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WOMEN *and*
COMPETITION

The Oxford Handbook of Women and Competition

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The Oxford Handbook of Women and Competition

Edited by

Maryanne L. Fisher

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The *Oxford Library of Psychology*, a landmark series of handbooks, is published by Oxford University Press, one of the world's oldest and most highly respected publishers, with a tradition of publishing significant books in psychology. The ambitious goal of the *Oxford Library of Psychology* is nothing less than to span a vibrant, wide-ranging field and, in so doing, to fill a clear market need.

Encompassing a comprehensive set of handbooks, organized hierarchically, the *Library* incorporates volumes at different levels, each designed to meet a distinct need. At one level are a set of handbooks designed broadly to survey the major subfields of psychology; at another are numerous handbooks that cover important current focal research and scholarly areas of psychology in depth and detail. Planned as a reflection of the dynamism of psychology, the *Library* will grow and expand as psychology itself develops, thereby highlighting significant new research that will impact on the field. Adding to its accessibility and ease of use, the *Library* will be published in print and, later on, electronically.

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Peter E. Nathan
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Maryanne L. Fisher is Full Professor in the Department of Psychology at Saint Mary's University in Halifax, Canada, and an Affiliate Faculty member at the Kinsey Institute in Indiana, USA. She is an award-winning educator and has published over 90 journal articles spanning a variety of topics, with most related to women's intrasexual competition. She has recently coedited *Evolution's Empress: Darwinian Perspectives on the Nature of Women* (Oxford University Press, 2013).

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The Oxford Handbook of Women and Competition represents a fulfilled goal. Twenty years ago, research by Sarah Hrdy, Anne Campbell, Helen Fisher, and David Buss (among others) provided me, the Editor, with inspiration to study women and intrasexual competition. I hoped that one day the field would progress to the extent that full volumes on the topic would be possible, and here is tangible evidence of this advancement. Collaborating with the contributors for the *Oxford Handbook of Women and Competition* has been a pleasure, and I am grateful for their hard work, patience, and shared vision in what the book was to become. I am also thankful for the support and assistance from the people at Oxford University Press (OUP), namely Abby Gross. Due to these individuals, OUP firmly remains one of the premier publishers for scholars to share their ideas. In addition, I thank Saint Mary's University for their openness to research topics that are at the edges of mainstream psychology and oftentimes controversial, and to my fantastic collaborators who have worked with me on various topics pertaining to women over the years. I also have a deep appreciation for the undergraduate students who have worked with me, especially their enthusiasm for research, as well as for my son (Maxwell) who greets the world with a highly curious mind. Thanks also to my nonacademic (and academic) friends and family who have had countless discussions with me on related topics, and to my husband, Mark, for his support from the very start of this project. I am grateful to all of you, and am delighted to have had this opportunity.

The Oxford Handbook of Women and Competition

SECTION 1

Introduction

Introduction

Maryanne L. Fisher

Abstract

The topic of women's competition has gained recent momentum, as evidenced by the proliferation of articles in the scientific literature. There has been a considerable body of new research highlighting competition in several domains, including access to and retention of mates, access to resources related to mothering, interaction with virtual media, issues faced in the workplace, and engagement with sport and physical activity. The chapters in this volume provide a definitive view on the contemporary state of knowledge regarding women's competition. The majority of chapters rely on an evolutionary framework; other chapters argue that sociocultural sources shape women's competition. While the book is primarily about women, some contributors focus on issues faced by adolescent girls, or mention developmental trajectories for young girls through adulthood. It is hoped that the information within this volume will serve as a source of inspiration to help guide future directions for research.

Key Words: women, competition, indirect aggression, behavior, intrasexual competition, same-sex, review

Introduction

For those of us with an interest in women and competition, it is truly an exciting era. Never before has there been such a dedicated focus on the topic, with numerous articles and books detailing the wide assortment of venues in which women engage in competition and associated behavioral, cognitive, and hormonal considerations. Indeed, the issue has gained significant momentum in the scholarly literature over the last two decades. These developments span a noteworthy range of topics, as exemplified in the chapters listed in the table of contents for this volume.

The goal of this volume is to provide a definitive overview of the field of women and competition. Some chapters expand this view to incorporate girls and adolescents, aiming to provide a fuller understanding of issues pertaining to women. A second, equally important goal is to shed light on topics that require further exploration, and thereby serve as a

springboard to help direct future research. Indeed, every chapter contains concrete ideas for new research directions.

To set the stage, I begin this introduction with a discussion on why this book is about women. Some readers may argue that such a section is entirely unnecessary, and that books that focus on men would not typically include such a review. However, I feel strongly compelled to document shifts in the scholarship over time, and to suggest plausible reasons that led to the dedicated study of women and competition. Such change has been slow and often difficult, and it has taken decades to arrive. Thus, I feel it must be documented for posterity, so that new generations of scholars may comprehend some of the hurdles researchers in this area have likely faced.

I then turn to a brief overview of the current theoretical state of the field, including a short discussion of areas that have remained seemingly

overlooked by the research community. This section is followed by a presentation of the layout of the book, and a short conclusion.

Turning the Focus toward Women

The overwhelming majority of modern research on competition pertains to that which occurs within-sex (intrasexual) rather than between-sex (intersexual). It is important to start with a clear statement that scholarly developments in the study of women and intrasexual competition have not been at the expense of understanding men and their forms of intrasexual competition, which was (e.g., Daly & Wilson, 1990; Fischer & Mosquera, 2001; Geary et al., 2003; Marlowe, 2000; Mazur & Booth, 1998; Polk, 1994; Symons, 1979; Van de Vliert & Janssen, 2002; Wilson & Daly, 1985)—and remains (see, e.g., Buunk & Massar, 2012; Ponzi et al., 2015)—a topic of much interest for researchers. Some of this past research, as well as current scholarship, reflects an interest in exploring the sexes together, showing how they converge and diverge in their forms of intrasexual competition. Indeed, some of the chapters in this volume similarly rely on comparisons of women with men, while others focus solely on women. Regardless, the constantly growing body of scientific literature shows that there is a need to understand the sexes both together and individually, in terms of their competitive behaviors, motivations, and cognitions.

It is indisputable that there has been an academic shift from the focus on men and competition to studying women and competition. There are several potential explanations for why this has happened, five of which are now discussed.

As mentioned, the majority of chapters in the current volume incorporate an evolutionary perspective. It has been reviewed elsewhere (Fisher, Sokol-Chang, & Garcia, 2013) that women are typically perceived as being relatively passive in the evolutionary process, particularly within the traditional evolutionary psychology paradigm (see Liesen, 2007, 2013). Viewing women as competitive therefore reflects a shift toward perceiving women as active agents. Moreover, much of the prior work pertaining to women and evolution has been oriented toward what happens *to* women rather than women's active influence on human evolution (Fisher, Sokol-Chang, & Garcia, 2013). Hence, this paradigm shift toward viewing women as active agents within the evolution of humans has directly led to an outpouring of new work.

Another reason underpinning the change may be temporal societal shifts. Societal views of women (and men) are revised over time, and for most Western cultures, this shift has meant a movement toward gender equality (see, e.g., Crompton & Lyonette, 2008). For instance, in 1977, 65% of interview respondents in the United States believed in “traditional” gender roles, where men should be the primary earners, with women taking care of the home and family, while in 2012, that number dipped to 31% of respondents (Roper Center, 2015). Inglehart and Norris (2003) state that while there is a general global movement toward gender equality, such that some countries have achieved major gains in legal, educational, economic, and political gender equality, “in many places, the lives of women remain wretched” (p. 3). This remaining cultural difference in gender equality may be due to numerous factors. Manago and colleagues (2014) document how environmental change in terms of increased urbanization, and technological and commercial growth, leads to a shift away from ascribed gender roles and toward chosen and equality-based roles.

Moreover, gender roles may directly impinge upon competitive attitudes and behaviors. Cultures that become less patriarchal show a decrease in sex differences in attitudes toward engaging in direct, overt competition. Andersen et al. (2013) investigated ball-throwing activity where there was an economic reward for performance when individuals outperformed others; they found that adolescent girls had a lower propensity than boys to compete in such a task in a patriarchal society, with no sex difference in a matriarchal society. They argue that traditional gender roles exhibited by patriarchal societies cause girls to typically show a decline in competitiveness during adolescence, and that this decline presumably decreases as society shifts from patriarchal to matriarchal (Andersen et al., 2013). Hence, by extension, if there is a cultural shift over time toward egalitarian gender roles, there should be less stigma associated with girls and women competing in a direct manner for the resources, mates, and status that they seek.

Perhaps this shift is also a result of the growing number of women involved in research. Reiter (1975), when discussing the study of women in anthropology, comments: “A great deal of information on women exists, but it frequently comes from questions asked of men about their wives, daughters, and sisters, rather than from the women themselves. Men's information is too often presented

as a group's reality, rather than as only a part of a cultural whole. Too often women and their roles are glossed over, under-analyzed, or absent from all but the edges of their description" (p. 12). With the growing number of women entering academia (e.g., CAUT, 2008), there is presumably an associated shift in the focus of research, coupled with new, critical questions about potential biases in past theories and findings.

Maybe, too, it is due to increasingly sophisticated methodologies. Hrdy (1981/1999, pp. 129–130) states that:

Women are no less competitive than other primates, and the evidence will be forthcoming when we begin to devise methodologies sufficiently ingenious to measure it. Efforts to date have sought to find "lines of authority" and hierarchies comparable to those males form in corporations. No scientist has yet trained a systematic eye on women competing with one another in the spheres that really matter to them.

Thus, she proposed that one of the obstacles to studying women's intrasexual competition is subtlety, and consequently researchers need to invent or discover research methods that are able to detect covert behaviors. Further, researchers need to determine the spheres in which women compete, rather than simply examine hierarchies and dominance, as women compete in many arenas and these traditional schemas may not be relevant. Turning one's research focus to these previously unexplored areas was critical, given that women's intrasexual competition rarely involves escalating contests (Clutton-Brock & Huchard, 2013), and that women suppress it when men are present in order to avoid seeming undesirable (Cashdan, 1999; Fisher et al., 2010). The chapters in this book indicate there have been sufficient advances in methodologies and research design that have enabled empirical examination of women's notoriously subtle and covert intrasexual competition.

The State of the Field

The topic of female competition has gained considerable recent momentum, as evidenced by the proliferation of articles in the scientific literature. This expansion of inquiry and theoretical development has been noticeable within the area of women's competition, as well as in the competition of other mammals and birds. Indeed, the general topic has developed to the extent that there was a recent issue of a top-tier scientific journal dedicated to this topic (i.e., Campbell & Stockley, 2013; a theme

issue on "Female Competition and Aggression" for *Philosophical Transactions of the Royal Society, Series B, Biological Sciences*). While there has been an absence of academic books singularly devoted to women's intrasexual competition, several authors have meaningfully raised the issue in the larger context of the evolved psychology of women (e.g., Campbell, 2002; Hrdy, 1981/1999) or while studying the similarities and differences between the sexes (e.g., Benenson, 2014). It should be noted that there have been a handful of books that have solely explored women and competition, but often these are more popularist accounts, with the majority using interview data and providing a look into individual experiences, or relying on general statements without academic support (e.g., Chesler, 2009; Holiday & Rosenberg, 2009; Shapiro Barash, 2007; Tanenbaum, 2002). These books remain informative works, certainly, but do not typically include the same level of scientific rigor as more academically marketed volumes. Looking more broadly, there are mass market books aimed at helping women remove themselves from competition altogether (e.g., DiMarco, 2008). Recently, there have been publications oriented toward addressing how women are treating themselves overly harshly, and thus acting as a "mean girl" to themselves and competing with imaginary rivals (e.g., Ahlers & Arylo, 2015). Regardless of the intended audience or approach, one fact is clear: collectively, these works provide direct evidence that there is an interest in the lives of girls and women, as pertaining to their aggressive and competitive interactions with same-sex others.

In my opinion (outlined in Fisher, 2013), one of the most influential catalysts that propelled scientific developments in the area of women and intrasexual competition was a call by Sarah Blaffer Hrdy (1981), quoted earlier in this chapter. Hrdy writes that when she originally published *The Woman That Never Evolved*, the field had only been examining female intrasexual competition within the context of nonhuman primates, not among humans. After the initial release of her book, articles started to appear that pertained to sex differences in competition (e.g., Cashdan, 1998), and some researchers focussed on these differences within competition for mates (e.g., Buss, 1988; Buss & Dedden, 1990). These developments were followed by early research on women's competitive tactics and behavior within an evolutionary context (e.g., Campbell, 1995, 1999; Cashdan, 1999; but see also an early mention in Fisher, 1983). More recently, there has been a growth

in the literature dedicated toward women intrasexually competing with friends (Bleske & Shackelford, 2001) or in the workplace (e.g., Buunk & Dijkstra, 2012).

I propose that once the door was opened by Hrdy (1981), researchers started to earnestly explore evolutionary accounts of women's intrasexual competition, and then this focus shifted outward, moving into domains outside of evolutionary-based (sub) disciplines. Although many scholars prior to Hrdy studied competition, they often concluded with the statement that girls and women are simply less competitive relative to boys and men (e.g., Skarin & Moely, 1976; for a review, see Cashdan, 1998). Such conclusions were based on overt, direct measures of competition, such as winning a game, or social comparison with friends and concerns with appearing to be inferior to them (e.g., Berndt, 1982). In many instances, sex differences typically manifest when competition is expressed using physical aggression, with men using this form far more than women (e.g., table 3, Cashdan, 1998). Thus, the critical catalyst that drove the academic movement toward studying women's intrasexual competition, and led to incredible progress over the past decades, was when Hrdy rallied scholars to start to examine women's competition in ways that truly mattered to them. Hence, there was a shift away from examining direct methods for establishing hierarchies, for example, and toward covert, indirect means to gain access to mates, status, dominance, or resources (e.g., Björkqvist, 1994; Björkqvist, Lagerspetz, & Kaukiainen, 1992; Campbell, 1999).

Researchers have proposed a link between aggression and competition, such that aggression is necessary for competition to occur (e.g., Schuster, 1983). Indeed, as may be deduced from this review thus far, there was a breakthrough when findings from studies on aggression began to be included in frameworks for examining women's intrasexual competition. Those studying aggression showed women's experiences in interpersonal relationships often led to gains with respect to resources, mates, status, or reputation (e.g., Burbank, 1987; Olson, 1994; Schuster, 1983, 1985). Those who linked the findings from indirect aggression with theories of competition were able to, at long last, comprehend the subtle nature of women's intrasexual competition.

Rather than provide an overview of developments since the integration of these areas, I leave it to readers to peruse the chapters of this book. The contributors provide evidence of the ways in which

women compete, and the underlying causes and motivations of their behavior. What is abundantly clear is that women do compete (typically with each other), and that the form of their competition is often indirect, covert, and circuitous. Many of the authors review how girls and women rely on indirect aggression to perform their intrasexually competitive acts. Based on the chapters in this volume, it is safe to conclude that women rarely compete via direct, physically aggressive means.

Future Research Directions

There are still many areas within women's intrasexual competition that are neglected by researchers; as mentioned, each chapter outlines directions for future work. However, for the sake of transparency, it is important to note that there are several omissions from this volume, which is primarily due to an overall lack of research on specific topics. I have identified six such areas, although I presume there remain others not listed here.

To begin, there is a mainly theoretical limitation regarding work that is situated using evolutionary theory. Darwin, in *The Descent of Man* (1871/1998), argued that the weapons and ornaments observed in males but rarely in females of many species were secondary sexual characteristics. These features were not primarily the result of increased survival, but instead the consequence of intrasexual competition for access to mates or to attract members of the opposite sex. Sexual selection, as Darwin named the process, was dependent on the advantages that some members of the species had over other members, exclusively framed in terms of reproduction. According to Clutton-Brock (2007, p. 1885), since the days of Darwin, sexual selection is now perceived to be

a process operating through intrasexual competition for mates or mating opportunities, with the result that selection pressures arising from intrasexual competition between females to conceive or rear young are generally excluded and sexual selection is, by definition, a process that is largely confined to males. An unfortunate consequence of this is that characteristics that increase the competitive ability of individuals are likely to be attributed to sexual selection if they occur in males—but not if they occur in females... [There remain] many important questions about the operation of sexual selection in females and the evolution of sex differences have yet to be answered. Where females compete directly with each other, it is often unclear precisely

what they are competing for. Where females have developed obvious secondary sexual characteristics, it is often uncertain whether these are used principally to attract males or in intrasexual competition for resources, and how their development is limited is unknown.

Thus, while we have made large strides in our understanding of women's intrasexual competition for limited resources (including quality mates), the ultimate motivation and consequences of competition is at times obscured.

The remaining five areas that are not addressed in this volume are less theoretical, but highly important. First, there is minimal research on mating psychology related to nonheterosexual women, as applied to competition for access to, and retention of, mates (see for exceptions, Li et al., 2010, who studied eating disorders; and Lindenbaum, 1985, who reports as a psychotherapist on competition within lesbian relationships). Indeed, while there exists work, for example, on women's sexual fluidity as a mechanism for shared parenting (i.e., allomothering; Kuhle & Radtke, 2013, but also Apostolou, 2016) as a form of cooperation, there remains a heteronormative bias in the literature for women's mating competition. Moreover, there is seemingly no literature addressing how nonheterosexual women compete for access to resources that are necessary for successfully raising children (who may be present from a prior heterosexual relationship, or a result of planned insemination), or access to resources that may assist their families' survival (for further reading, see Kirkpatrick, 1987).

Second, this volume only touches on co-wives and the forms of their competition among various cultures (see, e.g., the chapter by Sokol-Chang, Burch, & Fisher). There has been research on co-wives and competition within individual cultures (e.g., Burbank, 1987) and, albeit rarely, at a multicultural level (see Jankowiak et al., 2005; and for coding issues in the Standard Cross-Cultural Sample, see White, 1988). However, it remains vastly understudied and is rarely a central topic of inquiry. Related to this point, there is a lack of specific, focused investigation into issues faced by co-wives who are mothers, specifically dealing with the resources that they need to support their children, although presumably such data exist as part of other projects.

Third, there is also an apparent lack of investigation into the acute and chronic health consequences for women who engage in intrasexual competition

on a long-term basis in the workplace, within their families (e.g., in the case of co-wives, between sisters, or between mothers and daughters, or among in-laws), or for access to mates. In one study, young adult women reported higher levels of distress resulting from competition within their friendships and in academic domains (McGuire & Leaper, 2016), but the long-term outcome of this distress remains unknown. In this volume, the chapter by Miller and Rucas does partly address this topic, as they examine how the loss of sleep due to rumination over social situations with other women influences well-being and health outcomes. This topic is highly important, given the direct consequences for women's overall health and well-being, which affects not only themselves but also those who may depend on them for care, such as children, elderly parents, or mates.

Fourth, much of the work that conceptually relies on an evolutionary framework pertains to women's intrasexual competition for access to mates. In her chapter in this volume, Low discusses the theoretical underpinnings of women's intrasexual competition, and asserts, "Intrasexual selection always concerns resources important for survival and reproduction, or resources that have in the past filled that role" (p. 17). She states that the majority of work in this area deals with mating, yet it also plays a very important part in other areas of girls' and women's lives, starting in the womb. One explanation for the focus on mating is that Darwin considered intrasexual competition in his theory of sexual selection, such that it occurs when members of the same sex compete for access to mates. Perhaps scholars using an evolutionary perspective have been slow to move away from this limited scope and expand competition to being a phenomenon that happens in many life-stages and in a variety of contexts.

This focus on mating access has led to several areas of neglect; for example, competition for retention of mates, or competition among women who are already in a romantic relationship. Indeed, the overwhelming majority of the research findings are based on single young women participating in studies for course credit while at university, and hence, are members of a WEIRD sample (i.e., Western, Educated, Industrialized, Rich, and Democratic societies; Henrich, Heine, & Norenzayan, 2010). For example, it remains unknown how women who have been married for over a decade, with children or grandchildren, compete to retain their mates, or even if they engage in such activity. Moreover, we have no research on how these women would

compare if they lived in, for example, a Western and non-Western culture. This focus on younger women competing for access to mates has resulted in a lack of research on competition among women in their later reproductive years or among postmenopausal women; for a first exploration of these issues, see MacEacheron and Campbell in this volume. This lack of attention to older women is a noteworthy exception, given the research on the importance of grandmothers (see Sokol-Chang et al., this volume, for a review).

Fifth, there has been a dearth of research into the influence of individual differences on women's intrasexual competition (although see, for an exception, Buunk & Fisher, 2009). However, there needs to be much deeper exploration into factors related to, for example, personality traits, time perspective orientation, life history strategy, developmental history, self-monitoring, dominance seeking, and social conformity. Likewise, cultural influences remain overlooked, including how one's cultural orientation (e.g., collectivistic/individualist) plays a role. There is some promising recent work, though, which deals with individual differences in father presence versus absence within the Caribbean island of Curaçao (van Brummen-Girigori & Buunk, 2016).

Structure and Contents of the Book

This book consists of 39 chapters organized into 10 sections, with an additional concluding chapter. At times, there is some overlapping content in a portion of the chapters that helps to reinforce key points from multiple perspectives, while still enabling the chapters to stand alone.

Section two is devoted to theory and overview of women's intrasexual competition. Low opens the book with a broad overview of the types of female intrasexual competition, and outlines how it occurs over the span of a woman's lifetime, starting in the womb and then later in life for social status or mates. Given that the bulk of the existing literature pertains to mating competition, it was decided that the next chapter would deal specifically with theory surrounding this form of competition. Thus, Arnocky and Vaillancourt examine mating competition, as caused by biparental care and individual variation in men's mate value. To close this section and provide the reader with ideas about general sociality, and how competition may work in tandem with needs for affiliation and cooperation, Scott examines the sociality of female nonhuman primates. She extrapolates about the potential lives of women if they lived in various social environments.

