females are at least twice as large and sometimes several hundred times larger than males, has evolved repeatedly (Ghiselin 1974; Poulin 1996; Vollrath 1998). The most familiar example of this occurs in orb-weaving spiders (Araneidae), as illustrated by the example of *Argiope aurantia* at the beginning of this chapter, but dwarf males and giant females occur in several other spider families as well (Vollrath 1998; Hormiga *et al.* 2000; see also Chapter 7 in this volume). Even more extreme female-biased SSD, with females several hundred times larger than males, has evolved repeatedly in aquatic environments and examples can be found in several lineages of crustaceans, annelid worms, cephalopod mollusks, and deep-sea fishes (e.g. Gotelli and Spivey 1992; Raibault and Trilles 1993; Anderson 1994; Norman *et al.* 2002; Rouse *et al.* 2004; Zardus and Hadfield 2004; Berec *et al.* 2005; Pietsch 2005). In numerous cases, males have become structurally reduced sperm donors that live permanently in or on the female. Well-documented examples of this form of parasitic SSD include deep-sea marine tube worms in the genus *Osedax* (Rouse *et al.* 2004), the bottom-dwelling echiuran marine worm *Bonelia viridis* (Berec *et al.* 2005), and the barnacles *Trypetesa lampas* (Gotelli and Spivey 1992) and *Chelonibia testudinaria* (Zardus and Hadfield 2004). These examples from diverse taxa share a common mating system, where large, relatively sedentary females accumulate males throughout their reproductive lives, and the tiny, short-lived males compete for attachment sites on or within the female. Among vertebrates, several different lineages of deep-sea Anglerfishes (suborder Ceratioidei) have evolved a similar pattern of SSD in which dwarf males attach themselves to females hundreds of times their size (Pietsch 2005). In some of these species, males become structurally reduced, and remain permanently attached as parasitic sperm donors, and multiple males have been found on a single female. Although these examples suggest that dwarf males typically spend much of their lives attached to larger females, the most extreme female-biased SSD discovered to date occurs in the blanket octopus (*Tremoctopus violaceous*) where both sexes are free-living. In this species females are up to 2 m long and are 10 000–40 000 times heavier and at least 100 times longer than males (Norman *et al.* 2002). Like male *A. aurantia*, males of this species die after inseminating the female.

These examples serve to illustrate the astounding range of SSD. Even in this brief overview, general patterns begin to emerge, such as the relative dominance of male-biased SSD in endothermic vertebrates and of female-biased SSD in other groups. Another apparent trend is the association of extreme SSD with aquatic environments (spiders being a notable exception) and with skewed mating ratios wherein only the larger sex accumulates multiple mates. A third pattern, most obvious in cases of extreme SSD, is that divergence in body size between males and females is generally accompanied by divergence in life history and ecological variables. For example, SSD is frequently associated with differences between the sexes in age at maturity (Stamps and Krishnan 1997; Vollrath 1998; Blanckenhorn *et al.* 2007; see also Chapters 5, 15, and 20 in this volume) and survival or lifespan (e.g. Norman *et al.* 2002; Foellmer and Fairbairn 2003, 2004). Some degree of habitat or trophic segregation between the sexes is also common (Blanckenhorn 2005; Ruckstuhl and Neuhaus 2005). The striking variation in SSD and the covariation of ecological and life history variables provide powerful illustrations of the many ways that gender roles have evolved in organisms with separate sexes. Even within a single evolutionary lineage, the teleost fishes, the contrast between the shell-spawning, polygynous freshwater cichlid, *Lamprologus callipterus*, where males are 12 times heavier than females, and the deep-water, open-ocean Anglerfishes with attached, dwarf males hundreds of times smaller than females, could hardly be more extreme.

How and why such diversity has evolved is the subject of this volume. The chapters that follow are a compendium of studies of the evolution, adaptive significance, and genetic and developmental bases of SSD. In a series of separate overviews and case studies, evolutionary biologists attempt to answer the question: why do adult males and females so frequently differ markedly in body size and morphology? Throughout the volume the emphasis is on sexual dimorphism in overall size but the scope of enquiry encompasses gender differences in body shape, the size and structure of secondary sexual characteristics, patterns of growth (ontogeny), life history, and genetic architecture. From a variety of perspectives, the authors examine the role of natural and sexual selection in shaping these differences. Adaptive hypotheses allude to gender specific reproductive roles and associated differences in trophic ecologies, life-history strategies, and sexual selection. This adaptationist approach is balanced by more mechanistic studies of the genetic, developmental, and physiological bases of SSD. These describe how organisms have responded to gender-specific patterns of selection to produce present-day patterns of SSD and remind the reader that the evolution of sexual dimorphism occurs in the face of major biological constraints: divergent phenotypes must be produced from largely identical sets of genetic instructions.

