

COMPARATIVE AND THEORETICAL APPROACHES TO STUDYING SEXUAL SELECTION IN PRIMATES

Charles L. Nunn

Section of Evolution and Ecology, University of California, Davis, California, USA

INTRODUCTION¹

Primates exhibit amazing variation in traits that are likely to have arisen through sexual selection. Many of these traits play a role in visual or chemical communication. The striking countenance of a dominant male mandrill serves as a classic example [Setchell]. Scent marking in callitrichids is another form of communication that may be sexually selected [Heymann], while dichromatism is a complicated phenomenon that is likely to be influenced by many factors, including sexual selection [Gerald]. Other sexually-selected traits are behavioral, including female intrasexual competition for mates [Saltzman; Vervaecke et al.; Heymann], infanticide by males [Crockett] or females [Digby, 1995; Saltzman], and cryptic female choice [Reeder]. Finally, sexual selection itself may be influenced by the competitive regime, as mediated, for example, by demographic factors [Strier; Watson et al.].

Primatologists have made great strides in understanding sexual selection in primates. The chapters in this book, which I summarize here, highlight many of these exciting advances, while also illustrating the shift from descriptive accounts of primate biology to tests of hypotheses that have arisen from advances in mainstream behavioral ecology [Shahnoor & Jones]. One chapter in this volume, for example, investigates the potential for applying new models of reproductive skew to understand patterns of sexual selection in primates [Hager]. Skew models are one of the most influential conceptual frameworks to emerge in the last decade of behavioral ecology research [Clutton-Brock, 1998; Reeve et al., 1998; Johnstone, 2000]. Figure 1 shows the number of citations for “reproductive skew” in a search of ISI’s Web of Science for the years 1994 to 2001. When “primate” is included as an additional search term, however, no hits are obtained, illustrating the lack of attention by primatologists to this conceptual framework. Similarly, searching for the phrase “reproductive skew” produced only two

¹ Authors’ names cited without dates refer to chapters in the present volume.

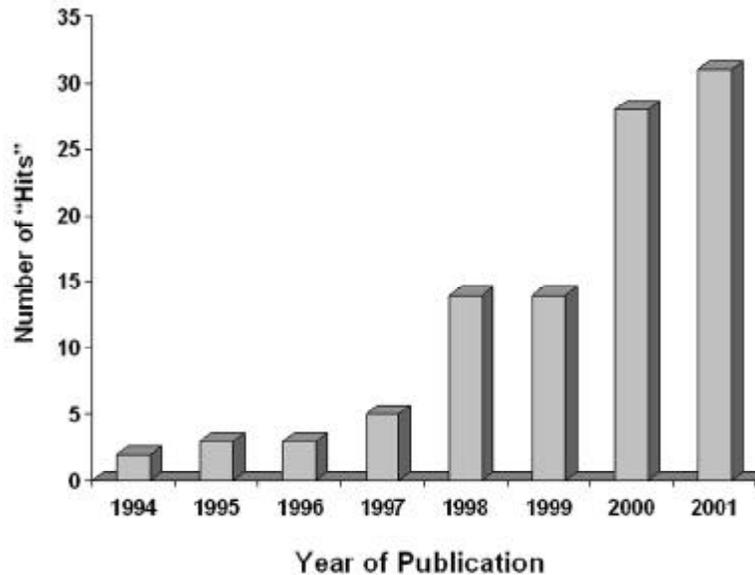


Figure 1. Research Interest in Reproductive Skew Models. Results are from searching for the term "reproductive skew" in ISI's Web of Science (<http://isi2.isiknowledge.com>) for the years 1994-2001.

"hits" on the most comprehensive compilation of primate literature on the World Wide Web (Primate Lit, <http://www.primatologist.wisc.edu/pin/>). One possible explanation for the lack of interest by primatologists is that the skew framework is not helpful for understanding primate biology. Counter to this explanation, however, Hager makes a compelling case for applying skew models to understand sexual selection and variation in reproductive output in primate societies [see also Palombit].

The present book also highlights some of the ways in which primatology has influenced behavioral ecology more generally. Primatological studies of sperm competition and cryptic female choice have influenced other areas of biology, particularly in path-breaking comparative studies of testes size [Harcourt et al., 1981, 1995] and the evolution of male and female genital morphology [Dixson, 1987, 1998; Dixson & Mundy, 1994]. The chapter by Reeder highlights the many fascinating ways in which female primates may bias paternity after copulation. Despite the influential role of primate comparative studies in understanding post-copulatory mate choice, however, remarkably little is known about the mechanisms mediating such processes in primates, as compared to other animals, such as insects [Eberhard, 1996]. Having access to a tractable experimental system obviously helps to understand complex physiological phenomena, especially phenomena that require invasive work on the female reproductive tract and biased sperm usage. Hence, the slow life history that characterizes primates

has limited research on cryptic female choice. The 17 potential examples of cryptic female choice in primates summarized by Reeder will serve as a useful guide for future research on this important topic.