Section three deals with social status and aggression. Liesen begins this section with an examination of women's aggression and status seeking within their social networks, arguing that they may be both supportive and competitive, and largely impact on women's lives, as well as the lives of their children. Gallup's chapter serves as an example of some of the arguments posed by Liesen, and he investigates adolescent girls' intrasexual peer aggression from an evolutionary perspective, positing that it serves to influence the dating relationships of rivals, as well as enabling one to gain access to desired partners. Rucas presents the idea of social capital as driving women's intrasexual competition, and investigates how relationships with particular individuals lead to benefits that offset costs in maintaining social networks, for example. Nagamuthu and Page-Gould explore women's same-sex friendships, and address whether intrasexual competition is highest among friends, or if friendship nullifies the existence of competition in favor of cooperation. Honey adds a different perspective, focusing instead on how the Dark Triad of personality traits (subclinical psychopathy, Machiavellianism, and narcissism) is used by women to exploit and manipulate others, often for purposes of gaining status, resources, or mates.

Section four pertains to communication and gossip. Anderson presents a model of women's communication of aggression, where women functionally match the form and frequency of their aggression to environmental triggers and individual differences between competitors. McAndrew turns the focus of the rest of this section to gossip. He explores women's use of gossip, and shows that it may be used in an aggressive, competitive way to effectively exclude potential competitors from the social group, as well as harming competitors' ability to establish or maintain a social network. Sutton and Oaten then use the perspective of gossip as informational aggression, and conclude that it is an effective, low-risk strategy to use in intrasexual competition for mates, particularly within the framework of altering reputations and poaching potential mates. Hess addresses coalitional relationships, and suggests that they serve aggressive functions in competitions involving one's reputation. She argues that intrasexually competing via gossip is typically more effective than using physical aggression for within-group competitive contexts.

Section five is centered on mate availability and mating relationships. Stone opens this section with a review of the research on how imbalances in the number of men and women (i.e., the sex ratio)

influence mating competition. Her investigation reveals that while men's mating competition is increased when there is a surplus of available mates, women's behavior is more mixed, possibly due to socioeconomic factors, patriarchy, or variance in mate quality. Dillion, Adair, and Brase take a closer look at sex ratios, focusing instead on the operational sex ratio (i.e., the ratio of men to women who are viable and available mates in a given mating market). They posit that women who are in environments where there is a surplus of women demonstrate systematic changes in their behaviors, including increased intrasexual competition. Continuing the theme of mating markets, Fisher and Fernández discuss strategies for intrasexual competition in relation to women's mate value, and suggest that mate value may be manipulated by rivals. Brewer adds novelty with her examination of the specific mating-related threats that women face, depending on whether they are single or romantically partnered, and how these threats influence their use of competitive tactics. Adair, Dillon, and Brase turn to how women may use the mating preferences of other women to provide information concerning their own mate choice (e.g., for the purposes of mate copying, mate poaching, or mate retention). They investigate how women's interest in other women's mate choice may lead to increased competition for mates, as well as the contexts in which this competition is most likely to be observed. In the last chapter of this section, Morris, Beaussart, Reiber, and Krajewski look at how women cope with the long-term effects of romantic relationship dissolution, and propose that associated negative emotions may provide motivation to avoid similar situations in the future. Specifically, they argue that dissolution due to women's intrasexual competition via losing a mate to a rival may lead to several advantages.

Section six details endocrinological and psychobiological considerations. Costa, Serrano, and Salvador suggest that women engaged in competition show a psychobiological response pattern that is effectively captured by their coping competition model. In this model, they propose a multistep process that emphasizes one's cognitive appraisal of the situation, which begins before the competition, as well as one's appraisal about the outcome, which influences future competitions. Using a narrower perspective, Cobey and Hahn exclusively focus on the hormonal regulation of competitive behavior in women, using a comparative and lifespan approach that ranges from birth through to after menopause. Nikiforidis, Arsena, and Durante narrow the

hormonal focus one step further and examine the influence of the ovulatory cycle on women's intrasexual competition. Their review highlights ovulatory influences on women's motivation to enhance their appearance for purposes of outperforming rivals, but also on patterns of consumption and financial decision-making as a way to compete in terms of status and resources.

Section seven pertains to topics spanning health and aging. Miller and Rucas examine how women's intrasexual competition and aggression within their social networks gives rise to problems for sleep, for example via ruminations or in sleep tradeoffs against waking activities, when more time and mental energy are needed for social actions. Sleep issues in turn impact on women's health and well-being. Turning to diet, Salmon reviews women's intrasexual competition for status and dominance, as well as for mates, and posits that it may lead to reproductive suppression. She proposes such suppression may be self-induced or caused by others, via extreme dieting behavior. In the last chapter of this section, MacEacheron and Campbell review potential factors that influence women's intrasexual mating competition as they age, arguing that the majority of research is exclusively performed on young women. To demonstrate potential areas of future development, they review reproductive advantages that women may experience when they are considered a successful mother.

Section eight focuses on motherhood and family. Valentine, Li, and Yong provide a thorough cross-species review of how mammalian mothers engage in various types of competition that ultimately influence the success of their offspring surviving and reproducing. In a related vein, Sokol-Chang, Burch, and Fisher focus on human mothers and separately investigate the advantages of cooperative versus competitive mothering, arriving at the conclusion that integrating both cooperation and competition is the most beneficial strategy. Kennair and Biegler extend the focus of this section to other family members and study mother-daughter conflict over choice of the daughter's mate, if the daughter's mate value is perceived as a valuable commodity in terms of a tradable resource for the family. In some cases, parents may provide benefits to some daughters, but not others, causing intrasexual competition between sisters. The section ends with Cousins' and Porter's examination of infanticide. They explore the specific circumstances that may lead to infanticide, such that it allows the mother to be able to intrasexually compete for access to better-quality mates.

Section nine presents chapters on physical appearance. DelPriore, Prokosch, and Hill begin this section with a focus on the advantages and disadvantages faced by beautiful women. They discuss how and why women strategically enhance their physical attractiveness to facilitate intrasexual competition. Dubbs, Kelly, and Barlow contend that women's fixation on improving their physical appearance for mating competition can lead them to take risks, such as unnecessary medical procedures. Shaiber, Johnsen, and Geher depart from examining individual attractiveness per se and instead present a review of adult and children's beauty pageants, arguing that they elicit competitive behaviors and strategies typically seen in mating contexts. Further, they suggest that the emphasis on status and resources that are bestowed on a winner enhance motivation to intrasexually compete. Johnsen and Geher examine fashion, viewing it as a tool women may use to enhance their attractiveness and hence effectively compete with rivals. They also review how women alter their clothing choices in relation to their ovulatory cycle status, in order to best compete for mating access.

Section ten deals with competition in virtual contexts. Yong, Li, Valentine, and Smith examine women's intrasexual competition for mates via virtual means. They propose that women engage in social comparison and competition with same-sex others who they see in print and electronic media, and explore the ways that women are influenced by this pervasive exposure. Keeping with the theme of virtual media, Guitar and Carmen examine a social network site, Facebook, and how it provides a novel platform for women to engage in intrasexual competition via behaviors such as stalking, bullying, and self-promotion, as well as other competitive strategies. Meredith turns to the issue of women's computer gaming, and contends that women engage in intrasexually competitive behaviors while gaming, if provided with the opportunities to do so. She argues that the style of women's play mirrors competitive strategies that have been documented in real life, including mating competitions, contests for status, and the formation and maintenance of alliances.

Section eleven pertains to competition in applied settings, and the included chapters span a wide assortment of areas. Kocum, Courvoisier, and Vernon investigate intrasexual competition among women in the workplace, and argue that zero-sum situations lead to the creation of intrasexual prejudice and discrimination. De Backer, Hudders, and Fisher examine the ways one may study competition in relation to food preparation and

consumption, and propose many lines of potential inquiry to bridge evolutionary theory with food studies. Varella, Varella Valentová, and Fernández discuss how women's interest in various artistic pursuits, such as bodily ornamentation, creating objects, and beautifying places, represent important venues for examining intrasexual competition. The final chapter of the book is by Russell, Dutove, and Dithurbide, and they review women's competition in sport and physical activity. They provide a developmental perspective on girls and sport, and then turn to how women learn about competition, issues surrounding dispositional competitiveness, outcomes of competitiveness, and general consequences for women's competition in sport.

Concluding Remarks

This volume represents a comprehensive examination of women's competition. The topic is highly important, given that competition has the potential to influence many aspects of women's lives, including their overall biological development, coupled with attitudes toward their physical health and appearance, their interactions with family members and same-sex friends, how they form romantic and sexual relationships, the ways they interact with virtual media, and their participation in sport and physical activity. The contributors address how competition starts early in life, even while still in the womb, and carries on throughout girlhood and adolescence into adulthood. The fact that competition is so pervasive throughout women's lives clearly indicates its importance as an area of academic study.

Collectively, we have made significant advances in the study of this topic. However, there remain areas that have yet to be examined. In addition, there are topics being explored that are not included in the volume (mostly due to their infancy). Two such examples are hormonal fluctuations in contest sports (Casto & Edwards, 2016), and interest in running for political positions (Preece & Stoddard, 2015). Clearly, there are no signs that the momentum of research on women's competition will slow in the near future.

This volume is timely and needed. There has been an exciting increase in the number of studies over the last decades pertaining to women's intrasexual competition in particular. Still, there has not been a parallel increase in the number of academic books on the topic. As mentioned, the majority of relevant books are oriented toward a popular-readership audience, with little examination of

the overall academic literature. What is truly novel about this volume is the definitive voice that the chapters provide on the academic study of women's competition. The chapters not only represent the current state of the field from multiple perspectives, but also provide solid guidelines for future directions for research. Hopefully, this volume will be an inspiring one for the next generation of scholars, and serve as a solid foundation to their work.

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SECTION 2

Theory and Overview

Competition Throughout Women's Lives

Bobbi Low

Abstract

From conception to the grave, girls and women face competition with others. In this chapter, I focus only on competition with other females: in the womb, the fetus's needs compete with her mother's and any sister's; after birth, she competes throughout her life: with her sisters, other female relatives, and unrelated female competitors for social status or mates. Although seldom as overt as male–male competition, female–female competition is equally serious in terms of lifetime impacts and may occasionally become violent. Here I follow a female lifetime, exploring the kinds, intensity, and impact of female–female competition.

Key Words: female–female competition, behavioral ecology, life history theory, lifespan, sex differences

The *Oxford English Dictionary* defines “competition” as “the activity or condition of striving to gain or win something by defeating or establishing superiority over others.” Today, we may find ourselves competing for prizes that are rather trivial in the sense of competition for real resources and their relationship to a struggle for existence: beauty pageants and high school athletic prizes, for example. Darwin, in making his argument for the existence of natural selection, was quite cogent about the importance of competition for limited resources in the “struggle for existence” throughout organisms’ lifetimes. His argument (somewhat rephrased) was simple. In any species (he gives a great example of elephants), (1) numbers increase geometrically: more individuals are produced than can be supported indefinitely by existing resources; (2) this geometric rate of increase is never seen; (3) this means that some struggle for existence (read “competition for resources”) must occur; and (4) heritable variation exists. We can infer, then, from his reasoning that in any environment, not all individuals survive and reproduce equally well. Of course, we have learned a considerable amount about genetics

and subtle environmental influences in the ensuing decades since Darwin. Nonetheless, in his basic points, Darwin (1859, p. 62) was quite prescient:

I should premise that I use the term Struggle for Existence in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny. Two canine animals in a time of dearth may be truly said to struggle with each other over which shall get food and live. But a plant on the edge of the desert is said to struggle for life against the drought, though more properly it should be said to be dependent on the moisture.

Darwin then went on to discuss competition issues for parasitic plants like mistletoe, which competes against other mistletoes and other fruiting plants to attract the birds that disseminate their seeds. Competition for resources, across many species and throughout lifetimes, was central to his work.

Darwin found it easy to see how surviving and reproducing would be favored by natural selection. At first, though, he had trouble seeing how

“ordinary” natural selection could favor risky and potentially lethal behaviors, so he separated sexual selection—the competition for mates—from ordinary natural selection. It was difficult for him to see the utility of behaviors, such as fights among elephant seals or red deer, that were dangerous and likely to get individuals killed. Today, because we understand the utility of risk-taking for high reproductive rewards, we consider sexual selection as a subset of natural selection (e.g., Mayr, 1972, p. 88). Much (typically male) intrasexual selection is simply a very high-risk, high-gain form of competition. For example, 30% of adult male red deer deaths arise from injuries received in fights; however, a male that does not fight has no reproductive success at all (Clutton-Brock, Guinness, & Albon, 1982).

For males, then, often being highly successful in reproducing involves taking serious, potentially lethal risks. Most mammals tend to have polygynous mating systems, because females are specialized for feeding newborns; males, thus freed from the utility of parental assistance, may then specialize in competing for mates (e.g., Clutton-Brock et al., 1982; Davies, Krebs, & West, 2012). In such systems—especially in terrestrial mammals—males are more expensive than females for a mother to produce successfully: males are carried longer in utero, they weigh more at birth, they nurse more often and consume more milk at each nursing bout, and they wean at a few days older so they can grow larger. Such trends result from the fact that, in physical combat, larger males are likely to be more successful than smaller males (Clutton-Brock et al., 1982; Le Boeuf & Reiter, 1988), especially in terrestrial (rather than aquatic or aerial) species. However, because of intense male intrasexual competition and resultant injuries, males die earlier than females.

Female mammals, in contrast, have the highest success when they can raise healthy, successful offspring. They are specialized to feed infants, and, being physically close, attend to much other parental care; as a result, there tends to be a sexual dichotomy: males spend effort on finding mates, whereas females spend more parental effort than males on their offspring.

In northern elephant seals (*Mirounga angustirostris*), although 82% of males die before reproductive age, and most males sire no offspring, the most successful male sires ten times as many offspring as the most successful female (Le Boeuf & Reiter, 1988). Thus, becoming a successfully reproducing male is a high-risk, high-gain endeavor. On the other hand, a male mammal that has been castrated lives

longer than its fertile competitors (e.g., Hoffman et al., 2013) but is unsuccessful at leaving offspring. Thus, male striving and risk-taking are important in terms of siring offspring: that is, not only *surviving*, but also *reproducing* successfully, are important. Today, then, we treat sexual selection as a part of natural selection, because reproduction is as important as survivorship in terms of lineage success. That is, natural selection and its subsets of sexual selection (e.g., attracting an excellent mate), social selection (e.g., having a successful lineage), and reciprocity (e.g., helping individuals who will return that help) all contribute to the differential success of individuals.

Importantly, although often so subtle as to go unnoticed, females, like males, undergo considerable intrasexual selection—competition with others of the same sex—principally for matings. This is in contrast to intersexual selection—mate choice by the opposite sex, in which the usual case is female choice of particular males.

In all cases, we are asking what traits, in any particular environment, help an individual to survive and reproduce and its lineage to persist and grow compared to another. We have come to understand that measuring and understanding these differences can be a complex and subtle business; maximizing reproductive success in terms of number of offspring may not lead to optimization of lineage persistence and growth relative to other family lines—it depends on the environment. For example, in highly competitive environments, every offspring may need great investment to be competitive. And there is a tradeoff: one cannot make more *and* larger offspring. So, when competition is low, high fertility—and low investment in each offspring—is common; when competition is high, the winning strategy is to make fewer but intensely invested offspring (Low, 2001, 2013; MacArthur & Wilson, 1967). In all these cases, competition, in the Darwinian sense, is focused on survival and reproduction, or, more properly, lineage persistence and relative lineage increase.

With this “large and metaphorical” understanding of competition, it is easy to see that each of us faces competition of various sorts at every stage in our lives. There are many ways to compete, as discussed at length in subsequent chapters: the actors can vary, the specific resources at stake (in terms of contributing to reproductive and lineage success) vary, and the strategies vary (e.g., having many babies with little care vs. few babies with intensive care). But, in all cases, competition is for rewards

(e.g., status, wealth, high-quality mates) that contribute to successful reproduction and to continuing family lineages. A moment's thought will probably reflect what we find in the literature. Although the specifics may differ between the sexes—in seeking a mate, men value youth or reproductive value more than do women; women value resources more than men—no one wants a sickly, socially inept, poor individual as a lifetime mate.

Particulars can also vary across societies. Thus, among the Ache of Paraguay, the best hunters, a form of status, have more wives over their lifetimes than do poorer hunters (Hill & Hurtado, 1996). Among the Yanomamö, if a man kills someone on a revenge raid, he is accorded the status of *unokai*; *unokai* marry earlier and more often than other men and have more children (Chagnon, 1988). Even in late-marrying, no-divorce nineteenth-century Sweden, wealthy men married younger wives than did poorer men and had, on average, 1.5 more children than other men (Low, 1994; Low & Clarke, 1991). In essentially every traditional or historical society for which these questions were asked, wealth and/or high status allowed men to increase their reproductive success.

At each stage in a woman's life history, the importance of any particular resource may vary. For example, nutritional resources in infancy help growth (and thus competitive ability), status in school or sports influences other students and perhaps even teachers to respect one, and being able to obtain the best available mate as an adult helps in a variety of ways: enhanced resources or an ability to have either more or better-invested children than others. In contrast, some types of competitiveness may be stable through several life history stages. Even though we think of nutrition as of highest priority in infancy, it remains an important resource through the lifespan. On the other hand, physical strength, hormonal balance, and other resources that require effort to develop may not be important until puberty. Similarly, both intelligence and knowledge become increasingly important as a child grows into an adult.

Intrasexual selection always concerns resources important for survival and reproduction or resources that have in the past filled that role. Probably the most-studied female–female competition is that centered on finding good (e.g., wealthy, high-status, companionable) mates—strategies such as derogation of competitors and self-promotion. These are covered in excellent detail in later chapters, so here I only leave signposts to them. Let us begin, then,

with conception and follow how competition plays out in each stage of a woman's life history.

Competition in the Womb

Even before the moment of fertilization, what may become a human female faces intense competition. Within the mother, whose sex chromosomes are XX, each protogamete, through the process of meiosis, produces four cells. There is competition to become a part of the new fetus because, of the four cells the mother produces, only one will become a viable egg; the others, which are called “polar bodies,” have almost no protoplasm and are not viable. There is considerable chromosomal influence and competition, at least in studies of mice (Wang, Racowsky, & Deng, 2011). It is even possible that the monthly process of egg and polar body production, the generation of one egg and three useless cells that will die, may contribute to menopause (Reiber, 2010). Thus, *whether and which* X chromosome from the mother, and its associated half-genome, make it into the functioning egg is an important example of intrasexual competition.

Men, who are XY, produce four sperm through meiosis. Some of these will bear an X chromosome, from the father's mother, and some will have a Y chromosome, from the man's father. Therefore, there is competition to determine whether an X-bearing or a Y-bearing sperm is the successful penetrator of the egg. Furthermore, if a man has what is called a “driving Y” chromosome, he will produce mostly or all Y-bearing sperm, and our protodaughter has little or no chance of entering the world (Hamilton, 1967).

Assume that fertilization has indeed produced a female fetus. The fetus's genes and her mother's genes are not identical, so neither are their reproductive interests. The fetus is always in competition with her mother for resources. The mother's interests often are best served by providing less investment than would be ideal for the fetus (e.g., if food is in short supply). Both the mother's own total reproduction and the interests of other offspring matter to the mother, but the interests of the fetus are simply to maximize what she alone can get from her mother (Hrdy, 1999). This means that mother and fetus compete both for simple nutrition and for essential nutrients like calcium. When conditions are harsh, it is not unlikely that the mother will reabsorb or spontaneously abort the fetus—a severe and deadly competitive loss indeed for the daughter fetus. Even when resources are relatively

rich and further maternal nutritional investment in this daughter would yield no increased survival or improved condition, the daughter's interests are still dedicated toward getting more resources for less effort, thus putting pressure on the mother's resources. This intense conflict over the distribution of the mother's resources is why Trivers (1974) noted the intense maternal–offspring conflict at the termination of parental care (e.g., weaning).

This maternal–fetal conflict is exacerbated by the fact that half of the fetus's genes come from the father, and the father's interests are allied with the fetus even if the mother's investment causes her harm (Haig, 1993). Neither the fetus nor the father bears the costs; the mother's body has the task of allocating effort in the optimal way for herself and *all* her offspring, which is of no import for the fetus or father—again, the fetus has an “interest” simply in getting the most investment possible. I return to this problem later because women face this problem again, from the other side, when they become mothers.

If our fetal girl shares the womb with siblings, competition is yet more severe. As an aside, this is especially true if she shares the womb with a male twin (intersexual selection). In virtually all mammals, males grow faster and are carried longer in utero. After birth, males nurse longer and more often than female offspring (e.g., Davies et al., 2012). All these conflicting interests regarding resource allocation—father's and fetus's interests against mother's—mean greater resource drains on the mother. Furthermore, if a male and female share the womb, there will be fiercer competition for female fetuses and infants against larger, stronger brother(s). But a female twin also imposes a cost on our focal female fetus, although not so severe as a male twin.

Preadolescence: Sugar and Spice— Are Little Girls Nice?

Cross-culturally, in the 93 odd-numbered societies of the Standard Cross-Cultural Sample (one of the standard ways to make cross-cultural comparisons), from about age 7 on, boys, but not girls, are taught to be aggressive and to show fortitude, whereas girls are taught to be industrious, responsible, and obedient. Curiously, there was no significant difference in the degree to which either sex was taught to be competitive (although it is not clear how this was defined; Barry, Josephson, Lauer, & Marshall, 1976; Low, 1989). So, although today we see many sex differences in type and apparent

intensity of competitiveness, in traditional societies, girls, as well as boys, were taught to be competitive.

Anyone who has spent time around small children will have noticed that even preschool children choose with whom to play; at this stage, inclusion/exclusion choices appear to be largely stereotypic and based on children's perceptions of social convention (Killen, Pisacane, Lee-Kim, & Ardilla-Rey, 2001). In many circumstances, little boys play in mixed-age groups more than do girls; boys engage in more rough-and-tumble play (Berenbaum, Martin, Hanish, & Fabes, 2008; DiPietro, 1981) and are often fiercely and overtly competitive, fighting for what they want. No matter how often an adult separates the fighters, boys tend toward head-on aggression more than girls do.