1.2 The major integrative themes: adaptive significance and genetic constraint

The broad sweep of research on SSD presented in this volume can be viewed in the context of two central questions. One question concerns the adaptive significance of SSD. What selective forces drive divergent evolution of the two sexes and maintain SSD in contemporary populations? On a general level, there is broad consensus that SSD primarily reflects the adaptation of males and females to their disparate reproductive roles (e.g. Greenwood and Adams 1987; Andersson 1994; Short and Balaban 1994; Fairbairn 1997; Geber *et al.* 1999; Mealy 2000; Blanckenhorn 2005; see also other chapters in this volume). Because body size tends to be related to reproductive success through different pathways in males and females, most typically through fecundity in females and through mating success in males, the body size associated with maximum fitness (i.e. the optimal body size) often differs between the sexes. In such cases, selection favors SSD, and males and females are expected to evolve toward their separate optimal sizes (Figure 1.3a). Sexual dimorphism in traits not closely related to reproductive function, such as feeding or locomotory structures, is less readily explained. Such differences are generally associated with ecological differences between the sexes and this has given rise to the hypothesis that SSD could reflect adaptation of the two sexes to different ecological niches rather than to different reproductive roles (Slatkin 1984; Hedrick and Temeles 1989). It seems unlikely that ecological niche divergence between adult males and females (more recently termed sexual segregation) is ever truly independent of sexual divergence in reproductive roles (e.g. Shine 1991; Braña 1996; Geber *et al.* 1999; Blanckenhorn 2005; Ruckstuhl and

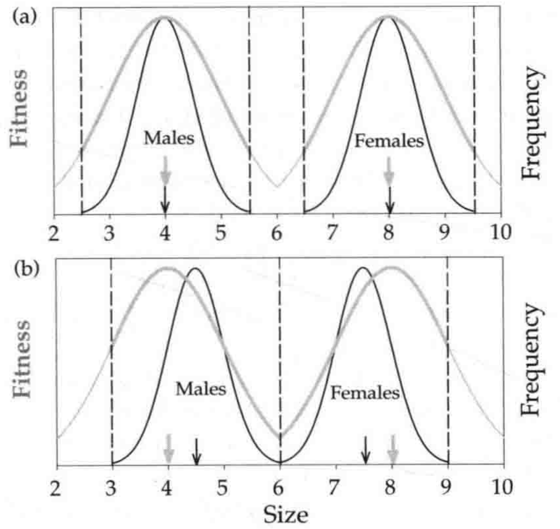

Figure 1.3 A schematic representation of selection on body size in which the optimal body size (i.e. the size that maximizes fitness) is higher for females than for males. The gray lines show lifetime fitness as a function of body size. The black lines are frequency distributions of body sizes for males and females in the population. (a) A population in which the mean sizes of the two sexes (black arrows) match the optimal sizes (gray arrows) and hence SSD is at evolutionary equilibrium. Within the range of sizes present in the population (bounded by the dashed lines) selection is stabilizing in both sexes. (b) A population in which the mean sizes of both sexes are displaced toward the common mean and away from their optimal values. Within the range of sizes present in the population, selection would appear as primarily directional and antagonistic (in opposite directions in males and females). This pattern is expected during an evolutionary transition to increased SSD and may persist for many generations if the genetic correlation between sexes is high (Lande 1980a; Fairbairn 1997; Reeve and Fairbairn 2001).

Neuhaus 2005; see also Chapter 5 in this volume). Nevertheless, whether ecological differences between the sexes are causes or consequences of SSD, or have evolved independently, is the subject of continuing research (e.g. Pérez-Barbería and Gordon 2000; González-Solís 2004; Forero *et al.* 2005), and selection favoring divergent ecological roles should be considered in any comprehensive explanation of SSD (e.g. see Chapters 3–5, and 9 in this volume).