Many chapters in this volume vividly illustrate the power of integrating proximate and ultimate questions. Proximate questions examine the physiological basis of a behavioral trait and its developmental basis, while ultimate questions investigate the adaptive function of a trait and its evolutionary history. Thus, Saltzman examines proximate and ultimate factors related to female reproductive competition in common marmosets. She notes that suppression yields obvious reproductive benefits for dominant individuals (an ultimate question), but the proximate mechanisms by which suppression is achieved differ among species, producing diverse patterns in interspecific comparisons. Similarly, a thorough understanding of alternative reproductive strategies in mandrills, or bimaturation in orangutans, requires knowledge of the physiological basis for different male morphs [Setchell; see also Gerald].

It is surprising how little is known about the most basic aspects of primate sexual selection. For example, what features do female primates prefer in their mates, and why [Andersson, 1994]? Even in mandrills, we lack conclusive evidence that females choose more colorful males [Setchell; see also Jones & Agoramoorthy; Robbins; Bergman & Beehner]. Why are some species dichromatic, and why do males more often exhibit the dark form of biphasic dichromatism? The chapter by Gerald provides a constructive framework for investigating these issues by classifying dichromatism into different categories. But even with this framework, interspecific patterns are not clear-cut and will require further comparative research. How does female choice interact with male-male competition? Some authors have proposed that the two aspects of sexual selection are linked, with female preferences for particular male attributes corresponding to traits used by males in intrasexual competition [Berglund et al., 1996; see also Setchell, for interaction of inter- and intrasexual selection]. Without detailed information on the signals used in mate choice and male intrasexual competition, however, it is impossible to examine the evolution of male traits and female preferences in primates. Finally, is female competition for mates as important as female competition for resources? And, if so, do males exhibit choice of mating partners? Such a reversal of sexual selection has been proposed to account for the evolution of exaggerated sexual swellings in catarrhine primates [Pagel, 1994], although this hypothesis remains controversial [Nunn et al., 2001; Zinner et al., 2002, in press].

Two broader conceptual frameworks are likely to be important in future investigations of sexual selection in primates and provide the structure for the rest of this chapter. First, understanding sexual selection in primate societies requires a dynamic perspective that investigates the correlation between male and female traits. Thus, rather than viewing sexual selection as an equilibrium or even static condition, it should be examined as a dynamic coevolutionary process that is rooted in conflict, or *antagonistic coevolution* [Rice, 1996; see also “conflict theory” in Shahnoor & Jones]. Second, it is critical to place sexual selection research within a socioecological framework that involves explicit comparison of different species and also investigates the suites of characters that are likely to influence (and be influenced by) sexual selection. Con-

sider, for example, the importance of life history traits in sexual selection research. The ratio of the duration of lactation to gestation alters the risk of infanticide by males [van Schaik, 2000], while body mass correlates with reproductive opportunities through its effects on interbirth interval and other traits [Mitani et al., 1996]. In what follows, I discuss insights provided by antagonistic coevolution and comparative primate socioecology in greater detail.

SEXUAL SELECTION AND ANTAGONISTIC COEVOLUTION

Intrasexual competition, such as sexually-selected male-male competition for mates, clearly involves conflict. But it is less often appreciated that sexual selection also involves conflict between the sexes. Intersexual conflict arises because males are not passive participants in female choice, but instead are expected to exert pressure to increase the chances that a female will mate with him. Smuts and Smuts [1993] identify such behaviors as sexual coercion, defined as male use of force (or threat of force) that functions to increase a female's chances of mating with the coercive male, at some cost to the female. By this definition, sexual coercion includes a variety of male behaviors, from the aggressive herding of females observed in hamadryas baboons [Kummer, 1968] and gorillas [Robbins,], to the forced copulations observed in orangutans [Mitani, 1985a]. Sexually-selected infanticide [e.g., Crockett; Palombit] also counts as a form of sexual coercion [Smuts & Smuts, 1993]. Because these male behaviors are costly to females, counterstrategies are expected [Smuts & Smuts, 1993].