So, are little girls really sweet and less competitive than little boys? Perhaps not. Girls do seem to be more subtle in the ways they compete (Benenson, Antonellis, Cotton, Noddin, & Campbell, 2008; Benenson, Hodgson, Heath, & Welch, 2008): they appear to avoid potentially risky direct aggression. Instead, they turn away at critical moments, shift their voice tone, and spread rumors. It would be hard to assess their behavior as less competitive than that of boys; the competition is just conducted differently (e.g., Kokko & Pulkkinen, 2005). These differences (e.g., girls competing by manipulating status and by exclusion) may underlie the fact that girls do not generally play in such mixed-age groups as do boys.

There is evidence that girls' patterns of competition and exclusion are somewhat malleable; usually this is noted in studies of sex differences in competition. Cotton et al. (2013) found, in repeated mathematics competitions in elementary school, that boys outperformed girls in the first competition but that, in later competition, girls were at no disadvantage and sometimes outperformed the boys. This raises the question of how girls are socialized to compete with each other. In a sample of girls slightly younger than age 15, Booth and Nolen (2012) found that girls from single-sex schools competed more like boys than did girls from mixed-sex schools: that is, with rougher play and more direct aggression. Similarly, we must be careful in trying to generalize about girls' competitive strategies from samples taken mainly from one or two countries. When Cárdenas et al. (2012) compared girls' competitiveness in Sweden (a high gender-equity country; Low, 2011) and Colombia, which ranks far lower in macro measures of gender equity, they found that boys and girls (aged 9–12) in Colombia were

equally competitive in all tasks and in all measures used. In Sweden, boys tended to be more competitive in general, but girls tended to be competitive about improving performance on tasks (e.g., school assignments, recitals).

For girls as well as boys, though, there are more- and less-aggressive individuals; by age 8, one can predict some important aspects about aggression in later life. Individuals with low impulse control and high aggressiveness can show these traits early and continue showing them throughout life. Furthermore, a variety of interventions (e.g., tutoring, peer-pairing) appears to have no impact on this pattern. That is, the level and type of aggressiveness (direct, verbal, or physical attacks) are relatively stable throughout life (e.g., Ogilvie, 1968; Salmivalli & Kaukiainen, 2004).

Adolescence and Young Adulthood

Not surprisingly, sex differences in competitiveness increase in adolescence as hormonal changes set the stage for direct mate competition. Overt female–female competition becomes heightened in adolescence and young adulthood, and its intensity continues through mating and marriage; at its extreme, it can become violent (e.g., Sikes, 1998). Competition can be a double-edged sword, as many other chapters in this volume illustrate (also, e.g., Hibbard & Buhrmester, 2010). At this life stage, too, the ways in which boys and girls compete tend to differ: although both sexes frequently express their motivation as competing to “excel” (e.g., to surpass a personal best), boys are more likely than girls to compete to “win.” In formal educational settings, girls are often as competitive as boys, but their competition takes different (less direct, more subtle) forms. In fact, for girls, formal competition to win may be associated with relatively high levels of depression and loneliness and fewer close friendships (Hibbard & Buhrmester, 2010).

Even from late primary school, popularity is a major aim of competition and a likely proxy for later success in mate competition. The “popular” girls get the higher-status dates and, perhaps later, higher-status mates. To be sought after is clearly advantageous, although this striving for popularity may be variously modeled (Read, 2011; Read, Francis, & Skelton, 2011). Duncan (2004) found that girls felt their relationships tended to shift once they entered secondary school from intimate dyadic pairings to more fluid—and strategic—groups often focused on sexual competition and popularity. Popularity is

often associated with cliques and with exclusionary “meanness” as individuals begin to sort themselves into groups of similar status (Merton, 2005).

Girls and young women tend to participate in organized sports less than do boys and young men. Cross-culturally, using the Human Relations Area Files (which contain more society data than the Standard Cross-Cultural Sample but may contain observations by others than experienced ethnographers), Deaner and Smith (2013) found that in 50 societies, there were more male sports than female sports and that some (e.g., hunting, combat sports) were exclusively male, thus reflecting a robust sex difference. In the contemporary United States, women represented 51% of noncompetitive exercisers, 24% of total sports participants, and 20% of team sports participants (Deaner et al., 2012). There was little evidence that these trends were reversing. As Deaner has noted, through evolutionary time, men likely gained status in a variety of male–male competitions, both as individuals and in teams; such competitors gained better access to mates. Perhaps it is not surprising that women’s intrasexual competition is far more common in other (e.g., individual, personal, and directly reproductive) contexts rather than, for example, in organized sports.

To infer the importance of socialization in female intrasexual competition, Andersen et al. (2012) found that, in the patriarchal society they studied, girls’ competitiveness declined as puberty began. Cross-culturally today, Finnish, Israeli, Italian, and Polish girls ages 8, 11, and 15 all used indirect aggression most commonly (e.g., subtle snubs, snide comments), followed by verbal aggression directed at the victim, with physical aggression least common (Österman et al., 1998). Which strategy is most common changes with age: from adolescence onward, *physical* aggression, typically in the context of attracting the approval of boys in the group, can increase in some circumstances. For example, female associates of gang members may try to prove they also are “tough” and therefore worthy and desirable (Levy, 2012), sometimes to the extent of considerable violence and even murder (Lin, 2011; Sikes, 1998).

Competition for Mates and Competition Among Co-Wives

As girls mature and become actively interested in mating and marriage, life becomes more complicated, in part because our lives today differ so greatly from our lives in the past. Across most mammals, including primates, as noted earlier, males compete

and display “good genes” as reflected by hierarchical status, fighting ability, and so forth. This has been studied more in nonhuman species and in traditional societies: in general, a male that can dominate is preferable as a mate than a male that loses to others, and, as with all behaviors, there are genetic as well as environmental and ontogenetic contributions. Frequently, we can see the gene–behavior connections most clearly in abnormal or pathological cases, although they are usually simplified examples. Consider the Dutch family in which a point mutation resulted in males showing borderline mental retardation and abnormally impulsive aggressive behavior (Brunner, Nelen, Breakefield, Ropers, & van Oost, 1993).

Humans are among the most intensely male-parental of mammals because human fathers tend to give more parental care than do males of other primates. Thus, finding an excellent husband usually becomes a matter of competition among families because free female choice—which is common in other mammals—was largely superseded by parents and often fathers and uncles who chose (and sometimes still choose) children’s spouses (Whyte, 1979). This appears to be true not only for traditional societies such as hunter-gatherers and agriculturalists, but also even in more recent recorded history. Shakespeare captured this in *Romeo and Juliet*: when 12-year-old Juliet complained as her father betrothed her to a middle-aged man (who would be a good ally for her father) although she loved young handsome Romeo. Her father responded (Act 3, Scene 5):

An you will not wed, I'll pardon you!
Grazed where you will, you shall not house
with me: . . .
An you be mine, I'll give you to my friend;
An you be not, hang, beg, starve, die in the streets,
For by my soul, I'll ne'er acknowledge thee
Nor what is mine shall never do thee good.

Even though female choice was not widespread in our evolutionary and historical past, women did and do have some ability to exert influence in some societies. Today, in large nation-states (in which most competition studies are done), most women have the ability to choose their spouse. At this point, female–female competition is critical. All else equal, those who excel at intrasexual competition will be favored by selection (e.g., Buss & Dedden, 1990).

Both men and women derogate their competitors. Women, far more than men, were likely to call other women promiscuous (a great threat to

male investment) and to degrade other women’s appearance. They also were more likely than males ($p = 0.047$) to question another woman’s fidelity. Other tactics women employed to “dis” other women were to spread rumors and to call other women unintelligent, insensitive, exploitative, and boring. Not all of these tactics were equally effective, especially when men’s tactics versus women’s tactics were analyzed (e.g., Buss & Dedden, 1990). But how are women who derogate their competitors viewed by men and by other women? Fisher et al. (2010) found that others’ perceptions do change. Men saw female derogators as less friendly, kind, and trustworthy and overall less desirable as a mate—so there may be costs to derogation. Women saw women derogators in similar ways but also saw derogators as less fit to be a parent and less attractive.

Derogation is certainly not the only competitive strategy women use; another is self-promotion: advertising one’s positive attributes such as, “I am intelligent, responsible, beautiful.” Fisher, Cox, and Gordon (2009) found that women tend to use self-promotion more than do men, whereas men derogated competitors more strongly than did women. Self-promotion was particularly apparent for individuals who were romantically unattached or dating compared to those in a committed relationship. Both derogation and self-promotion are more indirect and subtle forms of competition than, for example, overt aggression; it is clear that one can compete subtly or overtly and aggressively. The social environment may have strong influence here: depending on circumstances (gang members vs. professional women CEOs, for example), each can be highly effective.

From an evolutionary point of view, the fact that most peoples in traditional societies are polygynous suggests that competition and cooperation among co-wives have done much to shape modern female–female competition. It is true that co-wives can become allies (Yanca & Low, 2004), although this may not be the predominant pattern. In a cross-cultural study of 160 societies for which data exist in the Standard Cross-Cultural Sample (a standardized sample controlling for geographic region and, within region, language group, and for which trained ethnographers’ reports exist), Betzig (1989) found that conflict among co-wives was the eighth most commonly stated cause of divorce after such obvious causes as infertility. She also argued that because co-wives were in competition in polygynous societies, such conflict might reasonably be lumped with adultery. If this were done, such

conflict would be part of the second most common cause of conjugal dissolution. In a detailed study of 69 societies for which the ethnographers specifically commented about co-wife relationships, Jankowiak, Sudakov, and Wilreker (2005) found considerable pragmatic cooperation (e.g., in gathering) and a few life-long friendships among co-wives; nonetheless, they found conflict in the majority of co-wife relationships. They found that first wives (typically older than subsequent wives) frequently reacted with suspicion, fear, and anger to the addition of a new wife.

Pregnancy: Neither Rosy nor Romantic

Pregnancy has never been the rosy, romanticized picture some might imagine (Hrdy, 1999). In pregnancy, in addition to the fact that a woman must compete with her fetus for resources, a father's reproductive interests are also at stake—and not in the mother's favor. “Genomic imprinting” (Haig, 1993) reflects the fact that fetal genes from the father can act in the fetus's favor (i.e., forcing more parental investment by the mother even when that is counter to the mother's interests). So, for example, there are paternally imprinted genes (well-studied in rodents and humans) such as *Igf2* and *Pg1/Mest* that cause the fetus to grow faster and thus take more resources from the mother (Burt & Trivers, 2006). (These often help the offspring with early growth: bigger babies typically do better than smaller, thinner infants.) Other paternal genes have similar effects a little later: *Pg3* not only enhances embryonic growth, but also increases nursing behavior; *Rasgrff1* increases infant growth (again, at the mother's expense), with peak influence around weaning. In all these cases, the father's imprinted genes aid the fetus or newborn at little or no cost to the father but often at considerable cost to the mother. Because genomic imprinting occurs whether the fetus is a girl or boy, it obviously involves more than intra-sexual competition; nonetheless, a woman's ability to rebuff paternally imprinted genes may give her a competitive advantage against other women. Again, this is an arena for future work.

Mothers: Competing Through One's Children and Having It All

In life's next stage, women become mothers. Do mothers (or both parents) use their children to brag, to gain status? There are two main ways in which this is feasible. First, parents may use children as “billboards” of parental wealth in their social competitions, much as wealthy men may adorn their

wives in sexual competition (e.g., Low, 1979). Second, parents may both pressure children to excel (in academics or athletics, for example) and brag about their children's accomplishments to other parents, again in the context of social selection. There is little in the primary literature about these possibilities, but web sites and popular articles, from *Time* magazine's coverage of children's styles (e.g., dresses for 3-year-olds costing hundreds of dollars) to *Battle Hymn of the Tiger Mother* (Chua, 2011) and *Joy Luck Club* (Tan, 1989), suggest that this is a fairly common phenomenon and one ripe for study.

In the matter of women competing to “have it all” (i.e., to have both well-provided and well-taught children and high-level professional careers), early feminists in the 1970s seem to have had no idea of the difficulties inherent in becoming superwoman. Nonetheless, from a reading of *Lean In* (Sandberg, 2013), it is clear that with enough advantages, some women—supercompetitors—can become superwoman. . . if they can afford a nursery next to their CEO office.

Postreproductive Life: Do Grandmothers Compete?

Unless they die prematurely, all organisms experience senescence: the decay in system functions that comes with age. In humans, many systems (e.g., lung function, muscle amount and tone) show significant decay by the time a person reaches around 70 years of age. Of course, this can vary depending on such things as smoking or intense exercise. But human female reproductive systems senesce as early as 40–45 years of age, with an average in the 50s. Human females are unusual in living almost a third of their lifetime in the years after ceasing reproduction; in most other mammals, females might spend perhaps 10% of their lifetimes postreproductive. Why?

To take a comparative perspective, some other species do show early female reproductive senescence: odontocyte whales (Marsh & Kasuya, 1984, 1986), baboons (Packer, Tatar, & Collins, 1998), bonobos (de Waal, 1997), rhesus monkeys (Walker, 1995), lions (Packer et al., 1998), and elephants (Poole, 1997). Many of these species share with humans an intense level of maternal care and a long time to independence for offspring. These phenomena have given rise to the Grandmother Hypothesis (e.g., Hawkes, O'Connell, Blurton Jones, Alvarez, & Charnov, 1998, 1999), which argues that because children take so very long to become independent, very late-born children of late-reproducing mothers

might die, and grandmothers may work to help the success of their grandchildren. If this is so, then it would be competitively advantageous for mothers to switch relatively early from reproduction to simply caring for existing children.

Despite the attractiveness of this hypothesis, there are few data and results conflict. The first analysis of human lifetime fertility among women who stopped earlier versus later is that of Hill and Hurtado (1991, 1996), who worked with the Ache of Paraguay. They found some positive effects of grandmothers' help: men and women with a living mother experienced slightly higher fertility than did others, and children with a living grandmother survived slightly better than others. But these effects were small, and women who remained fertile longer had higher lifetime reproductive success than other women. Selection is weak at older ages because (1) it affects relatively few women (many have died), and (2) it affects little or none of their reproductive lives (Hamilton, 1966; Williams, 1957). Thus, grandmothering benefits (in terms of, e.g., enhanced survivorship of grandchildren or daughter's fertility) are not likely to be large enough to be highly beneficial (Kachel, Premo, & Hublin, 2011).

Because the value of a grandmother's efforts may vary with age-specific fertility and mortality patterns, a grandmother's value to a mother's fertility may vary across societies. Studies in the Gambia have found that maternal grandmothers improve the survivorship of their grandchildren (Sear, Mace, & McGregor, 2000) and that the presence of a woman's in-laws increases her fertility (Sear, Mace, & McGregor, 2002). In contrast, no such effects existed in Malawi (Sear, 2008). Similarly, conflicting results arise from cross-cultural reviews (Hill & Hurtado, 1991, 2009; Sear & Mace, 2008; Shanley, Sear, Mace, & Kirkwood, 2007). In different societies, various relatives may or may not affect women's fertility and children's survival. Strassmann and Garrard (2011), in a meta-analysis of 17 studies, found that the survival of the maternal (but not paternal) grandparents enhanced grandchildren's survivorship. Their results suggested another hypothesis: that of local resource competition, with individuals competing against relatives (often same-sex relatives) for resources, which is usually detrimental. Here, as Darwin might say, is a problem for future analysis.

Given the similarities to human female senescence in other species (e.g., with elephants, odontocete whales, baboons, lions, and rhesus monkeys), it

is worth asking if there is evidence of a grandmother effect in these species. Packer et al. (1998) tested the grandmother hypothesis with field data from baboons and lions—in these species, two results countered the grandmother hypothesis: first, old-reproducing females had no higher mortality costs of reproduction than younger females; and second, grandmother help did not improve the fitness of either grandchildren or reproductive-age offspring.

Are There Universals?

It is safe to say that some intrasexual competition exists in every stage of a human female's life; it can be severe, even lethal (ending up in a polar body or being shot by a rival girl-gang member), and there are often striking tradeoffs. Sometimes the competition is directly over survival and reproduction; often, competition is for proxies for these two central biological phenomena, such as gaining nutrition competitively as a child, joining the popular clique at school, or attracting an outstanding mate. Maternal–fetal conflict and genomic imprinting are likely to be similar in all populations, for example. On the other hand, the effect of kin on children's survival appears quite mixed across populations. Finally, at different life history stages and across populations, the particular proxies for survival and lineage success can differ greatly, depending on health, growth, competence as a result of intense schooling, and more (see Low, 2013). Nonetheless, the end point in most cases is to gain the best available possible mate, whether that is a corporate CEO or a successful drug dealer, and to have healthy, well-invested children. Today, in most developed nations, (some) women have the option of gaining CEO positions themselves; typically, this incurs a fertility cost as a result of long and expensive schooling, which usually delays the age at which a woman has her first child (the most important predictor of lineage growth) and reduces her total fertility (Low, Simon, & Anderson, 2002). For example, in 2005, the 87 male US senators had, on average, three children; the 13 female senators averaged 0.8 children (author's data). Thus, competition, conflicts of interest, and tradeoffs rule women's lives from before becoming an egg to grandmotherhood.

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Sexual Competition among Women: A Review of the Theory and Supporting Evidence

Steven Arnocky and Tracy Vaillancourt

Abstract

Darwin (1871) observed in his theory of evolution by means of sexual selection that “it is the males who fight together and sedulously display their charms before the female” (p. 272). Researchers examining intrasexual competition have since focused disproportionately on male competition for mates, with female competition receiving far less attention. In this chapter, we review evidence that women do indeed compete with one another to secure and maintain reproductive benefits. We begin with an overview of the evolutionary theory of competition among women, with a focus on biparental care and individual differences in men’s mate value. We discuss why competition among women is characteristically different from that of men and highlight evidence supporting women’s use of epigamic display of physical attractiveness characteristics and indirect aggression toward same-sex peers and opposite-sex romantic partners as sexually competitive tactics. Finally, individual differences in competition among women are discussed.

Key Words: female competition, parental investment theory, sexual selection, indirect aggression, epigamic display

The sexual struggle is of two kinds; in the one it is between individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive; whilst in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners.

(Darwin, 1871, p. 398)

Competition pervades many important aspects of human existence. Over the course of recorded history, individuals and groups have rivaled one another for status, wealth, territory, food, resources, and mating opportunities, with the victors typically gaining an advantage in terms of

survival and reproduction (Darwin, 1859, 1871). From an evolutionary perspective, such competition has been regarded to occur most frequently among males (Darwin, 1871) and only trivially among females who sometimes assume “characters which properly belong to the males” (Darwin, 1871, p. 614). Yet recent advances in evolutionary theory and supporting empirical evidence have begun to challenge this view, suggesting instead that female competition exists as an adaptive behavioral strategy in its own right: competition among females may aid in the acquisition of reproductively relevant resources (e.g., Clutton-Brock, 2009; Rosvall, 2011), as well as mating access (e.g., Campbell, 1995; Vaillancourt, 2005, 2013), and mate retention (Arnocky, Sunderani, Miller, & Vaillancourt, 2012).

In this chapter we provide an overview of the evolutionary view of competition as it applies to women. Toward this end, competition is first defined within the context of natural and sexual selection. The adaptive role of female competition is then reviewed and applied to human behavior, suggesting that female–female competition should be expected to occur among humans (Arnocky et al., 2012; Campbell, 1995, 1999; Rosvall, 2011; Vaillancourt, 2005, 2013). Two common forms of female competition are placed within this evolutionary framework: the use of physical attractiveness characteristics as a mechanism for attracting members of the opposite sex (i.e., epigamic display) and indirect aggression toward same-sex peers and opposite-sex romantic partners. Finally, individual differences in competition among women are discussed.

Why Do Humans Compete?

In the mid-nineteenth century, Charles Darwin (1859) put forth the theory of evolution by natural selection, which suggests that survival and reproduction become enhanced among organisms that are best suited to the prevailing environmental condition. The offspring of well-suited individuals will become more abundant, and the population will evolve according to their more appropriate characteristics (see also Darwin & Wallace, 1858). Darwin, however, noted many physical and behavioral characteristics that seemed to undermine his theory. One prototypical example is the brilliant plumage of the peacock, which is physically costly to produce and may detract from survival by increasing visibility to predators. This was a source of great frustration for Darwin, who wrote, “The sight of a feather in a peacock’s tail, whenever I gaze at it, makes me sick!” (Darwin, April 3, 1860, in a letter to botanist Asa Gray).

Darwin eventually came to recognize that such traits likely evolved in the context of reproductive success, even if at the expense of an individual’s survival. In his seminal work on the subject, *The Descent of Man, and Selection in Relation to Sex* (1871), Darwin proposed that sexual selection, as a special case of natural selection, is a driving force behind evolutionary change. Sexual selection refers to the success of certain individuals over others of the same sex, in relation to the propagation of offspring (Darwin, 1871). Specifically, it is the heritable traits possessed by successful reproducers that will be passed on to, and exhibited more frequently in, subsequent generations. In the case of the

peacock’s plumage, for instance, research has shown that train coloration predicts males’ mating success. Males with more brilliant plumage are more sexually desirable to peahens and may therefore have greater opportunity than males with duller coloration to pass on their genes to offspring who, in turn, will be more likely to possess similarly bright train feathers (Petrie & Halliday, 1994; Petrie, Halliday, & Sanders, 1991).