The second major question addressed in various ways throughout this volume is to what extent the evolution of SSD is constrained by the shared genomes of males and females. Selection that favors different optima in males and females, known as sexually antagonistic selection, results in genomic conflict if the traits are determined by the same genes in both sexes (Rice 1984; Gibson *et al.* 2002; Bonduriansky and Rowe 2005a, see also Chapters 16–18 in this volume). Theory predicts that, if there is no independent genetic variance for the trait in either sex (i.e. if the genetic correlation between sexes is perfect; $r_{\mathrm{Amf}} = 1$), SSD cannot evolve. In such a situation, antagonistic selection will result in a compromise, intermediate average trait value (Lande 1980a, 1987; Fairbairn 1997; Reeve and Fairbairn 2001; see also Chapters 8 and 16–18 in this volume). However, genetic correlations are seldom perfect, and provided that some independent genetic variation exists, trait values are expected to eventually reach their independent selective optima within each sex (Lande 1980a, 1987; Reeve and Fairbairn 2001). The major effect of the shared genes (i.e. genetic correlations) is to greatly slow the rate of attainment of equilibrium SSD so that the mean sizes of the two sexes may remain displaced from their optima for many generations (Figure 1.3b; Lande 1980a; Reeve and Fairbairn 2001; see also Chapter 18 in this volume). A second effect of strong between-sex genetic correlations is to produce correlated evolution of body size in males and females, even when selection is antagonistic. This is expected in the early stages of the evolution of SSD, when selection for increased (or decreased) size in one sex causes a lesser, correlated response in the other sex. Size initially evolves in the same direction but at different rates in the two sexes, resulting in a temporary covariance between the sexes and between mean size and SSD (Lande 1980a; Fairbairn 1997; Reeve and Fairbairn 2001). Such a scenario has been proposed as an explanation for the common pattern of interspecific allometry for SSD known as Rensch's rule (Maynard-Smith 1977; Leutenegger 1978). However, because genetic correlations between the sexes should produce such allometry only very early in the evolutionary trajectory, most authors have rejected this explanation (Clutton-Brock 1985; Fairbairn and Preziosi 1994; Abouheif and Fairbairn 1997; Fairbairn 1997). The only system in which this hypothesis has been specifically tested is that of allometry for SSD among populations of the water strider, *Aquarius remigis*, and there it was definitively rejected (Fairbairn and Preziosi 1994; Preziosi and Fairbairn 2000; Fairbairn 2005). Nevertheless, the extent to which genetic constraints and genomic conflict influence patterns of SSD is largely unknown.

These two themes, adaptive significance and genetic constraint, weave their way through the 19 contributed chapters that follow. In the first section of the book, six chapters describe broad patterns of variation in SSD within and among major phylogenetic lineages. The studies in this section combine literature reviews with new comparative analyses to both discern patterns and deduce broad-scale underlying evolutionary mechanisms. The second section of the book presents a collection of eight case studies where researchers have measured patterns of selection and genetic architecture within single species or groups of closely related species. These studies emphasize the mechanisms of adaptation and constraint within populations (i.e. at the microevolutionary level) and provide excellent examples of morphological evolution in response to selection for diverse gender roles. The final section of the book consists of five chapters that more directly address the proximate, functional basis of SSD. These studies describe how developmental and genetic mechanisms are able to overcome the basic constraints of a shared genome to produce males and females uniquely adapted for their disparate gender roles. The studies presented in the three sections represent diverse approaches for studying SSD and utilize many different taxa, but all authors emphasize common themes and general patterns. Brief introductions to each of three sections serve to summarize and highlight these.

1.3 Caveats and limitations of this collection of studies

The comparative analyses, case studies, and conceptual reviews that comprise this volume represent a very broad array of approaches to the study of SSD and utilize many different organisms at both macroevolutionary and microevolutionary levels. Both alone and in concert, the chapters provide comprehensive introductions to research on SSD and establish goals and directions for future research. Nevertheless, readers should be cautioned that the volume is not encyclopedic. Limitations on both the number of chapters and the length of each chapter meant that we could sample only some of the burgeoning literature in this area (an ISI keyword search uncovered 1469 papers using the term sexual size dimorphism published between 1976 and September 2006). Because each author was permitted only a limited number of citations, more recent review articles are often cited in preference to lists of the older, original studies. Readers are encouraged to refer to these reviews for the original citations. To help readers access the literature in more detail, a list of suggested readings is provided at the end of each chapter.