Intersexual and Intrasexual Selection

Sexual selection is the result of two important interrelated phenomena. First, *intersexual selection* refers to the degree of selectivity or choosiness of mating partners between the sexes. This choosiness is often based on epigamic display of secondary sexual characteristics, which are irrelevant to reproduction yet are attractive to members of the opposite sex because they indicate genotypic and phenotypic quality (Starratt & Shackelford, 2015). For example, peahens prefer to mate with brightly colored peacocks, perhaps because bright trains are a costly signal of a male’s genetic quality—only sufficiently healthy males will produce the brightest colorations (Zahavi, 1975). Second, *intrasexual selection* refers to competition between members of the same sex over contested mating resources and opportunities. Members of one sex rival one another by displaying their value to potential mates or through direct dominance and threat displays or other aggressive behavior (e.g., Thornhill & Alcock, 1983). For instance, among elephant seals, males engage in direct physical combat in order to acquire and control harems of females, with successful male competitors typically achieving the greatest reproductive success (Hoelzel, Le Boeuf, Reiter, & Campagna, 1999; Le Boeuf, 1974). It is important to note that intrasexual competition need not be limited to mate acquisition: after copulation, sperm competition, as a form of indirect competition, (Hoelzel et al., 1999) as well as mate-guarding behavior (Galimberti, Boitani, & Marzetti, 2000), also serve to maintain the likelihood of paternity.

Darwin observed a striking sex difference among the two aspects of sexual selection. He noted that, in the vast majority of species, adult males more often engage in intrasexual selection. Males are usually more “modified” and “fight together and sedulously display their charms before the female” (Darwin, 1871, p. 272). Conversely, females more often act as sexual gatekeepers, selecting their mates from the more competitive male population (see Andersson, 1994).

Yet Darwin was unable to determine the cause of this commonly reported sex difference (Cronin, 1991), and it took nearly a century for researchers to begin to understand why males are often considered to be more competitive than females and, importantly, under what circumstances exceptions to this phenomenon arise.

Differential Parental Investment Influences Sexual Selection

Sexual selection is driven by the reproductive constraints imposed on one sex by the other. Lindenfors and Tullberg (2011) noted that “most often it is females who are the limiting resource for the reproductive success of males due to a fundamental asymmetry between males and females in their defining characteristic, their gametes” (p. 10). Many researchers have suggested that by the time of fertilization, females have invested considerably more reproductive effort because of anisogamy; females produce a limited number of energy-rich eggs and males produce many energetically cheaper sperm (Dawkins, 1976; Trivers, 1972). Females, being limited by the number of eggs they can produce, will exhibit a corresponding limitation in reproductive outcomes. A female will produce roughly the same number of offspring in a given breeding season, regardless how many males she mates with. Conversely, male reproductive success increases significantly alongside the number of females they can access and inseminate (Bateman, 1948).

Sex differences in the energy expended toward offspring production and survival are by no means limited to anisogamous gametes. Parental investment theory (Trivers, 1972) contends that the expenditure of *any* parental effort, including time, energy, risk, feeding, and other resources toward the production and survival of offspring, carries with it a cost that could otherwise be spent on procuring mating opportunities or rearing additional offspring (Barash, 1979; Trivers, 1972). Females, when bearing the heavier parental investment, have the most to lose from making poor mating decisions and must therefore express greater choosiness in determining with whom they will mate (Trivers, 1972).

In turn, these differential reproductive constraints lead to greater variability in reproductive fitness among males. Some particularly successful males will access multiple females and produce many offspring, whereas many less successful males will be shut out from reproducing altogether

(Bateman, 1948; cf. Birkhead, 2001). Accordingly, males more than females exhibit behavioral biases toward preferring and competing for multiple mating opportunities; “there is nearly always a combination of an indiscriminating eagerness in the males and a discriminating passivity in the females” (Bateman, 1948, p. 365).

Due to increased competitive pressure among males, natural and sexual selection will, over deep evolutionary time, begin to favor the competitively adaptive morphological and behavioral male features of successful maters, leading to increased sexual dimorphism of those traits (Alcock, 2001; Lande, 1980; Moore, 1990; Selander, 1972). For instance, sexually dimorphic body size among species of snake in which males are larger than females confers a distinct competitive advantage in physical combat (Shine, 1978). As another example, the horns of male ungulates have evolved not for antipredatory defense but rather for fighting male competitors during rutting season (Lindenfors & Tullberg, 2011). Sexually dimorphic features become most pronounced among species with strong sexual selectivity (Alexander, Hoogland, Howard, Noonan, & Sherman, 1979). At the extreme end of this spectrum, male members of a highly polygynous gorilla species compete to control and mate with a harem of females. These males are typically twice as large as their female counterparts (Larsen, 2003; Plavcan, 2001; Robbins & Czekala, 1997). Conversely, biparental care in most monogamously mating species counters male reproductive variance and reduces sexual dimorphism (Archer & Coyne, 2005).

This trend has also been observed in sex-role-reversed species wherein males invest significant parental care and have a reproductive rate below that of their female counterparts. In sex-role-reversed pipefish, males are choosier in their mate selection, whereas females tend to exhibit mating effort by way of ornamentation/courtship displays toward males as well as dominance displays toward intrasexual competitors (Berglund & Rosenqvist, 2001, 2009).

A Framework for Female Competition

In more than 95% of mammalian species, females are the sole providers of parental care (Clutton-Brock, 1989, 1991; Kleiman & Malcolm, 1981; Woodroffe & Vincent, 1994). It may, therefore, be tempting to conclude that females are primarily passive mate selectors who engage in low levels of competition. However, recent evidence is beginning to challenge this assumption, suggesting

instead that evolutionary theory does not disqualify females from competing in order to benefit their survival and reproductive fitness (Rosvall, 2011; see also Hrdy, 1981). Across a wide variety of species, females have indeed been shown to compete over mating-relevant resources such as food (Baird & Sloan, 2003) and nesting sites (Rosvall, 2008), as well as for the protection of offspring (Christenson & LeBoeuf, 1978). Females have also been shown to engage in more direct forms of mating competition. Some intrasexually aggressive female birds are more likely to be monogamously (vs. polygamously) mated and may consequently receive increased benefits from males (e.g., Sandell, 1998; Searcy & Yasukawa, 1996). Among primates, dominant females have been observed to harass subordinate females. This harassment can cause enough stress that the female subordinates may fail to come into estrus or might spontaneously abort pregnancies (Campbell, 1995).

Rosvall (2011) argued that researchers' relative ignorance of female–female competition may be rooted in how researchers define sexual selection. If the definition is restricted merely to competition for the *number* of mates or copulations, as has traditionally been the case, then its applicability is biased toward males because female reproductive fitness benefits less from mating with multiple partners (Bateman, 1948). Conversely, if the definition of sexual selection is broadened to encompass all manifestations of competition for mates, including competition for mate quality and mating-relevant resources, then females' intrasexual competition should be viewed as compatible with that of males (Rosvall, 2011). For instance, in species with extensive female care and little male parental investment, female competition primarily surrounds accessing males who can provide good genetic benefits (i.e., copulating with visibly high-quality males; Fisher, 1930), as well as protecting offspring and accessing resources to bolster the capacity for maternal care (Rosvall, 2008). Among polygynous primates, females who achieve dominant status reach sexual maturity and conceive earlier, and they produce more offspring who live longer (e.g., Pusey, Williams, & Goodall, 1997). Conversely, when males engage in parental care, females often compete for exclusive mating access to the males who are most likely or able to provide parental care, resources, or territories (e.g., Andersson, 1994; Rosvall, 2011; Whiteman & Cote, 2003), as well as to prevent extra-pair mating (Roberts & Searcy, 1988). As the research literature grows in this area of inquiry, it is becoming

increasingly clear that female competition pervades a wide variety of species. These findings have led some researchers to suggest that female–female competition confers many benefits to survival and reproductive fitness and is therefore “unlikely to exist merely as non-adaptive byproducts of selection on males” (Rosvall, 2011, p. 1135). Researchers have recently begun to explore whether competition among human females might also have been sexually selected for, and, if so, how such competition might manifest within our modern social structure.

Applying Sexual Selection to Human Competition

Consistent with most mammalian species, human females have greater requisite parental investment than human males (Trivers, 1972). The internal fertilization process of human reproduction involves women bearing the greater cost of gamete production relative to men. For women, fertilization is then followed by a requisite nine months of gestation and up to four years of lactation, along with the caloric costs of carrying, protecting, and providing nutrition for the infant (Campbell, 1999). Anisogamy and differential parental care in humans suggests that women should be choosier than men when selecting their sexual partners. Research findings have largely supported this hypothesis, showing that women are less willing than men to go on a date with (and to have sex with) an attractive member of the opposite sex (Clark & Hatfield, 1989; Kurzban & Weeden, 2005; Townsend & Wasserman, 1998). Women's greater selectivity, in turn, leads men to compete with one another in order to gain and maintain mating access to choosy females (Campbell, 1995; Daly & Wilson, 1988).

Sexual selection explains many of the broad sex differences that exist in human behavior (e.g., Archer, 2009; Daly & Wilson, 1990). Men compete for dominance, resources, and social status among other intangibles that may contribute to reproductive opportunity or that serve to quell rivals (Daly & Wilson, 1988, 1994). For instance, men are more likely than women to signal their desirability by displaying high status and wealth (buying women nice dinners, getting a high-paying job, and flashing money; Buss, 1988). Men are also more likely to compete with one another using physical prowess and combat. Among men, one's proportion of fat-free muscle mass predicts his total number of past-year sex partners (Lassek & Gaulin, 2009). Some men use physical aggression in order to attain or guard sexual partners, even at the risk of incurring

injury or death (e.g., Wilson & Daly, 1985). The decision to utilize aggression hinges on a fundamental cost–benefit analysis. Men are more likely to aggressively compete if they perceive a high likelihood of coming out victorious (Archer & Thanzami, 2007; Parker, 1974). Across cultural and contextual boundaries, males engage in more risk taking as well as more physically and sexually aggressive behavior surrounding their status and mating relationships compared to females (Archer & Coyne, 2005; Daly & Wilson, 1983; Vaillancourt, 2005).

Biparental Care

At first glance, humans seem to fit well within the prototypical mammalian model of greater female choosiness and male competition for varied mating opportunities. Men can certainly benefit their reproductive fitness by increasing the number of women with whom they copulate. For instance, serially monogamous men (but not women) produce more children than those who remain in one purely monogamous pair-bond (Forsberg & Tullberg, 1995; Jokela, Rotkirch, Rickard, Pettay, & Lummaa, 2010). Although women might also improve their reproductive fitness by copulating with multiple partners via sperm competition (i.e., engaging in short-term mating with men who exhibit “good gene” characteristics such as physical attractiveness; Sunderani, Arnocky, & Vaillancourt, 2013; Weatherhead & Robertson, 1979), their mating strategies nevertheless also include a greater preference for establishing long-term pair-bonds with men who will contribute a significant degree of parental care toward offspring (Buunk & Fisher, 2009).

Why do women exhibit a preference for monogamy and biparental care? Researchers have suggested that, over our evolutionary history, an increase in men’s parenting efforts likely would have led to greater reproductive success (Miller, 1994). Evidence suggests that biparental care can enhance the survival and well-being of offspring. For instance, in preindustrial Europe and the United States, paternal investment has been linked to infant and child survival rates (Geary, 2000). Among the Ache, a Paraguayan hunter-gatherer society, father-present children are three times more likely to survive compared to father-absent children (Hill & Hurtado, 1996). Paternal investment is also indicative of offspring “quality.” Children whose fathers provide paternal investment tend to have better social and academic skills, as well as higher income during adulthood (Geary, 2000; Pleck,

1997). From a fitness perspective, it is therefore in a woman’s best interest to secure a man who can not only provide good genes but is also able and willing to invest in their offspring (Campbell, 2004). This is reflected in the priority of women’s mate preferences. Women are attracted to both good-gene indicators, such as facial symmetry and skin quality (Jones et al., 2004), as well as to behavioral and personality cues to a potential mate’s willingness to invest in her and her offspring (Buss, 2012).

Evidence of men’s increased monogamy and parental investment can be observed in the degree of sexual dimorphism of modern humans. Males and females of biparental species tend to be morphologically similar. Although men are on average larger (approximately 15%) and stronger than women, this appears to constitute a significant reduction in sexual dimorphism compared to that of our ancestors (Geary, 2000). Hominids preceding *Homo sapiens*, such as *Australopithecus afarensis*, are believed to have displayed greater sexual dimorphism, with estimates of males being significantly larger than females, and of mating polygynously while contributing little in the way of parental investment (Geary, 2000; Gibbons, 2007; Larsen, 2003; cf. Reno, Meindl, McCollum, & Lovejoy, 2003). Conversely, the mating system of modern human society is typically described as one of serial monogamy, mild polygyny, and biparental care (see Schmitt & Rohde, 2013).

By engaging in long-term mating relationships, men might increase the quality of mate they can attract, as well as their degree of paternity certainty (Buss & Schmitt, 1993; Starratt & Shackelford, 2015). Yet biparental care also constrains male reproductive variance. Fewer men will have a large number of offspring from numerous women, and many more men will find opportunity to mate (Geary, 2000). Thus, due to the “heavy commitment that he will make in their joint progeny, it pays a male to be choosy . . . [and] women must compete with one another to secure the best men, just as men vie for the best women” (Campbell, 2004, p. 17). Indeed, when men invest in a long-term mating strategy, they tend to be more discriminating in their mate choice than if they were adopting a short-term, low-investment strategy. For instance, Buss and Schmitt (1993) found that men tend to relax their standards for a potential mate when considering short-term but not long-term mating contexts. Not all men will be equal providers of good genes, of reproductively relevant resources (e.g., food, shelter, protection,

social influence), or of parental effort (e.g., teaching, emotional support). Thus, women must also exhibit competitive attitudes (Buunk & Fisher, 2009) and behavior (Griskevicius et al., 2009; Vaillancourt, 2005, 2013) toward same-sex conspecifics for access to the highest-quality mates, who may themselves be highly selective in their mate choice (Campbell, 2004). Females who could secure the most reproductively viable mates (e.g., men who will invest in offspring, provide resources, care, etc.) would have had the greatest opportunity of producing surviving offspring. For example, it has been noted that, in some preindustrial societies, the ability of a woman to secure a high-status man was linked to more surviving offspring compared to women with lower-status partners (e.g., Volland, 1990; Volland & Engel, 1990). Because these desirable men represent only a portion of the population, it is conceivable that competition for their favor will occur (Vaillancourt, 2005).

Mate Poaching

Women, like men, do not compete merely for mating access to unattached individuals. In all human societies, some individuals will attempt to attract mates who are themselves already in an existing romantic relationship, a behavioral tactic termed “mate poaching” (Buss, 2006; Schmitt & Buss, 2001). In a large cross-cultural study, Schmitt et al. (2004) found that 35% of women admitted to attempting to poach a man from an existing romantic relationship for the purpose of a short-term liaison, and 44% reported doing so for the purpose of establishing a long-term romantic relationship. Women can benefit their reproductive fitness through short-term mating with high-quality men via sperm competition—copulating with multiple men in a short period of time creates a scenario whereby the sperm of the best genetic quality may be more likely to fertilize the women’s egg (Baker & Bellis, 1995; Goetz et al., 2005; Weatherhead & Robertson, 1979). Women might also use short-term sexual encounters to “upgrade” to a better-quality romantic partner (Greiling & Buss, 2000). By poaching a man who has demonstrated his desirability and willingness to commit to other women, a female might benefit her long-term mating success (Schmitt & Buss, 2001). Arnocky, Sunderani, and Vaillancourt (2013) found that successful mate poaching by women predicted having had a greater number of lifetime sex partners, more lifetime casual sex partners, as well as more lifetime dating relationship

partners, indicating greater mating success among those women willing to compete for mates who are already “taken.” Consistent with findings from studies of intrasexual competition among women, physically attractive women are more frequently the targets of a male mate poacher’s desire and are more successful in their own poaching attempts compared to less physically attractive women (Sunderani et al., 2013).

Divergent Sexual Strategies and Strategic Interference

The competitive strategies of women are by no means limited to intrasexual (female–female) conflict. Women can also benefit their reproductive fitness by competing with mating partners in order to express their preferred sexual strategy. For example, it is well established that men, more than women, prefer sexual variety (Symons, 1979). For women, however, a long-term partner’s infidelity is undesirable given that it can result in the division of important financial, social, and emotional resources with other women (Buss & Shackelford, 1997b), or in relationship dissolution, leading to significant loss of investment, resources, and parenting assistance (see Buss, 2003; Fisher, 1992). It may therefore benefit women to employ various mate-guarding tactics (Buss, 2002). Such behavior is common, with approximately 75% of married women (and men) reporting that they engage in some form of mate-retention behavior (Buss & Shackelford, 1997a). For women, the most common mate-retention strategies were providing love and care, physical appearance enhancement, and physical possession signals. In attempting to retain a mate, women are more likely than men to engage in appearance enhancement, verbal possession signals (e.g., discussing being off the market), and threatening punishment for a mate’s infidelity (e.g., notifying her partner that she will dissolve the relationship if he cheats on her); such tactics are most likely to be employed by women who are paired with a desirable mate who is high in income and/or status striving (Buss & Shackelford, 1997a).

Why Competition among Women Differs from That among Men

The competitive strategies employed by women seem to differ fundamentally from those of men. Women, in comparison to men, less often exhibit extreme forms of overt physical and sexual aggression (Archer, 2004; Daly & Wilson, 1988; Vaillancourt, 2005). Women have more to lose in

terms of reproductive fitness from potential physically damaging confrontations (Daly & Wilson, 1989). Campbell (1999, 2004) has argued that females' greater parental investment requires greater risk aversion. Even though humans are effectively a biparental species, women still provide the bulk of *obligatory* parental care (Hrdy, 1999). Thus, a mother's death is more debilitating to a child's survival compared to the death of a father (Sear, Mace, & McGregor, 2000). Whereas a man's inclusive fitness may rely on copulatory opportunity, a women's inclusive fitness relies more heavily on her successfully rearing her children through early life (Campbell, 2004). Accordingly, the costs associated with direct aggression and other risky forms of competition become amplified—for a woman (and for other female nonhuman primates), it is more important to remain alive in order to rear their offspring (see also Björkqvist, 1994; Campbell, 2004; Liesen, 2013; Smuts, 1987). It has been suggested that women instead compete using a variety of epigamic-display tactics and (relatively) less risky aggressive strategies in order to achieve dominance, attract mates, and quell rivals (Archer & Coyne, 2005; Vaillancourt, 2005, 2013). In the following section we review the evolutionary underpinnings of two commonly researched forms of competition among women: epigamic display (appearance enhancement) and indirect aggression.

Epigamic Display: Competition over Physical Attractiveness Characteristics

Across diverse human cultural groups, men are remarkably consistent in their expressed preference for physically attractive women (Buss, Shackelford, Kirkpatrick, & Larsen, 2001; Cunningham, Roberts, Wu, Barbee, & Druen, 1995). Men find attractive women who best display various cues to health and fertility. These include youth, lustrous hair, clear skin, feminine and symmetrical facial features, and a low waist-to-hip ratio (WHR; ranging between .67 and .80), typically constituting an hourglass-like figure (Buss, 1989; Fisher & Voracek, 2006; Gangestad & Scheyd, 2005; Hinsz, Matz, & Patience, 2001; Singh & Randall, 2007; Symons, 1979). Given men's selectivity in choosing long-term mating partners, women should be expected to compete with one another in the display of these desirable characteristics (Symons, 1979). Indeed, when asked how they compete with rivals and attract mates, women often report attempting to enhance their appearance (Cashdan, 1998) through the use of makeup, suntanning, nail polish,

and flattering clothing (Tooke & Camire, 1991). In their book titled *Why Women Have Sex*, Meston and Buss (2009) review evidence that women, more than men, attempt to enhance their physical appearance as a competitive mating strategy. Women are twice as likely as men to spend more than one hour working on their physical appearance each day. Western women are also 50% more likely than men to bronze their skin and are willing to spend almost ten times the amount of money that men spend on appearance-enhancement products (Meston & Buss, 2009). Seock and Bailey (2008) found women to enjoy shopping more, and to be more brand-conscious (aware and desiring of high-end brands) compared to men. For women, shopping seems to be more closely linked to enhancement of their self-image (Dittmar & Drury, 2000).

A woman's effort toward enhancing her appearance may therefore be an adaptive competition tactic. Hill and Durante (2011) found that women who were primed with intrasexual competition motives (by viewing photos of attractive women and rating their attractiveness, friendliness, and extraversion) were more willing to take health risks in order to enhance their physical appearance (via skin tanning and taking diet pills) compared to women in a control condition. Single women were also more likely to engage in risk behavior when exposed to a mating prime (viewing photos of men and rating their attractiveness, friendliness, and extraversion). Hill, Rodeheffer, Griskevicius, Durante, and White (2012) have further shown that in an economic recession (when spending on most products decreases), women nevertheless exhibit a propensity toward increasing spending on appearance-enhancing products (termed "the lipstick effect"). The researchers found that such spending is driven largely by an increased desire to attract mates with resources. Indeed, physical attractiveness is positively related to women's mating success. Rhodes, Simmons, and Peters (2005) found that women with highly attractive faces became sexually active earlier in life (i.e., had a longer period of reproductive potential) and had more long-term dating partners, compared to their less attractive peers. Physically attractive women are also more adept at stealing desirable men from already-existing romantic relationships (Sunderani et al., 2013). Rhodes et al. noted that "Attractive traits can certainly be altered by grooming practices and need not be entirely honest signals of mate quality" (p. 198). In other words, if a female can mimic or enhance facial attractiveness through the use of products and/or

grooming, she may, to a degree, be able to improve her long-term mating success. Women are also more likely than men to report attempting to enhance their physical appearance as a mate-guarding tactic (Buss, 2002).

Rhodes et al. (2005) also note that the association between features of attractiveness and health and fertility is clearer for bodies (Singh, 1993) than for faces (Rhodes, Chan, Zebrowitz, & Simmons, 2003). Disordered body image and eating disordered behavior have been conceptualized as being born out of competition for mate acquisition and retention (Abed, 1998). This is because a low WHR in women is viewed as an honest signal of her health, indicating a greater estrogen-to-androgen ratio and greater fecundity. For instance, in a sample of women presenting for artificial sperm donor insemination, Zaadstra et al. (1993) showed that an increase in WHR predicted a statistically significant decrease in the probability of conception. WHR was a stronger predictor of fecundity than either age or obesity. Perhaps, then, it is not surprising that males find women with a low WHR to be more physically attractive, healthier, and reproductively viable than women with a higher WHR (Singh, 1993).

This raises the question of whether women compete within the domain of body shape. The uniquely human cognitive ability to link food and exercise to body weight and shape affords individuals the capacity to purposefully alter their WHR (Abed, 1998). In extreme form, women who are unhappy with their body's appearance might engage in excessive compensatory behavior in attempting to lose weight and are at an increased risk for developing an eating disorder (Parry-Jones & Parry-Jones, 1995). Abed et al. (2012) have argued that competition over displaying youth and thinness has become intensified in recent decades due in part to declining fertility (leading to extended periods of "pseudonubility" among older women who remain thinner), increased sexual autonomy, and high concentrations of attractive same-sex competitors in our local mating environments. This may help to explain the concurrent rise in eating disorders over the same time period (Abed et al., 2012). For example, eating disorders are significantly more common among heterosexual women who are in their prime reproductive years, compared to men, older women who are outside of reproductive age, and homosexual women (e.g., Abed et al., 2012; Li, Smith, Griskevicius, Cason, & Bryan, 2010). Moreover, intrasexual competition for mates has been shown to correlate positively with body dissatisfaction,

drive for thinness, and disordered eating behavior in both cross-sectional and experimental studies (Faer, Hendriks, Abed, & Figueredo, 2005; Li et al., 2010). For example, Li et al. (2010) exposed participants to one of two photo conditions depicting either (a) high-status competitive or (b) low-status noncompetitive intrasexual rivals. Results showed that heterosexual women (but not men or homosexual women) were more likely to report body dissatisfaction and more restrictive eating attitudes following exposure to the high-status but not low-status competitor photos. Eating disorder behavior has also recently been shown to be predicted by a fast life history (i.e., greater reproductive and mating effort) among college-age women (Abed et al., 2012). Taken together, these findings suggest that competition via the epigamic display of a desirable body morphology may, in some women, lead to the use of extreme and disordered attempts at weight loss. Recent research suggests that enhancing one's own physical appearance is merely "half the battle" in the struggle for mating success. Women sometimes also seek to disparage, exclude, humiliate, and derogate their competitors along dimensions of status, fidelity, and physical attractiveness, through the use of indirect aggression.

Indirect Aggression

Evidence suggests that the degree to which women compete extends beyond mere epigamic display (i.e., attempting to attract desirable men by demonstrating the characteristics most valued by men). Women have also been shown to compete via attack on rivals' social status, attractiveness, and sexual reputation (Campbell, 1995, 1999; Vaillancourt, 2005, 2013). These attacks are often covert and surreptitious, reducing the likelihood of retaliation and of physical, social, or legal consequence (Björkqvist, 1994; Campbell, 1999; Vaillancourt, 2005, 2013). Indirect aggression involves purposefully and often covertly manipulating interpersonal relationships through acts of social exclusion, gossip, and rumor spreading in order to harm others (Crick & Grotpeter, 1995; Lagerspetz, Björkqvist, & Peltonen, 1988). The vast majority of peer aggression occurs within rather than between the sexes (Gallup, O'Brien, White, & Wilson, 2009), and a greater proportional amount of aggression among girls and women is indirect in nature (Vaillancourt et al., 2010). This is not surprising given that women's use of indirect aggression has been shown to increase the perpetrators' status within the social hierarchy (Vaillancourt

& Hymel, 2006; Zimmer-Gembeck, Geiger, & Crick, 2005) and to promote depression, lower self-esteem, school dropout, and suicide among victims (e.g., Marr & Field, 2001; Owens, Slee, & Shute, 2000).

Interestingly, the content of women's indirect aggression corresponds to men's mate preferences. For example, given the degree of paternity uncertainty associated with human reproduction, men value sexual fidelity in a romantic partner. Predictably, girls and women often verbally attack female competitors' sexual reputation (e.g., by calling other women promiscuous or by calling them a tease; Buss & Dedden, 1990) and will limit their social interactions with those deemed to be promiscuous (see Campbell, 2004, for review). Similar indirect attacks surrounding women's physical appearance are common. Vaillancourt and Sharma (2011) showed that almost all women who were randomly exposed to an attractive female confederate engaged in derogatory behavior toward her when she was dressed in sexually provocative versus conservative clothing. Indirect attack of a woman's physical appearance may have adaptive value. Derogatory statements made about a woman's physical appearance can in fact reduce men's perceptions of that target woman's attractiveness and are more likely to be perpetrated by women who are, at the time, high in estrogen and thus maximally fertile (Fisher, 2004). Women have also been found to use indirect aggression during intersexual conflict. For instance, women are more likely than men to flirt with someone in front of their romantic partner as a mate-retention strategy (Buss, 2002).

Arnocky and Vaillancourt (2012) explored whether peer aggression does in fact confer mating benefits to perpetrators. The researchers followed adolescents over the course of one year. At time 1, participants completed both self-report and peer-report measures of physical and indirect aggression, as well as self-reports of peer victimization. At time 2, participants reported on their current dating status. Controlling for age, initial dating status, popularity, and physical attractiveness, results demonstrated that for both males and females, indirect aggression at time 1 predicted having a romantic partner one year later. In addition, being victimized by one's peer group negatively predicted having a dating partner at one-year follow-up.

Individual Differences in Competition

It is important to note that the basic principles of sexually selected female competition outlined

in this chapter are contingent on various environmental factors that can either increase or decrease the propensity for competition among individuals. One condition driving the frequency and ferocity of competition among humans and other vertebrate species is the operational sex ratio, or the proportion of fertilizable females to sexually active males in a given population (Emlen & Oring, 1977). When the sex ratio is skewed, members of the scarcer sex have better mating prospects (Fisher, 1930) and can therefore express greater choosiness regarding with whom they mate (Berglund, 1994). Conversely, mating opportunities are scarcer for the abundant sex, resulting in greater intrasexual competition (Emlen & Oring, 1977). In India, for example, there are more males than females in large part because of sex-selective abortions (Jha et al., 2006). This leaves many men (typically those of low socioeconomic status) lacking mating opportunity. Research has found a strong correlation between the operational sex ratio in various states in India and homicide rates, even after controlling for urbanization and socioeconomic status (Drèze & Reetika, 2000).

Women have been found to engage in more casual sex under conditions of relative mate scarcity (perhaps conforming to a male-biased mating strategy; Schmitt, 2005; South & Trent, 1988; Stone, Shackelford, & Buss, 2007). If indirect aggression has evolved among women for the purpose of mate competition, then its use can be expected to increase under conditions of women's abundance relative to men. To test this hypothesis, Arnocky, Ribout, Mirza, and Knack (2014) exposed participants to one of two bogus magazine articles, one reporting fictitious research findings suggesting that quality mates are a scarce resource and the other suggesting that quality mates are easy to come by. The researchers found that women were more intrasexually competitive, more jealous, and more willing to use indirect aggression against a same-sex rival after being primed to believe that mates were scarce (vs. abundant). Future research would benefit from exploring whether epigamic display variables (e.g., cosmetic use, perceived skin-tanning risk, desire to diet) similarly increase in mate-scarcity versus mate-abundance conditions. Indeed, research has found that under conditions of mate scarcity, women tended to wear more revealing clothing (Barber, 1999). Cross-culturally, competition among women seems to be contextually sensitive in that it becomes intensified when suitable

men are a scarce commodity (Campbell, 1995). See chapters 14 and 15 of this book for additional review of how the operational sex ratio influences competition among women.

Mate Value

Competition may be more frequent and extreme among those who are otherwise limited in their mating opportunities. Mate value is defined as “the total value of the characteristics that an individual possesses in terms of the potential contribution to his or her mate’s reproductive success” (Waynforth, 2001, p. 207). Men and women share many similarities in terms of what they consider to be a high-mate-value partner. Buss and Barnes (1986) found that both men and women desire kind, healthy, intelligent partners with exciting and easygoing personalities. However, Buss also observed sex differences in that men more than women preferred physically attractive partners, whereas women more than men preferred mates with good earning capacity.

Research has previously shown that men who do not conform well to women’s mate preferences may compete more intensely for mating opportunities or for mating-relevant resources. For example, Wilson and Daly (1985) showed that poor or unmarried men were more likely to commit murder than were their wealthier or married counterparts. Men are also more likely to engage in mate-retention tactics when they are of particularly low mate value (Miner, Starratt, & Shackelford, 2009) or when they are mated with a woman of particularly high mate value (Buss & Shackelford, 1997a). Men are also more likely to engage in mate retention when they perceive an increased likelihood of a partner’s infidelity (Starratt, Shackelford, Goetz, & McKibbin, 2007). This phenomenon is likely grounded in our ancestral past, whereby unnecessary or misdirected attempts at retaining partners would have detracted from other important mating and survival functions (Graham-Kevan & Archer, 2009). Thus, individuals who could best approximate the need for such efforts would probably have been more likely to survive and reproduce. Being of relatively low mate value is one particularly salient cue to an increased likelihood of cuckoldry or partner defection from the relationship, qualifying the expenditure of mate-retention effort (Arnocky et al., 2012).

If women have simultaneously evolved a propensity for the use of competitive strategies to attain and maintain desired mating opportunities, then

women should also be expected to exhibit more competition and mate-retention behavior in the face of increased reproductive threat. In support of this argument, Graham-Kevan and Archer (2009) found both men and women of low mate value to exhibit increased controlling behavior compared to their high-mate-value counterparts. Arnocky et al. (2012) found that women who perceived themselves to be of low physical attractiveness compared to their friends were more likely to perpetrate indirect aggression toward both peers (as a form of intrasexual competition) and partners (as a form of mate retention). Moreover, highly attractive women reported being indirectly victimized by their peers to a greater extent compared to less physically attractive females (Arnocky et al., 2012; Leenaars, Dane, & Marini, 2008). Arnocky et al. have suggested that low-mate-value women may be at particular risk of partner defection, given the greater proportion of more desirable competitors within the local mating market. Less attractive women (and men) have been found to worry more about a partner’s potential involvement with others compared to their more attractive counterparts (e.g., White, 1980). Women who perceive themselves as being less physically attractive are also more romantically jealous (Arnocky et al., 2012). This may, in turn, warrant the perpetration of indirectly aggressive measures as a strategy for both intrasexual competition and mate retention. Future research would benefit from examining these links experimentally. Cross-sectional data are limited in that directional conclusions about the effects of low perceived mate value and jealousy on female competition cannot be made. By temporarily priming low versus high self-perceived mate value, researchers could effectively examine group differences in inducing competition, be it indirect aggression, enhanced orientation toward epigamic display, or other competition-related variables.

Conclusion

Studies of human sexual selection have disproportionately focused on the relevance of competition for men, neglecting the potential evolutionary origins of competition among women. Yet it has become increasingly clear that competition among women may be an adaptive behavioral strategy meant to augment mating and reproductive success. The amount of parental investment provided by men is unparalleled by any of our closest primate relatives (Geary,

2000). Parental investment constrains reproductive variance and increases men's choosiness in selecting long-term mates (Campbell, 1999). Because men also vary considerably in their own mate value, both in terms of their willingness and ability to invest in partner(s) and offspring as well as in their genotypic and phenotypic quality, women can bolster their reproductive fitness by competing for the most desirable mates (Arnocky et al., 2012; Vaillancourt, 2005, 2013). Buss and Dedden (1990) have argued that successful intrasexual competition relies on enhancing one's desirability to members of the opposite sex by (a) causing rivals to be less appealing and/or (b) enhancing one's own appeal. Each of these goals may be satisfied through successful competition along dimensions of men's mate preferences for physically attractive, youthful, and sexually faithful mates (Buss, 2012). Evidence supporting this hypothesis has been robustly observed in terms of both women's epigamic display (i.e., self-promotion via physical appearance; Abed, 1998), as well as in their use of indirect aggression perpetrated against their peers (Arnocky et al., 2012). Physically attractive (Buss, 1989; Walster, Aronson, Abrahams, & Rottman, 1966) and indirectly aggressive girls and women have been shown to be more likely to attract mates (e.g., Arnocky & Vaillancourt, 2012; Gallup et al., 2011). Conversely, women who are victimized by their peers may be viewed as lustful or unfaithful, as less physically attractive, and as less desirable to men (Arnocky & Vaillancourt, 2012; Fisher, 2004; Vaillancourt, 2005, 2013). Though there remains much to be discovered, it seems to be the case that competition among women is intimately tied to the competition for mating success. The strategies employed by women do not merely mimic those employed by men but rather appear to reflect behavioral adaptations that are unique to the struggle for female mating success, suggesting that female competition exists not merely as a spandrel derived from sexual selection among males but rather as an adaptive behavioral strategy in its own right.

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Female Intrasexual Competition in Primates: Why Humans Aren't as Progressive as We Think

Nicole M. Scott

Abstract

Males and females compete with each other and amongst their own sex, but often for different reasons. This chapter enriches current understanding of female-female competition in humans by examining competition in other primates; it explores why females compete and discusses when affiliation and cooperation may lead to better outcomes. Socioecological constraints on a species—such as social organization, food competition, and dispersal preference—play a major role in the structure of female-female relationships; notable attention is given to factors that affect social relationships: food competition, reproduction, dispersal, and dominance. Bond maintenance behaviors and communication strategies are also discussed relative to female-female relationships. Three nonhuman primate societies are examined, and potential lessons from these structures are gleaned where possible. The chapter reviews human progress in overcoming phylogenetic and ecological constraints in favor of women's societal liberties.

Key Words: socioecology, primate sociality, resource competition, phylogeny, chimpanzee, dominance

Introduction

In recent decades, researchers have increasingly recognized that females can be competitive and aggressive (for possible historical reasons on the delay of interest, see Hrdy, 2013b). Although the immediate, or proximate, function of competition and use of aggression by females differs from that of males, the ultimate (in the sense of Tinbergen, 1963) reasons are similar: to increase their *fitness* or reproductive success. It is now evident that female competition and aggression occur throughout the animal kingdom (e.g., chimpanzees: Goodall, 1986; Pusey et al., 2008; Scott, 2013; cichlids: Tubert, Lo Nostro, Villafane, & Pandolfi, 2012; Walter & Trillmich, 1994; blackbirds: Yasukawa & Searcy, 1982; to name a few). Sources, or proximate causes, of female aggression stem from many levels of explanation: from population-level social structure to molecular-level circulating hormone concentrations

(Nelson, 2006). Humans are subject to many of the same physiological, ecological, and social constraints that other animals experience. This chapter is focused on female-female competition in human's closest relatives, the other primates. I specifically focus on three primate species—chimpanzees, hamadryas baboons, and ring-tailed lemurs—giving special consideration to the different ecological and social pressures of these and other species.

I have three goals for this chapter beyond providing an introduction to primates. The first goal is to place female-female competition and aggression in an evolutionary context to better understand the evolutionary advantage of the different strategies for dealing with each. Specifically, a number of theories regarding primate social relationships will be described. The second goal is to discuss competition in a variety of primate species while highlighting some of the general factors underlying

competition. The third goal is to describe the lives of female primates from three diverse social structures: chimpanzee multimale-multifemale societies, hamadryas baboon harems, and ring-tailed lemur female-dominated hierarchies. These three species provide insights into the lives of females living under different societal pressures, sharing different relationships with group males, and balancing different levels of aggressive and affiliative interactions with a special emphasis on cooperation. The main goal of this chapter is to thus provide an evolutionary story of women's social relationships by presenting information on female nonhuman primates; I refrain from making direct comparisons between the two and, instead, invite readers to keep the nonhuman primate story in mind as they continue to read the other chapters in this volume (see also Hrdy, 2013a).

In this chapter, I present an ethological approach to understanding the evolutionary values of aggression and competition. I discuss the current evidence suggesting that female primates compete for social status, for access to the best resources, and for the opportunity to raise healthy offspring. However, I also illustrate that aggression is not the only means for attaining those goals. Affiliation (via mutualism, kin selection, or coalitionary support) is the other side of the competition coin, and I spend some time discussing how it at times can be more useful than aggression. One common mechanism of competition shared between the contexts of affiliation and aggression is cooperation because cooperation often involves affiliation between individuals who then direct aggression against a third party. I highlight some of the evolutionary and environmental adaptations shared by women and other female primates in the context of primate social evolution. There exists a misconception that humans are the pinnacle of evolution. This chapter will highlight areas of primate life where humans could, in observing particular patterns of behavior in other primates, use that knowledge to understand its underlying causes and take note of when aggression is typically useful in competing or perhaps when more affiliative cooperation is better in navigating social life.

Introduction to Primates

It is likely that the first primates were nocturnal, insectivorous, and limited in their gregariousness (Charles-Dominique, 1977). From the last common ancestor, primates evolved and diversified into many ecological niches, dietary preferences, and social categories. There are two major divisions

of primates—made according to when they split from a shared common ancestor—that are useful in comparing primate species: Strepsirrhines (previously referred to as prosimians) and Haplorhines—which are further divided into Tarsiiformes (which will not be discussed further) and Anthropoids (Fleagle, 2013; see Appendix). Anthropoids are further divided into Platyrrhines (also known as New World monkeys) and Catarrhines (which include Old World monkeys and apes; see Fleagle, 2013). Each of these divisions and their respective species has experienced different evolutionary pressures and adapted accordingly; therefore, a myriad of traits have been added, subtracted, and modified in a nonlinear, temporally sporadic fashion that has added to diversity both within and between divisions. Recently, the evolutionary relationships or *phylogeny* among primates has been questioned and re-evaluated according to a number of different traits (e.g., Arnold, Matthews, & Nunn, 2010). As additional traits continue to be included in analyses of phylogeny, these relationships will continue to change. This chapter refers only to broad phylogenetic relationships because the order of divergence is widely accepted even if the approximate dates are not.

The Strepsirrhines or *prosimians* retain many ancestral traits in addition to their more recently derived traits and are estimated to have diverged from the other primates around 76 million years ago (mya; Horvath et al., 2008; Matsui, Rakotonirarany, Munechika, Hasegawa, & Horai, 2009; although see Steiper & Seiffert (2012) for a more recent divergence). The earliest lemur colonization of the island of Madagascar is estimated to be around 65 mya (Horvath et al., 2008; Matsui et al., 2009), where they diversified and continue to live today. New World monkeys split from Old World monkeys and apes around 35–45 mya (Goodman et al., 1998; Schrago & Russo, 2003), whereas Old World monkeys and apes separated around 20–30 mya (Goodman et al., 1998; Kumar & Hedges, 1998). Humans split from chimpanzees and bonobos around 5–7 mya (Goodman et al., 1998; Kumar & Hedges, 1998; Robson & Wood, 2008). The appendix at the end of this chapter maps out the relationship of each species mentioned in this chapter and indicates to which division a species belongs.

One of the hallmarks of primates is their ability to fill ecological and social niches (Fleagle, 2013); thus, the ecology of species within taxonomic divisions is almost as diverse as it is between divisions.

For instance, lemurs, one taxonomic family of primates that has been recently popularized in movies and television, are found only in Madagascar. The “land of lemurs” has few predators (Goodman, O’Connor, & Langrand, 1993), and their uniquely low predation risk likely played a role in their adaptation (Macedonia, 1993). New World monkeys—such as tamarins, spider monkeys, and squirrel monkeys—are only found in the Americas (hence the name), from northern Argentina through central Mexico. The ancestral monkeys who first colonized the Americas adapted according to the demands of a forest environment (despite having access to other biomes) and without competition from other, established primate orders. Old World monkeys—such as baboons, macaques, and patas monkeys—and nonhuman apes are found throughout Africa and parts of Asia and Europe, and their habitats include forests, savanna and open grassland, mountains, and even deserts. Complementing these diverse ecologies and adaptive pressures, primate social relationships exist in many varieties and complexities: some societies are more prone to aggressive interactions while others tend toward more affiliative behaviors wherein levels of competition drive the emphasis of each. This observation illustrates how it is key to view primate sociality in light of the environment or local ecological pressures in addition to considering phylogenetically inherited traits. After all, adaptation can only work with the materials that phylogeny has given to a species.

Although they are intimately intertwined, both ecology and sociality are potential common denominators when contrasting different primate groups. However, primate sociality can be assessed in three different ways: based on social organization (e.g., spatial proximity and ranging behavior), social structure (dyadic relationships and group hierarchies), or mating system (Schülke & Ostner, 2012). At this point, it should not be surprising that primate social groupings range the full spectrum from predominantly solitary living within a loose social group, pair-bonding, one-male-multifemale group (e.g., harem), and multimale-multifemale group (Fleagle, 2013; Schülke & Ostner, 2012). In some species, groups splinter and form smaller foraging parties only to come together at the end of the day to sleep as a large group (e.g., hamadryas baboons; Kummer, 1968) or come together days or weeks later (e.g., chimpanzees; Goodall, 1986)—a practice commonly referred to as *fission-fusion*. Societies can be male-bonded (in which males form strong social bonds), female-bonded

(in which females form strong social bonds), or both and may have linear and stable or nonlinear dominance hierarchies. Mating may occur between only the dominant female and males living in her social group (e.g., tamarins: Terborgh & Goldizen, 1985), between an otherwise solitary male and female (e.g., orangutans: Galdikas, 1981), between a bonded pair (e.g., gibbons: Carpenter, 1940), within a one-male-multifemale group (e.g., gorillas: Harcourt, Stewart, & Fossey, 1981; hamadryas baboons: Kummer, 1968), or within a multimale-multifemale group (e.g., chimpanzees: Goodall, 1986; Tutin & McGinnis, 1981; ring-tailed lemurs: Jolly, 1966; Sauther, 1991).

In general, female primates are free to choose their mating partner; however, their choice is generally limited with respect to the social structure, mating strategy, and various instantiations of coercion (Kappeler, 2012). One type of coercion, rape, is relatively rare within the different primate species with the notable exceptions of orangutans and humans (Muller & Wrangham, 2009; Muller & Thompson, 2012). Different societal structures can exist between species of a taxonomic grouping, as just illustrated in apes (orangutans, gibbons, gorillas, and chimpanzees; see also Jolly (1998) for a similar contrast in lemurs) as well as within a single genus (e.g., squirrel monkeys: Strier, 1999). Along a similar vein, social structures and, subsequently, social relationships are largely habitat-specific, and differences are evident between wild and captive populations (see Gartlan (1968) for discussion), although there is also evidence of species-specific (or phylogenetic) constraints (Thierry, 2007). Overall, and generally speaking, primates—humans included—are social, adaptive, and diverse. The overlapping diversity of social and environmental characteristics shared by human and nonhuman primates—along with their close genetic relatedness—lends a fruitful comparison in the endeavor to elucidate humans’ propensity to certain behaviors.