We have not attempted to include studies of every major organismal lineage and the empirical studies clearly emphasize tetrapods, insects, and spiders. These lineages all offer abundant data on many different species, facilitating broad inferences about both pattern and process. Plants are represented by only a single chapter, Lynda Delph's case study of *Silene latifolia* (Chapter 11). Studies of sexual dimorphism in plants have tended to emphasize the evolution of dioecy itself or differences between sexes in physiology, life history, flower size, or flower number, rather than dimorphism for overall size, and, as a result, it remains difficult to discern general patterns of SSD (Dawson and Geber 1999; Geber *et al.* 1999). Nevertheless, the concepts and theories applied to the evolution of sexual dimorphisms in plants are the same as those applied to animal systems (Geber 1999), and there is nothing to suggest that generalizations cannot be made across the two kingdoms. Excellent introductions to the literature on sexual dimorphism in plants are provided by Lloyd and Webb (1977) and in the edited volume by Geber *et al.* (1999).

Fish are also conspicuously absent from our empirical chapters, an omission that is particularly regrettable given the extreme range of SSD even just within the teleosts. As illustrated by the examples in the introductory paragraphs, the magnitude and direction of SSD in fish appears to be strongly related to the breeding system (e.g. Clarke 1983; Parker 1992; Roff 1992; Erlandsson and Ribbink 1997; Schütz and Taborsky 2000; Pietsch 2005). The available data suggest that fecundity selection generally favors large size in female fish and that female-biased SSD is the more common pattern, particularly in open-ocean species. Male-biased SSD tends to be associated with contest competition among males to defend resources or females, or provision of parental care by males, and may be more common in shallow-water and reef fishes. These generalities are tentative, however, and await more rigorous, phylogenetically controlled comparative analyses.

Aquatic and parasitic invertebrates are also absent from our collection of empirical studies. As illustrated in the introductory examples, extreme female-biased SSD has evolved repeatedly in this group (e.g. Ghiselin 1974; Gotelli and Spivey 1992; Poulin 1996; Vollrath 1998; Norman *et al.* 2002; Rouse *et al.* 2004; Zardus and Hadfield 2004; Berec *et al.* 2005). The little evidence available suggests that male dwarfism tends to evolve in aquatic habitats when larvae are pelagic and mature females are rare and widely dispersed. Transition to a parasitic lifestyle may also promote increased SSD through either increase in female size or decrease in male size (Poulin 1996; Vollrath 1998). Unfortunately, for most lineages of aquatic and parasitic invertebrates we lack sufficient data to make valid generalizations about the frequency and causes of SSD. When such data become available, it will be interesting to discover whether patterns common in insects and tetrapods, such as the association between male-biased SSD and sexual selection favoring large males (but not necessarily the reverse) and the pattern of allometry for SSD called Rench's rule, also hold in these lineages. Evidence from parasitic crustaceans and spiders suggests that these patterns may not be general in taxa with extreme female-biased SSD (Poulin 1996; Vollrath 1998; Hormiga *et al.* 2000; see also Chapter 7 in this volume) but quantitative and comparative studies of other lineages are sorely needed.

1.4 General methodological issues in estimating SSD

Although the term sexual size dimorphism can refer to sexual dimorphism in the size of a particular body component, most studies in this volume refer to dimorphism for overall body size. Unless otherwise specified, this is the sense in which we use the term and its abbreviation, SSD. Three basic methodological issues arise when we attempt to estimate SSD, and I will consider these in turn.