Why Compare Nonhuman Primates to Humans

Understanding the societal pressures and adaptive behavior of other primates helps to explain why people behave the way they do. Nonhuman primate behavior not only helps explain the current pressures experienced by women, but also elucidates how past pressures shaped the evolution of ancestral women. Uncovering the social structure and behavior of ancestral humans is more difficult than uncovering their fossils. Reconstructing

the behavioral repertoire of extinct species requires comparisons to extant species under a range of assumptions. These assumptions include the idea that limited evolution has occurred for certain traits (e.g., life histories: Jones, 2011; Robson & Wood, 2008; Roff, 1992), that suboptimal traits have been retained via strong phylogenetic inertia (see Blomberg & Garland (2002) for a review), or that the same trait has evolved in different species by means of convergent evolution (Fleagle, 2013). Thus, the process of reconstructing the behaviors of our ancestors culminates as a number of approximations toward the truth as additional evidence is collected. For instance, studying percussive stone tool use in monkeys and apes aids in hypothesis testing of how this technology emerged in early humans (e.g., Whiten, 2013; see also Hall, 1968).

One specific reason to compare nonhuman primate behavior to humans, rather than the behavior of other animals, is close genetic relatedness. For instance, chimpanzees and bonobos (sometimes referred to as pygmy chimpanzees) are humans' closest living relatives, sharing 90–99% of the same genetic information, depending on the level of genetic analysis (e.g., Anzai et al., 2003). The great apes, in particular, are the group most often studied for identifying how our proto-human ancestors behaved. Much has been learned about our own behavior from observing these animals. However, these apes do not always make for the best comparisons to humans because evolution does not necessarily lead to constancy in behavioral repertoires across closely related species. For instance, orangutans spend much of their time in solitude, so their social interactions, when they occur, likely do not reflect common human experience. On the other hand, chimpanzees and gorillas lack the pair-bonding common in many human societies, and their social relationships are shaped accordingly. Therefore, it is important to note where there are similarities and where there are differences and then select and construct comparisons appropriately.

In summary, taking phylogeny into account when comparing socioecological traits is important for understanding adaptive strategies of species and how these transform over evolutionary time. As mentioned, adaptation can only work with the materials at hand, which are constrained by phylogeny, and prepare the individual for the environment in which it lives. When phylogenetic constraints are appropriately applied, then more meaningful comparisons can be made (e.g., Arnold et al., 2010). However, convergent evolution—where the same

trait evolves in different lines—can muddle the picture and may lead researchers to misattribute phylogenetic origins or their subsequent constraints. Therefore, the remainder of this chapter will largely ignore phylogeny and will mostly be concerned with the ecological and social pressures that shape female-female social relationships.

Evolutionary Context of Competition and Aggression

Viewing female-female competition and aggression in an evolutionary context illuminates the adaptive benefits of each despite their associated costs. There are many factors that play into competition and aggression, but it is extraordinarily difficult to account for all of them within a single theory or model. Therefore, this section discusses a number of general theories of how primate social relationships evolved, including their merits and shortfalls. I also give consideration to general factors affecting female-female relationships, including food competition, reproduction, dispersal, and dominance.

Theories of Primate Sociality

Many attempts have been made to explain social relationships in primates (Silk, Cheney, & Seyfarth, 2013), and many theories have been devised to explain the evolution of primate social relationships (e.g., Clutton-Brock & Harvey, 1977; Isbell, 1991; Isbell & Young, 2002; Kappeler & van Schaik, 2002; Sterck, Watts, & van Schaik, 1997; van Schaik, 1989), but it was Wrangham (1980) who first used female behavior as a central explaining factor. Many of these theories have attempted to categorize female social behavior by its various traits (see Table 4.1; see also Isbell & Young, 2002). In some cases, all social categories can be found within a single taxonomic family, although family trends can be also apparent (e.g., hamadryas baboons are an exception to the otherwise “typical” baboon trend of matrilineal group organization and strong female bonds; see Cords, 2012). The different traits that make up a social category cannot be attributed to a single cause, and the diversity of social categories makes it difficult to develop a single, compatible theory of how primates evolved these systems. Figure 4.1 illustrates some of the factors that affect female social relationships—and female sociality more broadly—and demonstrates how these factors interact. These factors will be discussed throughout this section and the next section.

Theories for explaining primate social relationships range from attributing change in social

Table 4.1. Categories of Female-Female Relationships in Nonhuman Primates.

Social Category ¹	Competitive Regime ²				Social Response		Example ¹
	Contest Competition		Scramble Competition		Female Philopatry	Female Dominance	Species
	Within-Group	Between-Group	Within-Group	Between-Group			
Dispersing-Egalitarian	Low	Low	Low ³	Low	No	Egalitarian	Chimpanzee, Ring-tailed lemur, Hamadryas baboon
Resident-Egalitarian	Low	High	Low ³	High	Yes	Egalitarian	Patas monkey
Resident-Nepotistic	High	High? ^{4,5}	High ⁵	High	Yes	Nepotistic, Despotic	Japanese macaque
Resident-Nepotistic-Tolerant	High? ⁵	High	High ⁵	High	Yes	Nepotistic, Tolerant	Sulawesi macaque

¹ Sterck, Watts, & van Schaik (1997)

² Modified from Isbell & Young (2002)

³ Classified as *high* in van Schaik (1989)

⁴ Classified as *low* in Sterck, Watts, & van Schaik (1997)

⁵ Classified as *low* in van Schaik (1989)

Categories are described by the type and amount of feeding competition and the social response to female gregariousness. Table is modified from Sterck, Watts, and van Schaik (1997), but similar categories proposed by other authors are also included. Differences between authors' categories are noted.

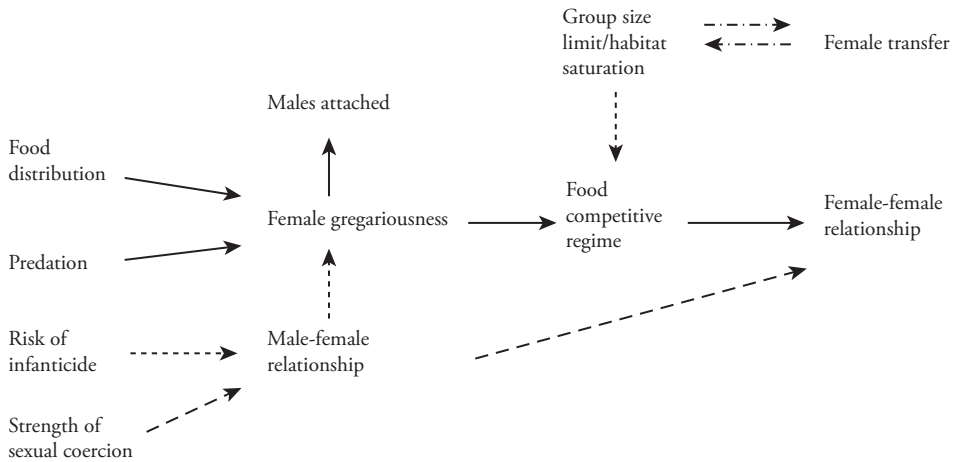


Figure 4.1 Schematic of factors affecting female-female relationships in nonhuman primates. Solid lines represent factors explained in van Schaik (1989). Dotted lines represent factors explained in Sterck, Watts, and van Schaik (1997). Dashed line roughly represents factors explained in Brereton (1995). Compound dash-dot lines represent likely other factors.

structure to primarily male-driven causes to primarily female-driven. Specific theories stretch from the idea of a reproductive arms race—in which males and females evolve to counteract each other's adaptation to secure fitness and mate choice (Brereton, 1995; see also Treves, 1998)—to protection from predators (see Sterck et al., 1997; see Figure 4.1). For instance, Brereton (1995; see also Hrdy, 1977; van Schaik & Kappeler, 1993; Watts, 1989) suggested in the *coercion-defense hypothesis* that males who live in societies where females choose their mating partner and who remain unselected by a female will develop coercive strategies to gain access to sex—such as by developing a larger body size or another method of overpowering females to force the matter (however, see Plavcan (1999) for a discussion of other possible factors affecting the evolution of sexual dimorphism). On the other hand, females adapt to this threat by evolving new traits, such as forming coalitions with other females against these “undesirables” (see the section “Dispersal, Dominance, and Female Sociality” for a discussion of female coalitions), by recruiting a higher-ranking male for support, or by concealing estrus (i.e., the point in the female's reproductive cycle when she is receptive). The “undesirables” would have to respond to regain a reproductive advantage, so they (i.e., the next generation or so) further evolve new traits, such as committing infanticide or some other abuse, and so the war rages on (i.e., because natural selection works only on those who succeed in reproducing). Building on previous work on female choice (Trivers, 1972; see also Smuts & Smuts (1993)

for review), Treves (1998) modified this dynamic approach of males and females directing adaptation in the *conspecific threat hypothesis*, which explains shifts in sociality as primarily caused by fluctuations in the probability of males who are not part of the group or other unrelated males interacting with females. This theory places a greater emphasis on the selective pressure exerted from the general aggressiveness of an unrelated male toward a female (and her offspring), whereas the previous theory focuses primarily on sexual coercion alone without regard to group membership.

Both the coercion-defense and conspecific threat theories explain current primate behavior but do so under different assumptions of female response and adaptations to male aggression (see also Smuts & Smuts, 1993) and are narrowly focused on reproductive strategies. An ecologically based model, on the other hand, assumes that primate sociality is an adaptation to a particular ecology rather than to social pressures (e.g., male aggression), although some of these models place a greater emphasis on the energetic costs to the individual (e.g., Isbell, 1991; Isbell & Young, 2002) rather than on group-level competition (van Schaik, 1989; Wrangham, 1980). This perspective places a greater emphasis on the selective pressures supporting social organization than on social interactions.

An *ecological model* (according to van Schaik, 1989) assumes that female gregariousness is determined by a combination of food distribution and predation risk (see Figure 4.1). Female gregariousness, in turn, determines male distribution within their

social group as well as female competitive regime, within and between groups, in terms of food availability. The interaction of these factors results in the varied social relationships seen in female primates. There is support for this version of the model in the observation that females use aggression to manipulate the number of males associated with their social group (e.g., squirrel monkeys: Baldwin, 1968; talapins: Rowell & Dixon, 1975; ring-tailed lemurs: Sussman, 1977; olive baboons: Packer & Pusey, 1979). For instance, female Japanese macaques limit the number of males in their troop by acting aggressively toward an unwanted male, thus driving him to withdraw from their troop (Packer & Pusey, 1979). This may reflect a female strategy of limiting competition for food or other resources, especially in species where size dimorphism (in this case, when males are larger than females) is not great or where males are less likely to provide protection or parental care (Clutton-Brock & Harvey, 1977; Packer & Pusey, 1979). For instance, hanuman langur females form coalitions against aggressive males, and the size of these coalitions increases as the number of aggressive males increases (Hrdy, 1974, 1977; Sommer, 1987; Treves & Chapman, 1996).

Despite the power in explaining certain tendencies, the ecological model is not always directly supported. The female-female relationship classes are derived from an ecological standpoint in consideration of both individual- and group-level competition, however, there are shortfalls which can be addressed by adding an additional layer of explanation. A *socioecological model* (Sterck et al., 1997) is based on the ecological model but adds demographic components to help account for the behaviors of species that the latter cannot explain. This model has the added power of accounting for social phenomena such as group size limits (i.e., habitat saturation) and infanticide (see Figure 4.1). For instance, an ecological model (see van Schaik, 1989) considers female relationships with males as a byproduct of female sociality rather than as a contributing factor (i.e., feedback loop).

Although the socioecological theory does well in explaining female-female social relationships, Sterck, Watts, and van Schaik (1997) discussed other alternative theories concerning demographics and social issues. Concerning demographic influences, they presented female philopatry (i.e., remaining in the natal group rather than dispersing) with kin selection as the ultimate source of female-female social relationships. They also suggested that interbirth interval (i.e., the time between births) could

be a supporting factor, but then argued against both interbirth interval and philopatry as prominent producers of female sociality. In terms of social issues, they discussed male policing, male harassing (i.e., the coercion-defense hypothesis), and costly reproduction, but only supported costly reproduction as a viable source of influence, citing the other two as failing to account for the full variation of female relationships. They also suggested that it could all just be an ecological effect of between-group competition. This could be especially true when the individual female and her dependent offspring are considered to be the main social unit.

As yet, there is no single theory that completely explains primate sociality, but it is clear that aggression and competition are not the only contributing factors to female social relationships. Cooperation and affiliation are important factors in female sociality, and the influence of these factors should not be underestimated (Sussman, Garber, & Cheverud, 2005). These are discussed in detail in the section "Female Competition and Cooperation in Primates;" however, to establish a background, the general principles that affect female sociality will be discussed first.

General Principles Affecting Female-Female Sociality

Sterck, Watts, and van Schaik (1997) described in detail the different types of female social relationships of primate groups (see Table 4.1), as well as how social relationships evolved (see Figure 4.1). Throughout the remainder of this chapter, a number of contributing factors to primate sociality will be discussed, especially with respect to how these factors affect female social relationships. Specifically, the effects of food competition, dispersal, and dominance (see Table 4.1) will serve as recurring themes in the following sections.

With respect to existing models of primate social evolution, the effects from predation, female transfer, group size limits, group cohesiveness, and within-group competitive regime have been recognized as major contributing factors determining female social relationships (see Figure 4.1); however, the importance of the interaction of these factors with phylogeny, demography, sexual and social selection pressures, and life histories is still being debated (see Strier (1999) for discussion and references). In this section, different aspects of female primate social life will be considered with respect to their effect on female-female social relationships and sociality.

FOOD COMPETITION AND FEMALE SOCIALITY

Competition for high-quality foods affects both a female primate’s interpersonal relationships and her group’s social structure (see Table 4.1). Particularly, the distribution of food in her environment influences the level and type of feeding competition (Isbell & Young, 2002; van Schaik, 1989; Wrangham, 1980). Feeding competition comes in two intersecting sets: *scramble* or *contest* and within or between groups (Figure 4.2). Scramble competition is indirect, whereby the first to arrive at a food patch has sole access to it (by virtue of being the only one there) and otherwise cannot monopolize the bounty (unless they deplete the food before company arrives). Contest competition is direct, and the winner is based on dominance or agonistic exchange, although it can also promote the formation of alliances. These types of competition and the resulting social structures vary with diet (see Isbell (1991) for discussion). Preferred foods found in clumped, defensible patches, such as fruit, promote within-group contest competition, and females benefit from remaining in their natal group and forming affiliative and agonistic dominance relationships (Wrangham, 1980). In this case, nepotism—favoritism granted to kin—would benefit all kin, and dispersal would be costly to the individual. This type of distribution also promotes between-group competition, which itself promotes cooperation within the group in protecting food patches. Food that is abundant and evenly distributed requires less competition both between and within groups and incurs a lower cost to a dispersing female because it would not be likely that she would wander into a desolate area where she would starve. In this case,

Competing how?	
Competing with who?	Within-group scramble
	Within-group contest
	Between-group scramble
	Between-group contest

Figure 4.2 Matrix of the two intersecting sets of competition types. As illustrated, scramble and contest competition strategies can occur within or between established groups. A group will experience one type of within-group competition and one type of between-group competition.

agonistic or dominance relationships provide little added benefit to the female.

As just illustrated, scramble and contest competition occur between and within groups and factor into group structure and social relationships. Within-group scramble competition is nearly unavoidable (Isbell, 1991), whereas within-group contest competition depends on the available resources (e.g., abundance, distribution, and quality; Sterck et al., 1997; but see Pruett & Isbell (2000) for emphasis on food depletion time). More generally, between-group competition appears more dependent on food abundance according to diet (i.e., fruit vs. leaves vs. insects), whereas within-group competition is tied to food distribution (Isbell, 1991). When foods are spatially clumped and of high quality, females are more likely to be philopatric (stay within their group) and exhibit strong aggression toward other groups because such food patches are defensible (Isbell & Young, 2002; Wrangham, 1980). However, if there is typically variable food quality within patches, then females will form dominance relationships within their group, and nepotism will likely be prevalent (Isbell & Young, 2002; Wrangham, 1980; see next section for a more detailed discussion). According to specific diets, insectivore primates have a greater preponderance of solitary life because their food is highly dispersed and not defensible, whereas folivores (i.e., leaf-eaters) have an abundance of greens to chew on, and, for them, the costs of grouping are much lower (however, for a discussion of food competition in folivores, see Snaith & Chapman, 2007). On the other hand, frugivores (i.e., fruit-eaters) rely on seasonal, highly dispersed, patchy fruit distribution; for these species, both within- and between-group competition are high, and the benefits of social grouping outweigh the costs. Due to the variability in social grouping in the face of diet and subsequent competitive regime, each factor should be considered as one of many that affect social relationships rather than as defining factors. This goes for predation (van Schaik, 1989) and the other myriad of factors that affect social grouping and female-female relationships, in particular.

DISPERSAL, DOMINANCE, AND FEMALE SOCIALITY

As just described, the different types of feeding competition help to shape the social structure of the group, especially female-female relationships. There are four types of female-female relationships that can describe a group (see Table 4.1; Sterck et al., 1997; see also Isbell & Young, 2002).

These relationships are partly delineated and identified according to the social category continua described by Vehrencamp (1983) as egalitarian-despotic, individualistic-nepotistic, and tolerant-intolerant. The first is called *dispersing-egalitarian*. In this type of society, females disperse from their natal group and enter into their new group without the aggression associated with dominance relationships because these societies have no or poorly defined hierarchies; therefore, females share relatively equal access to resources. The second type of female-female relationship is *resident-nepotistic*, and it is described as females inheriting their mothers' ranks (or rank closely to her and any sisters) in a highly hierarchical, female-philopatric society. In this type of society, aggression would be used early in life to assert the female's inherited position and her privileged access to resources. She would do this by instigating fights with her playmates only to be supported by her mother in any counterattack from the assailed playmates' mothers. The third type, *resident-nepotistic-tolerant*, is similar to the second, but, in this society, aggression directed up the hierarchy (i.e., toward higher-ranking individuals) is more common. Reconciliatory behavior following aggression is also common in this social structure. Relationships benefit from mending after aggressive interactions, and such mending helps to secure coalitionary support from the aggressed in the future. Such support is imperative for rank maintenance. The fourth type of female-female relationship is *resident-egalitarian*. In this society, females remain in their natal group within a poorly defined dominance hierarchy.

It is important to note that these female-female relationship classes can exist within phylogenetic taxa (e.g., genera, species) and so cannot be used to define a particular phylogenetic group (taxon). This observation highlights the importance of ecology over a purely phylogenetic explanation of social relationships, although the observation that these systems tend to be maintained even in captive groups suggests that species-typical patterns may persist in a wide range of ecological settings. Take for consideration the observation that, compared to eastern chimpanzees, female western chimpanzees have higher grooming frequencies and form alliances and strong bonds with each other (Boesch, 1996; Boesch & Boesch-Achermann, 2000) even though chimpanzees as a species were classified as dispersing-egalitarian (Sterck et al., 1997) at a time when such population differences were not considered. Additionally, it should be noted that these

social relationship categories have limited descriptive fidelity in terms of capturing the specifics of female-female relationships, despite their usefulness in partitioning species into comparative groups. For instance, chimpanzees, ring-tailed lemurs, and hamadryas baboons are all considered dispersing-egalitarian despite the three species having very different social organizations (see the section "Lessons from Three Primate Species" for further discussion).

As noted earlier, coalitionary support is key to maintaining dominance. Coalitions can form between close relatives (e.g., mothers or sisters) or between unrelated group members (see Langergraber (2012) and Gilby (2012) for discussions). Coalitions can be formed against lower-ranking individuals, higher-ranking individuals, or against an individual ranking between the coalition members, and females decide who to compete with versus assist depending on the immediate (e.g., resource access) or long-term (e.g., reinforce rank) benefit (Chapais, 2006). For instance, a lower-ranking sister may join an unrelated individual in a dispute with her higher-ranking sister in order to acquire a higher rank, even though the higher-ranking sister likely helped the lower-ranking sister acquire her current (albeit lower) rank (Japanese macaques: Chapais, Prud'homme, & Teijeiro, 1994). Generally, coalitionary support decreases with decreasing maternal relatedness, and this pattern likely supports the maintenance of matrilineal dominance hierarchies within groups (Chapais, Girard, & Primi, 1991; Chapais, Girard, Prud'homme, & Vasey, 1997; Silk, Alberts, & Altmann, 2004).

Infanticide is a less mutualistic mechanism of dominance ascension or maintenance that is also used as a general competitive tactic. Simply put, infanticide is often attributed to being an evolved trait in males because they benefit from stopping the mother's lactation—which suppresses estrus—thus returning her to estrus sooner (Hrdy, 1974; Palombit, 2012). However, competing females also use infanticide to their advantage. Females have been observed killing the infant of another female (e.g., chimpanzees: Goodall, 1986; Pusey et al., 2008; marmosets: Saltzman, 2003) or indirectly causing the death of another's infant (e.g., lemurs: Jolly, 1998). Female-led infanticide can be the result of a lack of available food or a lack of help in rearing the infant and is sometimes inflicted by the mother rather than by a dominant female (Culot et al., 2011). Early on, it was thought that infanticide was rare in nonhuman primates (Goodall, 1986; Palombit, 2012), but more cases have been

observed as field studies continue. Some researchers have suggested *disequilibrium* (Sterck et al., 1997), a situation of nonadaptive change, such as change resulting from habitat fragmentation or human pressure, as an explanation for this otherwise difficult-to-explain phenomenon, but others maintain that infanticide is an evolutionary adaptation (e.g., Hausfater & Hrdy, 1984; Lyon, Pandit, van Schaik, & Pradhan, 2011; Wilson et al., 2014) and is the result of competition for survival within a stressed group (e.g., Townsend, Slocombe, Thompson, & Zuberbühler, 2007).

Summary on Social Evolution

Essentially, predation risk favors group formation in females whereas food availability limits grouping (see Figure 4.1). Competition for food and other resources within a group strains female-female relationships and leads to aggression; thus, mitigating behaviors, such as affiliation and reconciliation, and cooperative behaviors, such as coalition formation, developed to promote group cohesion. Males go where the females are located and respond according to female social and grouping strategies (Wrangham, 1980). The proposed ecological and socioecological models do reasonably well in predicting the social relationships of female primates and other mammals, and these predictions are generally supported by what is observed in the wild, although exceptions have been found (e.g., Pruett & Isbell, 2000).

So why, then, is it surprising to hear new evidence showing the aggressiveness of and competition between females? Perhaps it is historical and is owed to the male-dominated academy's failure to consider competition in females as a viable topic of study in parallel to the study of male traits (e.g., Hrdy, 2013a, 2013b). Or, perhaps it is because these are "animals," and there is a tendency to view humans as separate from the other animals, in which case there would be no useful parallel to consider. There, historically, has been a sense of human superiority over animals such that the selective pressures and the principles that govern animal behavior are not viewed as equally constraining human behavior (e.g., Hume, 1777/1975). In line with that view, some researchers believe that human behavior differs from other animals in kind rather than in degree; however, in these last two sections, I make an effort to illustrate parallels in human and nonhuman primate lives. I draw specific examples of the social and ecological pressures experienced by females from a number of different species,

including how these affect aggression and cooperation. This theme will continue in the final section of the chapter with a discussion of female life in three distinct species of nonhuman primates—chimpanzees, hamadryas baboons, and ring-tailed lemurs—with special consideration directed as parallels in modern women.

Female Competition and Cooperation in Primates

In discussing the value of a social life, primatologist Hans Kummer (1979) described an individual A's need to view any group member, B, as a potential resource of some future benefit. In this sense, B is a resource for present or future ecological, social, emotional, or psychological benefit, and each interaction with B is an investment in their social bond. However, every time A meets B, their social bond is tested and evaluated as ally or competitor. These tests come in the forms of agonistic encounters, displays of ability, greetings, affiliative behaviors (such as grooming), and even play. Only through the creation and maintenance of social bonds can the benefits of social living—improved access to food, protection from predators, access to mates, and help caring for young (see discussions in Fleagle (1988) and Silk (2012))—be reaped by primates; however, social living also results in competition and, inevitably, conflict.

The varied types of competition are mediated differentially by aggression, but there are situations in which aggression is useful and others in which more affiliative behaviors may lead to a better outcome. Examples of such situations—which have been discussed throughout this chapter—include dispersal, dominance, and reproduction. Communication is a key mechanism for addressing aggression and cooperation, and so it will be discussed where applicable. For instance, a number of species use gestural (apes and monkeys: Call & Tomasello, 2007; Pika & Liebal, 2012) or vocal communication (chimpanzees: van Hooff, 1973; baboons: Cheney, Seyfarth, & Silk, 1995) to signal friendly intent or express submission (i.e., in order to avoid attack from another), to signal a threat of attack, or to recruit an ally for coalitionary support. Mechanisms of bond maintenance, such as grooming, can also aid in dampening the effects of competition and even foster cooperation in some future event. Grooming, in particular, has the added advantages of decreasing stress for both the groomer and the groomed (e.g., Boccia, Reite, & Laudenslager, 1989; Shutt, MacLarnon, Heistermann, & Semple, 2007) and inhibiting aggression (Carpenter, 1964, in Coelho,

Turner, & Bramblett, 1983). Bonding mechanisms will be discussed also in this section; however, it should be noted that the full function of grooming is still contested (see Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Colmenares, Zaragoza, & Hernandez-Lloreda, 2002; Seyfarth, 1977, for discussions).

Female Dispersal

Dispersal is an important means of avoiding inbreeding and, consequently, of maintaining genetic diversity within a group. In some primate species, females typically disperse from their natal group (chimpanzees: Goodall, 1986; hamadryas baboons: Abegglen, 1984; but see Swedell, Saunders, Schreier, Davis, Tesfaye, & Pines, 2011), whereas in other species it is males who typically disperse (ring-tailed lemurs: Sussman, 1991; olive baboons: Packer, 1979; Smuts, 1985) or sometimes both sexes disperse to varying degrees (gorillas: Watts, 2003). Sometimes females (or males) disperse from their natal group with a kin or age cohort member (also referred to as *co-transfer*: ring-tailed lemurs: Sussman, 1991). However, dispersal does not always occur by choice. Sometimes females leave their natal group in response to male coercion (e.g., hamadryas baboons: Swedell & Plummer, 2012). Sometimes females are pushed out of their group by other females through targeted aggression only to be met with similar aggression by the females in their new group (Kappeler, 2012). In these situations, resident group members will likely be unwilling to share resources with the new immigrant member. Aggression serves the residents in establishing priority access to the group's resources, whereas aggression would not benefit the immigrant who needs to be accepted into the group; in her case, it would be better to show affiliation. For example, when a male (of almost any primate species) immigrates into a new social group, he will benefit from resorting to aggression against resident males to secure his new residency (and place in the hierarchy) and aggression against resident females in the form of infanticide (to increase his own fitness; see Smuts & Smuts, 1993, for discussion), whereas aggression will work against a female immigrant because males will likely come to the aid of a resident female who is under attack (as will other resident females). Instead, an immigrant female benefits most from finding a "sponsor" in either a resident male (e.g., chimpanzees: Pusey, 1979; mantled howler monkeys: Glander, 1992) or female (e.g., bonobos: Idani, 1991) and befriending

the sponsor while slowly gaining acceptance by the remaining residents.

Individuals who disperse from their natal group experience different ecological and social pressures than do conspecifics who remain in their natal group (Isbell & van Vuren, 1996). Within an established social group, members of the philopatric sex are likely to be more closely genetically related to each other than are members of the sex that disperses (see Di Fiore (2012) for discussion). Therefore, individuals who remain in their natal group have the potential to form longer-lasting, more positive social bonds than if they had left their natal group under the assumptions that (1) time spent together and familiarity can increase social bonding (e.g., Hinde, 1977; Langergraber, Mitani, & Vigilant, 2009), and (2) kin selection (i.e., the phenomenon of showing preference to more closely related individuals as a means of increasing one's own fitness; Hamilton, 1964a, 1964b) promotes bonding. In turn, these individuals have more to gain from maintaining social bonds with their philopatric peers because those are the individuals whom they will need for future coalitional competition, kinship aside. In other words, a large repertoire of affiliative behaviors may be more beneficial than an arsenal of aggressive behaviors. Such affiliative interactions should be expected to occur more often, at least for those who remain in their natal groups, because these individuals will need to establish and service a large and complex network of long-term relationships (see Scott (2013) for evidence in communication strategies). Because aggression certainly has its place in maintaining one's position in the social hierarchy, it would be expected that aggressive interactions would still be necessary.

From this point, it may be expected that differential bonding and communication strategies of the philopatric versus the dispersing sex would be evident. In agreement with this argument, an immigrant female might use affiliative behaviors, such as grooming, to create a new social bond (Dunbar & Schultz, 2010), whereas a resident female will (and does) groom selective peers in order to maintain valuable social relationships (Aureli, Fraser, Schaffner, & Schino, 2012). Current evidence suggests that the philopatric sex spends significantly more time involved in grooming than does the dispersing sex (e.g., Assamese macaques: Cooper & Bernstein, 2000; bonnet macaques: Sugiyama, 1971; patas monkeys: Kaplan & Zucker, 1980; spider monkeys: Slater, Schaffner, & Aureli, 2009), including a higher proportion of time in same-sex

rather than mixed-sex grooming. Similarly, evidence from a number of primate species (e.g., vocal communication: red-capped mangabey: Bouchet, Pellier, Blois-Heulin, & Lemasson, 2010; rhesus macaque: Greeno & Semple, 2009; vervet monkey: Locke & Hauser 1999; gestural communication: spider monkey: Slater et al., 2009) indicates that the philopatric sex has a much greater reliance on communication in terms of frequency. However, similar studies of chimpanzees found no clear differences between the sexes in the general rate of production of vocalizations (Clark, 1993; Marler, 1976) or gestural communication (Scott, 2013), although differences did emerge when contexts of dominance and competition were examined more closely (sex: Mitani & Gros-Louis, 1995; Wilson, Hauser, & Wrangham, 2007; submission: Clark, 1993; Scott, 2013).

Female Competition for Food and Social Resources

Given that many species exhibit a positive relationship between social status and reproductive success (females: Pusey, 2012; Silk, 2012; males: Alberts, 2012; but also see Gartlan (1968) for exceptions), competition surrounding dominance relationships can be intense. An individual can establish dominance through his or her physical attributes, direct and indirect aggression, inheritance, or sometimes cooperation. For instance, in nepotistic societies such as Japanese macaques, close maternal kin (i.e., grandmother, mother, sister) will provide coalitionary support to a young female until she can dominate all other females that her mother outranks, including her older sisters (Kawamura, 1958; see Cords (2012) and Langergraber (2012) for discussions). However, as discussed earlier (see the section “General Principles Affecting Female-Female Sociality”), maternal kin also compete with each other to gain a higher rank and will sometimes gain the coalitionary support of an unrelated individual in order to rise in rank (e.g., Japanese macaques: Chapais et al., 1994). The influence of paternal relatedness is currently being investigated for similar effects (e.g., Schülke & Ostner, 2008).

Female dominance hierarchies are common when there is within-group contest competition (Chapais et al., 1991; see also Schülke & Ostner (2012) for discussion) because food distribution for these groups is patchy and varies in quality (Isbell, 1991). In this environment, it would be energetically beneficial to defer the better patches to the more dominant group members rather than fighting

for them; thus, the most dominant individual gets the largest, highest-quality patch and so on down the hierarchy (Schülke & Ostner, 2012). However, these conditions also promote coalition formation (Chapais et al., 1991), especially among relatives (Sterck et al., 1997; van Schaik, 1989; Wrangham, 1980). For example, by providing friends with access to highly desired foods, as is the case in meat sharing by chimpanzees, the “fruits” of contingent reciprocity may be reaped or future coalition partnering may be “bought” (see Mitani (2006) and Gilby (2012) for discussions). Even if playing favorites or buying favors is not the impetus for food sharing, in the very least, individuals benefit from their own generosity by giving in to those who harass them for a share: the more quickly they give in to such coercion, the more quickly they can continue eating (Stevens & Gilby, 2004; see Gilby (2012) for discussion). On the other hand, when food competition between groups is high, then cooperation in protecting food sources within their home range or territory becomes necessary, and dominance relationships may become more lax (van Schaik, 1989).

Friendships are an important means of staying competitive beyond just preferred access to food. There are adaptive benefits in terms of psychological and physiological health as well as reproductive success (Langergraber et al., 2009; Silk et al., 2009). In fact, it may be common for female primates to “tend and befriend” rather than “fight or flee” each other (Taylor et al., 2000). If females completely lacked affiliative bonds such as friendship, then not only would they suffer, but so too would their offspring. For instance, the infants of females who share strong social bonds with other females live longer than do infants of females who share weak bonds with others, surviving longer even in adulthood (baboons: Silk, Alberts, & Altmann, 2003a; Silk et al., 2009). The active maintenance of friendships through affiliative behaviors such as grooming also provides benefits by lowering anxiety and stress, as measured by glucocorticoid levels (baboons: Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008). On the flip side, following the death of a friend, the survivor may show higher levels of glucocorticoids (chacma baboons: Engh et al., 2006), indicating that she feels anxiety (or some other form of stress) in face of her social loss.

That is not to say that friendship or coalitionary support is free, as alluded to earlier in this section with the example of meat sharing. The cost of kin support is presumably usually outweighed by the ultimate (indirect) gain in fitness (Langergraber,

2012). Like any (human) friendship, supporters need something in return. This can come in the form of contingent reciprocity, mutual benefit, or market value (Gilby, 2012; see also de Waal & Brosnan (2006) for altruistic reciprocity). For example, longtailed macaques trade grooming for sex, and the rates for the grooming–mating exchange were influenced by social rank and the supply of available partners (Gumert, 2007). Grooming is a common commodity across primate species and can be used to drive up an individual's market value (by providing extended grooming services) or can be used in a more “I'll scratch your back if you scratch mine” kind of deal (e.g., contingent reciprocity: Gilby, 2012; or reciprocal altruism: Mitani, 2006). Other currencies of friendship include returned coalitionary support, sex, and food sharing (see Gilby (2012) for discussion and additional references). In fact, having male friends provides the female with the added benefit of infant protection (Setchell, 2008; see also Smuts & Smuts, 1993). In baboons, this friendship is initiated and maintained by the female after she has copulated with the male (possibly as a source of paternal confusion) and ends if the infant dies (Palombit, Seyfarth, & Cheney, 1997). One negative to having a male friend is that other males may indirectly attack him through a direct attack on his close female friend (chimpanzees: de Waal, 1982; baboons: Smuts, 1985).

Overall, friendships often exist outside of dominance and kinship boundaries (e.g., Gilby, 2012; chimpanzees: Langergraber et al., 2009; baboons: Silk et al., 2009) and are not limited to the same sex. Friendships are useful in competitive societies because they can provide coalitionary support against aggressive interactions or in cases of dominance disputes. They also have the added benefits of providing preferred access to food (e.g., food sharing). However, by simply being more dominant than others, an individual can eschew “payment” and directly gain preferential access to food and coalitionary support.

Competition for Mating Opportunities

Reproduction is the major source of competition in primates, although it can be considered to be the ultimate source of all competition. As discussed in the section “Theories of Primate Sociality,” some theories center on reproductive competition as the source of the evolution of social traits in primates. Females evolved social or morphological traits to aid them in competing for mating opportunities. These adaptations include behavioral responses that have

direct (e.g., infanticide) or indirect (e.g., reproductive suppression) influences on the reproductive success of other females, as well as on the physical development of secondary sexual characteristics (e.g., sexual swellings).

Infanticide is one example of a social strategy for reproductive competition. Typically, when the male is the aggressor, he is an outsider to the group and the alpha male has already been killed (by the intruder or other causes; Palombit, 2012). When the attacker is a female, though, she is usually a resident of the group, and the attack occurs outside the view of the alpha male (if the societal structure includes a male-dominance hierarchy). For instance, one account reports the continued harassment and attack on a lower-ranking female and her infant twins by a small group of resident females over the span of days during which the victim sought passive protection from resident males and in which infanticide was prevented (chimpanzees: Pusey et al., 2008). One way a female can avoid infanticide is by maintaining a male friend, as discussed in the previous section, who will protect her from attacks by males and females alike. Another strategy is to use the space in their group's territory that is best protected by resident males and offers the best source of food: females who spend the majority of their time in these spaces have higher reproductive success than do females who range elsewhere or who switch groups (chimpanzees: Williams, Pusey, Carlis, Farm, & Goodall, 2002).

Another example of female-female reproductive competition is reproductive suppression, in which one female, usually the most dominant female, suppresses the reproduction of other female group members (see Kappeler, 2012; Pusey, 2012). She can do this directly by preventing or interrupting mating (Setchell & Kappeler, 2003) or indirectly by hormonal suppression (Abbott, 1989; cotton-top tamarins: Snowdon, Ziegler, & Widowski, 1993). Daughters are not immune to this treatment or from getting kicked out of the group once they reach a “critical” size (lemurs: Vick & Pereira, 1989). Hormonal suppression is reversible and may actually benefit a subordinate. By waiting until she obtains the dominant position in the group, she gains mothering experience, and, upon achieving breeding status, she gains alloparenting resources from her subordinates, thereby increasing her reproductive success (for species and discussions see Setchell (2008) and van Noordwijk (2012)). However, it is also possible that the costs associated with waiting to reproduce do not create enough

pressure for evolving a counter-strategy, rather than there being any actual benefit.

Alternatively, females can prevent the pregnancy of a rival by physically intervening in the mating process. The competing female can use aggression or other harassment to disrupt or prevent mating (Kappeler, 2012; Setchell, 2008). For example, the presence of a dominant female may be enough to halt any interactions between a subordinate female and a nearby male before mating ever begins (e.g., brown capuchins: Janson, 1984, in Setchell, 2008). Like males, female primates in some species have evolved morphological traits, such as increased canine size (Plavcan, van Schaik, & Kappeler, 1995), to help them compete with others of their own sex.

In summary, female primates have evolved a number of behavioral and physiological traits that help them to compete for reproductive success through dispersal patterns, competition for food and social resources, and competition for mating opportunities. Cooperation is also prevalent and can occur between kin and unrelated individuals, as well as between the sexes. However, when it comes to pregnancy and birth, competition is fierce between family and friends alike.

Up to this point, a basic introduction to primate sociality has been laid out. In the next section, the information will be applied in a discussion of three distinct primate species. In discussing each species, the general principles affecting female-female sociality will be discussed in greater detail. Examples of female competition and cooperation as these pertain to the general principles will be considered with respect to the social structure and social organization of each species.

Lessons from Three Primate Species

Up to this point, a number of aspects of primate competition have been discussed, including a number of theories that have been devised to explain the evolution of and variations in female-female relationships. The third and final goal of this chapter is to illustrate where lessons may be gleaned from other primates with respect to similarities found in human cultures. Specifically, the aspects of dispersal, reproduction, dominance, and friendship will be described in further detail for three distinct species. The species to be evaluated are from three distinct clades (see Appendix): ape (chimpanzees), Old World monkey (hamadryas baboons), and prosimian (ring-tailed lemurs). Chimpanzees, hamadryas baboons, and ring-tailed lemurs provide examples

of female-female competition from distinct societies and evolutionarily distinct paths (see Appendix).

Reviewing these three species provides the opportunity to view the life of females through a different lens: a lens through which women would view the world if humans had a social structure more like these species. Because every aspect of social life is interconnected and also connected with the greater environment, when certain aspects of life get shifted, then the entire social system shifts as well. In the case of chimpanzees, their social structure is in many ways like modern (Western) humans in terms of (historically) female dispersal and male dominance. Hamadryas baboons live in harem societies that characterize some modern societies and some ancestral traditions, as well as reflect what life is like when groups depend on a centralized male protector. Lemurs, on the other hand, live in a female-dominated society, and their experiences may shed some light on what we could expect if women ruled the world. This section will conclude with some remarks on what can be learned about female life in each of these species and how women can apply knowledge gleaned from these observations to navigate their own social structures.

Chimpanzees

SOCIAL STRUCTURE

Chimpanzees live in a multimale-multifemale fission–fusion society of up to 150 individuals, although they spend the majority of their time in groups of 1–20 individuals (Goodall, 1986; Lwanga, Struhsaker, Struhsaker, Butynski, & Mitani, 2011; Nishida, 1968). Some of the traits that chimpanzees exhibit appear human-like; including tool use, communication strategies, and lethal intergroup aggression (or what may be referred to as “war” in human culture). Although differences have been found between chimpanzee communities (e.g., Whiten et al., 1999; Wilson & Wrangham, 2003), these differences are attributed to habitat and cultural traditions rather than genetics (Boesch & Boesch-Achermann, 2000; but see Langergraber & Vigilant, 2011). For instance, chimpanzees exhibit intelligent strategies for visits to border regions of their territory (border patrols), including traveling in larger groups and adjusting the volume of their vocalizations, assumingly to remain undetected or to advertise their territory ownership and coalitionary strength (Wilson et al., 2007; see also Clark (1993) and Fedurek, Donnellan, & Slocombe (2014) for other social and ecological contexts affecting call rates). Overall, males in chimpanzee

society tend to be more gregarious than females (Boesch & Boesch-Achermann, 2000; Kawanaka, 1984; Nishida, 1968), although a female's participation in cooperative group activities, such as border patrols and hunting, is largely dependent on her stage in estrus (Goodall, 1986).

The fission–fusion society of chimpanzees means that individuals travel in parties of varying size to forage, sleep, or copulate. The advantages of this societal structure include decreased competition on a day-to-day basis, but there are disadvantages, too. One disadvantage is the excitement caused by group fusion when members of the group reunite. Reunions entail affiliative gestures, a chorus of vocalizations, and sometimes violent displays (Goodall, 1986). Displays advertise male might and often end with the displayer beating (hands and feet) on another chimpanzee. Infants are not immune to these indiscretions, sometimes getting picked up and flung if caught in the path of the displayer. One solution that chimpanzees have developed is signaling with *greeting* gestures that mitigate fusion excitement and redirect the energy of potential aggression. In fact, chimpanzees have a large repertoire of vocalizations, gestures, postures, and facial expressions that function to promote affiliation, cooperation, aggression, and dominance (Goodall, 1986; Pollick & de Waal, 2007; Scott, 2013; van Hooff, 1973). Overall, communication is a key aspect of chimpanzee life, acting to create, maintain, and mend friendships, as well as to avoid or threaten aggressive action.

DISPERSAL AND REPRODUCTION

In chimpanzee society, a female and her offspring form the basic social unit. When a female reaches sexual maturity around the age of 10–11 years (Goodall, 1986), she may transfer to a new group where she can start a family. Female dispersal helps to avoid incest, but the transfer may only be temporary, and she may return to her natal group after some time. Transfer usually involves aggression once she has joined her new group, and she will typically stay close to a resident male (a new friend) for protection (Pusey, 1979) because all males are more dominant than all females in most situations (for contexts of situational dominance see Noë, de Waal, & van Hooff, 1980). This arrangement benefits the male because he is most likely to copulate with her in the near future (an example of mutualism or reciprocity).