1.4.1 Measuring body size

The first methodological issue is simply choosing how to measure body size. Standard measures exist but differ among taxa. For example, snout–vent length is the standard for snakes, lizards, frogs, and salamanders (see Chapters 4 and 5 in this volume) while body mass is the most common measure for birds (see Chapter 3). Body mass is the most general measure in mammals (see also Chapter 2 in this volume), but skeletal measures such as skull length or shoulder height are also used (see Chapter 12). In insects, head width, lengths of leg segments, wings, or wing covers (tegmina), or total body length are all used (e.g. see Chapters 6 and 8–10), whereas in spiders, maximum carapace width and total body length are most often used (Hormiga *et al.* 2000; see also Chapter 7). While it is appropriate to use any measure of size that is repeatable within and between individuals, if the goal is to study SSD for overall body size, not all measures are equally desirable (Lovich and Gibbons 1992; see also Chapter 6). Although mass might seem the gold standard for estimating overall size, it can have poor repeatability within individuals because of the effects of food in the gut, hydration, nutritional status, and reproductive condition. Skeletal measures may have the advantage of higher repeatability but tend to underestimate the variance in body size. This is because, for any isometric change in body dimensions, a change in length or width by a factor of z will increase volume (and hence mass) by z^3. Thus, a sexual size ratio of 2 based on a length measure (e.g. males twice the length or height of females) would correspond to a weight ratio closer to 8. Using any single skeletal measure as an index of overall size is also problematic because it assumes a strong and isometric relationship between the trait measured and overall body size. Although multivariate morphometric analyses invariably find strong positive correlations among linear measures of body components, each trait shows some independent variation and thus the correlations are not perfect. Further, allometric growth of body components is the rule, not the exception, leading to variation in organismal shape as well as size (e.g. Gould 1966; Baker and Wilkinson 2001; Bonduriansky and Day 2003; Emlen and Allen 2004). The pattern of selection may also differ among body components so that the perceived adaptive significance of SSD may depend upon which measure is used as an index of size (e.g. see Chapters 3, 5, 7, and 9–11). The take-home message is that no single measure, including mass, is ideal for estimating overall body size and, by extension, for studies of the evolution and adaptive significance of SSD. Researchers (and readers of this volume) need to be aware of the limitations of the measures used, and comparisons among studies using different measures should be made with caution.

1.4.2 Estimating average size of males and females

The second methodological issue concerns selecting an appropriate parameter for estimating the average size of adult males and females. In organisms such as insects and spiders that have determinate growth (i.e. skeletal growth stops at the final molt), mean body size estimated from an unbiased sample of adult males and females in a given population or species should suffice. However, many organisms, including most vertebrates other than birds, continue to grow after reproductive maturity. In these species, sex-specific patterns of growth or survival after maturity can alter SSD with age. Depending upon the question of interest, it may still be appropriate to estimate SSD using the mean sizes of all adult males and females in the population. However, parameters of the growth curves such as size at maturity, asymptotic size, or maximum size may be more appropriate measures of adult size in each sex. I refer readers to Stamps and Andrews (1992), Stamps (1993), and Chapter 14 in this volume (Box 14.1) for more detailed discussions of this problem. Chapters 5, 15, and 19 in this volume also provide brief discussions and explain how this problem has been resolved for different study systems.

1.4.3 Selecting an appropriate index for SSD

Once a measure of average size and has been adopted, researchers face the final challenge of deciding how to quantify SSD. Numerous quantitative indices exist in the literature, but no single index has emerged as the standard. Lovich and Gibbons (1992) and Smith (1999) provide excellent critical reviews of these methods and I will only highlight a few key issues here. Most commonly, SSD is expressed as a raw size ratio between males and females (M/F or F/M) or a proportional difference in size, as I have done in the examples in this chapter. These are both ratio estimators and are readily interchangeable (e.g. $(M-F)/F = (M/F)-1$). Unfortunately, although superior to difference estimators, ratio estimators tend to be statistically problematic and suffer from lack of standardization among studies (Lovich and Gibbons 1992; Smith 1999). For example, raw ratios have a highly asymmetrical distribution because values over 1.0 are unbounded, while values below 1.0 can vary only between 1 and 0. This exaggerates our perception of the magnitude and variance in SSD for ratios greater than 1.0 relative to those less than 1.0. For example, if females are twice as large as males, the size ratio equals 2 if female size is the numerator, but 0.5 if male size is the numerator. If females are 10 times larger than males, these values are 10 and 0.1, respectively. Because of this asymmetry, ratios are never a good choice for comparisons among taxa or traits unless the same sex is always larger, the convention in that case being to put the mean for the larger sex in the numerator (Smith 1999).

Following the arguments of Lovich and Gibbons (1992) and Smith (1999), we can define four characteristics as desirable for estimators of SSD. The first is linearity: a doubling of the magnitude of the dimorphism should cause a doubling of the estimator. The second is symmetry: males twice the size of females and females twice the size of males should yield values equidistant from the

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