Females generally have the choice to mate, but sometimes the matter is forced on the spot or in the form of a consortship (de Waal, 1982; Goodall,

1986; Muller, Emery Thompson, Kahlenberg, & Wrangham, 2011; Yerkes & Elder, 1936). A consortship is the chimpanzee equivalent of a weekend vacation to a bed-and-breakfast whether she likes it or not: an unwilling female can incur aggression until she either gets help from others nearby in resisting his advances or is finally coerced into following the male (Goodall, 1986). When the female is mature, experienced, and familiar with the courting male, she has complete control over when the copulation occurs and for how long, but an inexperienced female easily can be coerced by an assertive male even when she is not in estrus (Muller, Emery Thompson, & Wrangham, 2006; Yerkes & Elder, 1936; but see Muller et al. (2011) for other factors affecting female choice). In some communities, males may show remarkable tolerance when ignored by females and may not force the situation nor attack (western chimpanzees: Goodall, 1986); however, when a female is at her most fertile point in estrus and thus most likely to conceive, then males may maintain high aggression rates against her in order to secure paternity (eastern chimpanzees: Muller et al., 2011).

Male tolerance is one example of the conditions under which females have influence in a male's social life despite the dominance discrepancy. Males may involve females in rank disputes through election by female choice (e.g., western chimpanzees: Goodall, 1986; captive chimpanzees: de Waal, 1982), and males will sometimes defer access to intriguing objects to females (captive chimpanzees: Noë et al., 1980). However, the full reality of female choice is still debated (Muller et al., 2011; Muller & Wrangham, 2009), although the extent to which choice varies by population has yet to be determined. Furthermore, although adolescent males batter and harass females while climbing the status ladder, adult males will not try to dominate their own mothers and continue to show respect to them (Goodall, 1982), although males have been reported to sire offspring with their mothers (Wroblewski, Murray, Keele, Schumacher-Stankey, Hahn, & Pusey, 2009). Females appear to take full advantage of males' dependence on their future support—for instance, in future coalitions—by sometimes taking a passive role when recruiting a male ally (e.g., she stays behind and watches as her male friend exacts the punishment; Goodall, 1968). However, there may be population differences between eastern and western chimpanzees (e.g., Whiten et al., 1999), as well as between captive and wild chimpanzees

(e.g., Arnold & Whiten, 2001), so generalization is fairly limited until further studies are conducted directly comparing these populations. Overall, females seem to enjoy some situations of special social status but only in the case of their relationships with males; female–female relationships can be more contentious.

DOMINANCE AND FRIENDSHIPS

Females are less gregarious than males, but this is confounded by dependent offspring. Females with dependent offspring tend to spend time either away from others as a family unit or with a nursing party of other family units (Goodall, 1986; Nishida, 1968). Current evidence suggests that females at some sites share same-sex relationships that are more similar to male–male relationships than previously believed (western chimpanzees: Lehmann & Boesch, 2008, 2009). Although evident, the dominance hierarchy of females is typically difficult to assess and describe, so it is best described as nonlinear (e.g., Goodall, 1986; Nishida, 1970; but see de Waal (1982, p. 186) for an exception in a captive group) or categorical (e.g., high rank, middle rank, or low rank; Scott, 2007).

Some of the factors that affect rank for females differ from those for males, such as how many offspring she has in the community, especially in terms of her number of sons, but similarities exist, too, such as her ability to recruit allies and form coalitions (Goodall, 1968). Some researchers have described female dominance as primarily attributed by respect from below or what has been called a *subordination hierarchy* (de Waal, 1982; Rowell, 1974) because aggression does not appear to be a factor in determining rank (i.e., dominance cannot be assessed from the *winner* of fights, but rather is determined from direction of greeting and reassurance; Scott, 2007). This may be true in maintaining rank in an established group, but, in captivity, females seem to go through the same processes as males when establishing rank in a new colony (Yerkes, 1943).

Without clear-cut dominance relationships, female–female aggression appears to result from competition rather than from power struggles for status. Subsequently, female chimpanzees lack the motivation to mitigate their agonistic acts toward other females, although they do share these signals with males. Reconciliation is important for maintaining rank, yet, unlike males, females do not use signals of reassurance following acts of aggression. The same pattern of same-sex interactions

and different-sex interactions exists for contexts of submission (another important context for securing social status; Scott, 2013). That is not to say, though, that female chimpanzees completely lack social bonds with other females.

Females may lack the buffering mechanisms that mitigate the effects of aggression (de Waal, 1986; see Benenson et al. (2014) for a similar argument in humans) but may still manage to share strong, long-lasting social bonds with another female. These bonds resemble male–male social bonds and can exist outside familial bounds (Gilby & Wrangham, 2008; Langergraber et al., 2009; Lehmann & Boesch, 2009)—these are often referred to as *close friends*. As mentioned previously, the gregariousness of females is not to the same extent as it is in males (e.g., Goodall, 1986, p. 156): rates of male–male association are higher than female–female rates (Langergraber et al., 2009) and so are intrasexual grooming rates (Stumpf, 2007). Despite the lack of large-scale bonding, females may sometimes form a coalition against a male when he tries to force a consortship or copulation and otherwise act aggressively toward another female (captive chimpanzees: de Waal, 1982; see discussion in Smuts & Smuts (1993) for examples in other species). Females can also solicit the help of a more dominant female when an altercation with another female is imminent or occurring, as illustrated in this example from de Waal (1982, p. 47):

Jimmie and Tepel are sitting. . . while their two children play. . . . Between the two mothers the oldest female, Mama, lies asleep. Suddenly the children start screaming, hitting and pulling each other's hair. Jimmie admonishes them. . . . Tepel anxiously shifts her position. . . and eventually Tepel wakes Mama by poking her in the ribs several times. As Mama gets up Tepel points to the two quarrelling children. . . . Mama takes one threatening step forward, waves her arm in the air and barks loudly [and] the children stop quarrelling.

In light of this example, female chimpanzees use gestures more sparingly and more acutely than do males, seemingly catering their communicative exchange to the identity of their partners (Scott, 2013). This not only highlights the social intelligence of this species, but also may suggest that females value a stable network of social bonds. Males, by contrast, appear to treat all other adults the same regardless of their sex—at least in terms of their gesture use (Scott, 2013)—and constantly strive to assert themselves in their ranks and their

needs. This sounds similar to behavior in humans (e.g., Luxen, 2005), so what can we learn?

In summary, female chimpanzees are able to come together when there is physical threat or other altercation; if only they could assert themselves and act as a cohesive unit more often, they just might enjoy more dominance privileges than they currently do, although males do defer to females in certain situations. Furthermore, when emigrating, females are most at risk of severe attack when they are alone near the border regions of neighboring communities, especially when anestrus (i.e., not cycling). Immigrants often face aggression, particularly from resident females, although it does seem to bring together otherwise competing females to redirect their aggression away from each other and toward the new female. This may be a rather small benefit, but it serves to illustrate that cooperation is possible despite the lack of reconciliatory behaviors. In chimpanzee society, females are generally dependent on males for protection, as in the case with immigration, although it should now be clear that in the rare case when females team together they can overcome their subordinate position under males and maintain the social order themselves (at least in captivity, e.g., de Waal, 1982). The advantage of this type of society is that politics is everything. That certainly seems to be the case in humans, too.

Hamadryas Baboons

SOCIAL STRUCTURE

Like chimpanzees, hamadryas baboons (*Papio hamadryas*) live in a sexually dimorphic (males are bigger than females) fission–fusion society. These baboons gather in troops numbering in the hundreds, but form separate one-male units in which they do their feeding, mating, and most of their socializing. These one-male units, also referred to as *harems*, consist of a single dominant adult male, one or more females, and sometimes one or more *follower* males (Abegglen, 1984; Kummer, 1968). These units were initially characterized by male–female relationships because it appeared that females shared comparatively weak bonds; however, more recent evidence suggests that females can share social bonds within their unit and sometimes with a female from a different unit (Swedell, 2002). The troop is characterized by male–male relationships because the majority of communication between units in the troop occurs between dominant males, and the majority of social mixing is performed by

infants, juveniles, and subadult males (Kummer, 1968).

This one-male unit social structure is maintained by male aggressiveness to other males and to females of his own unit. A male maintains the cohesiveness of his unit by *herding* his females, usually by staring at an individual and sometimes by biting her neck after she moves too far away from him (Kummer, 1968). This kind of aggression is similar to that experienced by a female during chimpanzee consort formation. The cohesiveness of the entire troop is maintained by male–male relationships through aggressive interactions and cooperative support surrounding the control of and access to females. This can be likened to an honor system in which males do not cheat with another male's female.

DISPERSAL AND REPRODUCTION

A female hamadryas typically becomes part of a one-male unit before she is sexually mature, some time between the ages of 1 and 3 years, and as the result of an adult male forcing her into consortship through repeated aggression until she willingly follows him (Kummer, 1968). If she lags behind as the group moves, he will swiftly bite her on the nape of the neck. If she struggles in her movements, though, he may carry her on his back (Kummer, 1968). In fact, male hamadryas baboons display care-taking behaviors, and these could be an important root for the formation of the one-male unit (e.g., Kummer, 1967); this situation has clear benefits for females and would explain females' tendency to organize around a central individual. Following their care-taking tendencies, males act as the main protector of their units. During aggressive interactions, a female will rush to be close to her leader male and either turn to threaten her aggressor from his side or solicit him, such as by presenting her rump (a common *asking* gesture in other primate species: e.g., chimpanzees) to threaten the aggressor instead. Sometimes the alleged victim deceptively instigates the interaction on an unsuspecting victim, as in this example from Kummer (1967, p. 66):

Adult IV quietly sat cradling her infant. Subadult female 3a lingered around without being noticed. Suddenly 3a started screaming, rushed past IV pulling her tail violently, and ran on to their group leader. Female IV jumped to her feet, screamed, and ran toward the male, where 3a was already in the protected threat position. The male aimed a slight brow-lifting threat at IV.

DOMINANCE AND FRIENDSHIPS

Like chimpanzees, adult hamadryas females are known to form positive, stable social bonds with other females. Unlike chimpanzees, some female baboons show evidence of bonding outside their primary social unit, although this phenomenon appears to be closely tied to the number of other females in her unit (Swedell, 2002) and may be tied to kinship (see Schreier & Swedell, 2009; but additional evidence is needed). This could be an effect of the leader male's decreased ability to watch all of his females because it does not appear to be an effect of the leader male's unavailability as a social partner. One reason that females seem to be drawn to other females, even those from outside their social group, is access to infants (e.g., Kummer, 1968; Swedell, 2002). Many baboon species use grunts to signal benign intent when approaching a mother to request to hold her infant (Crockford et al., 2008; Silk, Rendall, Cheney, & Seyfarth, 2003b), but no work has been done to my knowledge on female hamadryas. Without this positive signal, mothers would likely move away to avoid potential harm coming to their infants. Another reason that females momentarily seek the attention of others is personality: some females appear more intrinsically motivated than others to seek out and maintain positive interactions with other females (Swedell, 2002). However, the identity of *others* as kin could be an important factor (e.g., Chalyan, Lapin, & Meishvili, 1994, in Swedell, 2002). Age seems to be an important factor as well because juvenile females are much more likely to socialize with other females, especially females of other groups (Kummer, 1968).

Within the one-male unit, females are rather undifferentiated in rank in wild populations (Abegglen 1984; Swedell, 2002) but can show linear dominance hierarchies in captivity (Kummer, 1968; Leinfelder, de Vries, Deleu, & Nelissen, 2001); however, the degree of female bonding is highly variable in the species as a whole and seems to be dependent on the size of one-male units (Colmenares et al., 2002; Swedell, 2002). In circumstances under which the dominant male is removed from the group, a female will take his place as most dominant, and the typical interactions with respect to this rank will resume (e.g., Coelho et al., 1983; Stambach, 1978). This tendency of females to organize around a central dominant individual appears to be instigated by the females rather than imposed on them by a male (Coelho et al., 1983; Stambach, 1978). Females do not compete with each other for rank or

food, but rather appear to compete for the right to groom their leader (Kummer, 1968; Swedell, 2002).

What can we learn from hamadryas baboons? Generally, female competition is limited: mate choice is constrained by her recruitment into a one-male unit, and access to food is abundant. The greatest competition is for attention from the central individual. Female baboons are drawn to a central, dominant individual and choose to be subordinate under that individual, even if the dominant other is another female. Personality clearly is an important factor in females' decisions on what constrains their social world and whether they choose to lead or follow. This could be the result of evolutionary adaptation (e.g., as response to paternal care of infants or group protection by males), but individual choice (in the face of local pressures) seems to provide the simplest explanation. The male social code makes it difficult for females to choose a male or to change social units without changing troops (hence leaving her family behind). Nevertheless, some females seem to be more outgoing than others, much like humans, and seek friends outside of their units. Effective communication plays a key role in this social mixing. The advantage to this society is the unconditional protection provided by the leader male, and his security in knowing the integrity of his fellow troop males allows the female to pursue her social interests.

Ring-tailed Lemurs

SOCIAL STRUCTURE

Ring-tailed lemur groups consist of a few adult males, a few adult females, and their young offspring making up a group of 15 individuals, on average (Jolly, 1966; Sauther & Sussman, 1993). These lemurs share many attributes with (savanna) baboons in their societal structures but not with the peculiar hamadryas baboons. Ring-tailed lemur societies consist of polygamous kin groups with dominant males and dominant females (Jolly, 1966). One important difference from savanna baboon society is that, for lemurs, society is unconditionally female-dominated. However, there are many other differences. For instance, typical (savanna) baboon dominance structures radiate from large kin groups (Smuts, 1985), whereas lemur dominance relationships are mainly dyadic and clear-cut—either the pair is wholly affiliate or wholly agonistic (see Jolly, 1998, for discussion). Unlike chimpanzees and baboons, however, this is not a sexually dimorphic species, meaning that males and females are the same size. In terms of female-female bonds, as in

some chimpanzee groups, mothers and daughters may share strong bonds, and affiliative interactions are generally between kin (e.g., Jolly, 1998; Taylor & Sussman, 1985). Also like chimpanzees, social groups can sometimes fission, and severe aggression between former groupmates may follow (Hood & Jolly, 1995).

DISPERSAL AND REPRODUCTION

Like other species of lemurs, female ring-tailed lemurs have seasonal receptivity in which all females of a social group (and surrounding groups) are in estrus for only a few hours out of the year (Jolly, 1967). Females will mate first with the group's dominant male and then with other group and immigrant males (Sauther, 1991). Male mate competition with female choice is the rule, although both sexes show increased aggression during the mating and birthing seasons (Jolly, 1967; Vick & Pereira, 1989); however, dominance hierarchies appear to remain intact (Pereira & Weiss, 1991; Sauther, 1991). Male-female aggression is especially high during the breeding season, as is male-male aggression (Jolly, 1967). Aggression between males and females is often instigated by males, but females usually win (Jolly, 1966). This is true even in pair-bonded lemur species (indri: Pollock, 1979). Rates of female-female aggression usually peak during the birth season when the risks of infanticide (e.g., Hood, 1994; Pereira & Weiss, 1991; although see Sauther & Sussman (1993) for possible arguments) and feeding competition are highest (Jolly et al., 1993).

Males typically disperse to new groups during the birthing season, and females must be wary of male infanticide (Pereira & Weiss, 1991), although other females may become responsible for the death of a groupmate's infant. For instance, a mother may be chased and subsequently drop her infant. When she attempts to retrieve her infant, the other group members may chase her away repeatedly (Gould, 1990): without access to its mother, the infant eventually dies. Taylor (1986, cited in Gould, 1990) noted that some infants were injured or killed when a higher-ranking female attacked the infant's lower-ranking mother as the infant was clinging to her body.

During the birth season, males may transfer to new groups in pairs, which they do every 3–4 years (Sussman, 1992). Males transfer to new groups regularly, and this serves as an indication of their low paternal investment—lack of rearing or other infant care. With so little investment in offspring, and without dominance over females, males provide

little agonistic support to females in disputes, and, in return, they receive little agonistic support from females when they are similarly imperiled (Pereira & Kappeler, 1997). This is different from both chimpanzee and baboon intersexual relationships.

As with chimpanzees and baboons, troop fission can occur, and the new and “parent” troops may fight despite their recent positive associations—moving out of the “us” group entails moving into the “them” group. Lemurs appear to have an exceptionally high degree of physical conflict with their formerly same-group female kin (Hood & Jolly, 1995; Ichino, 2006). This emphasizes an *every female for herself* attitude, especially considering the almost complete lack of male agonistic support.

DOMINANCE AND FRIENDSHIPS

Unlike baboons, lemurs are not nepotistic: daughters do not inherit their mother's rank, and mothers do not intervene in conflicts against their daughter, although mothers and daughters may cooperate in aggression against another (as do sisters; see Jolly (1998) for a discussion; Kappeler, 1993a, 1993b; Pereira, 1995). Rank-reversals can occur yearly, especially around the breeding season when all females in the group enter estrus at the same time (Jolly, 1967), and dominance can be circular (i.e., A is dominant to B who is dominant to C who is dominant to A; Pereira, 1995). Females associate preferentially with each other, although generally they have few close friends and show little affiliative behavior outside of grooming (Kappeler, 1993a, 1993b; see also Jolly (1998) for discussion).

Female lemurs are more aggressive than males: females exchange more aggression within and between troops (Jolly et al., 1993; Kappeler, 1999; Sauther & Sussman, 1993; although see Jolly, 1966). Lemurs lack the social repair mechanisms seen in baboons and chimpanzees, such as reconciliation. Reconciliation after conflict is rare (Kappeler, 1993b), as is coalitionary support in terms of recruitment of allies during an attack against another or in terms of retaliation against an attacker, although polyadic attack can occur (see Jolly, 1998, for discussion). Lemurs may target specific individuals, including members of their troop, and repeatedly attack them, sometimes leading to expulsion from the group or death (Jolly et al., 1993; Vick & Pereira, 1989). This occurs in other primate groups as well (see discussion in Sterck et al., 1997).

In summary, female ring-tailed lemurs have the advantage of dominance over males, leading to a decreased threat of male aggression. It has been

suggested that females have this advantage over males because they are in higher need of limited available resources (e.g., food), and their similar size to males makes them good contenders in a fight and because male paternal investment is low (Dunham, 2008). So, the cost of being dominant and non-pair-bonded is raising young without the help of the father. Lemurs are, however, female-bonded, wherein mothers and daughters or sisters share the strongest bonds. Despite this, there are still high rates of female-female aggression within the troop, including targeted aggression that can result in group expulsion for some unlucky females. One issue to consider in making comparisons to humans is that lemurs may be constrained in their social development by their limited ability to identify each other at a distance (as a result of their relatively poor eyesight compared to other primates: Pereira, 1995; see also Kappeler (1999) for discussion). So, they may not be able to monitor the activities of others from a distance, thereby severely limiting their ability to intervene in unsanctioned interactions. Some researchers consider this to potentially limit their social intelligence, but, in considering their many shared societal attributes with savanna baboons and other cercopithecines, their behavior is likely more reflective of their socioecology than of any physiological constraint. The most important lesson to be learned from lemurs is that even when females are the most dominant individuals, female-female aggression and competition are still high, even between kin. An *every female for herself* attitude has its personal benefits, but it also has its societal limits.

Conclusion

Overall, the aim for this chapter was to provide a detailed account of female competition in other primates in order to put into perspective the types of female-female competition that occur in human societies. Within this chapter, I provided a number of examples in which other primates appear to mirror human behavior in a similar situation. The main focus has been concentrated on describing nonhuman primate behavior without making direct comparisons to humans: readers can make those assessments as they continue reading this volume. Rather, this chapter has provided an assessment of the value of aggression, cooperation, and competition from the viewpoint of nonhuman primates with respect to the social and ecological factors they may face. The different social structures and

relationship types that exist throughout the primate order emerge from the intertwining of many factors (e.g., phylogenetic, biological, ecological, psychological), and these factors should be similarly considered in studies of human behavior.

The socioecological constraints on a species have been given notable attention, and much discussion proceeded from this approach. The behavioral repertoires used for aggression and affiliation were explained largely from a socioecological standpoint, and many examples of species that fit the model (or are exceptions) were provided in an attempt to provide a holistic view of the many factors that played into human evolution and the behavioral consequences seen today.

It appears that there is no single solution for female primates to the problem of competition. The discussion in the final section involved the effects of social structure on female choices and, subsequently, what kind of life females could expect in that situation. Excluded from the discussion was an example of monogamy, although there are some clear advantages to it in terms of female-female competition: competition would move from day-to-day battles for resources to solely battling to keep her mate's eye from straying. That is not say, however, that aggression would mostly disappear; instead, it would be used more often in territorial battles and within family unit disputes—given that dominance would be shared between the male and female (e.g., gibbons: Carpenter, 1940).

The question remains: why are humans not as progressive as expected compared to the other primates? There remain many parallels between women and other female primates, many of which I have presented in this chapter. Like women, female primates compete for social status, for access to the best resources, and for the opportunity to raise healthy offspring. More times than not, females are alone in their battles, especially when they fight against their own kin. In few primate species do males provide a supportive role to females outside the realm of physical aggression toward an aggressor—including in the rearing of offspring. So, the answer is simple: it is because humans are subject to the same phylogenetic and environmental constraints as the other primates, and these constraints impose limits on all aspects of social life that are difficult to rise above despite humans' "superior" cognition or morality. However, as humans, women (and men) are supposed to have the advantage of using

contemplative decision making to make the more difficult yet more beneficial choice that leads to the more positive outcome in their social relationships, especially while knowing that the outcomes of certain social situations typically and consistently emerge in specified ways. However, humans have yet to fully illustrate this ability (or “superior” morality), as evidenced by the observation that women in many countries (e.g., Saudi Arabia, Yemen, Syria) do not enjoy the same liberties as women in other societies, and they currently lack many of the rights men enjoy (e.g., right to an education, right to bear witness) or the same protections under law (as in cases of rape or other abuse). In fact, it was only relatively recently that women in some of the most liberal countries (e.g., United States) were granted similar rights to men, such as the right to vote (19th Amendment to the US Constitution in 1920) or equal pay (Equal Pay Act of 1963; Civil Rights Act of 1964; although this is yet to be fully realized in practice). As is the case in many primate species, there is a continued absence of both intra- and intercultural harmony.

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