Along with sperm competition and cryptic female choice, intersexual conflict is an area in which primatology has contributed to mainstream biology [Hrdy, 1974; Smuts & Smuts, 1993; Clutton-Brock & Parker, 1995]. But recent years have seen a flood of research activity on antagonistic coevolution in non-primate biological systems [Rice, 1996; Gowaty, 1997; Holland & Rice, 1998; Arnqvist & Rowe, 2002a, b; Chapman et al., 2003], whereas research progress has been slower in primatology. Antagonistic coevolution may even play a role in speciation in insects [Arnqvist et al., 2000; also see Gavrilets, 2000], a question that is of significance to primate studies [Bergman & Beehner; Froehlich]. Thus, it has become increasingly clear that important gaps remain in our understanding of intersexual conflict in primates, and primatologists would benefit from considering the conceptual frameworks that have been developed to understand this phenomenon in other organisms.

The term "antagonistic coevolution" captures the idea that male and female interests are inter-related, since each sex requires the other for reproduction. But conflicts of interest between the sexes result in antagonistic coevolution, with female counterstrategies arising in response to male strategies at manipulating females, male counter-counterstrategies arising in response to female counter-strategies, and so on, in cycles similar to those observed in host-parasite coevolution. As stated by Chapman and Partridge [1996, p 190], "...in an apparently unchanging sexual interaction males and females may be running frantically to stand still." The cyclical nature of sexual selection and intersexual conflict is under-appreciated in primate sexual selection, which tends to focus conceptually at equilibrium conditions in broad phylogenetic scales or at a single generation in field studies on primate social groups [see also Strier].

Several exciting developments have emerged to examine sexual selection as a dynamic process involving antagonistic coevolution [Chapman et al., 2003]. Many of these conceptual frameworks offer promise for understanding sexual selection in primates [see also Shahnoor & Jones; Jones & Agoramorthy]. For example, consider the **chase-away model** [Holland & Rice, 1998]. This model of sexual selection begins with a pre-existing sensory bias – a trait that increases a male’s attractiveness to females, such as bright or contrasting coloration. This trait induces females to mate with individuals that express the trait, and to mate more often than is optimal given the benefits received. As a result, selection favors female counterstrategies (resistance) to the male trait. Males are therefore selected to express the trait in increasing degrees to overcome the female resistance threshold, or to evolve new traits that exploit other sensory biases in females. This model produces a dynamic series of moves and counter-moves, and thus fails to reach a long-term, stable equilibrium. Cycles of coevolution occur as males attempt to increase their attractiveness to females while females evolve further resistance to male attempts at exploiting female sensory biases. One consequence of the chase away process, however, is that at any point in time males will be burdened with a variety of costly traits resulting from their attempts to stimulate females to mate.

How might the chase-away model apply to primates? Most obviously, the model may help to understand male traits that stimulate females to mate. For example, perhaps the colors of the male mandrill’s face exploit sensory biases in females for the colors of fruit? The chase-away model also may apply in counterintuitive ways, including in the evolution of exaggerated sexual swellings [Zinner et al., in press]. In species in which social groups contain multiple females and males, females may benefit from mating promiscuously with all males in the group. In this way, females reduce the risk that any given male will commit sexually selected infanticide [van Schaik et al., 2000], since males that mate with a female are less likely to kill her dependent offspring [Crockett; Palombit]. The exaggerated swellings found in Old World primates, especially those in multimale-multifemale groups, may therefore represent female attempts to overcome male resistance to mate, with the swelling operating on existing male biases for signals of fertility [e.g., small swellings present in ancestral primates that indicate timing of maximum fertility; see Nunn, 1999a]. Under this hypothesis, exaggerated swellings are a form of antagonistic coevolution, expressed in females as a response to threats of male sexual coercion involving sexually-selected infanticide [Zinner et al., in press].

In the remainder of this section I consider two ways that primatologists can apply the conceptual framework of antagonistic coevolution to understand sexual selection in primates – by using new perspectives rooted in phylogenetic comparative methods and by implementing computer simulations to better understand intersexual dynamics in biological systems [see also Chapman et al., 2003].

Phylogenetic Approaches to Studying Intersexual Conflict

To illustrate how coevolutionary dynamics can be explored in a phylogenetic context, consider comparative research conducted by Arnqvist and Rowe [2002a] on 15 congeneric species of water striders (*Gerris* spp.). In this system, mating is often characterized by violent struggles between males and females, with males preferring to

mate more frequently, and for a longer duration, than females. Males possess morphological adaptations to overcome female struggles, including exaggerated clasping genitalia, while females possess counter-adaptations to reduce male efforts to successfully “clasp” them, including abdominal spines. The expression of these male and female traits varies across species [Arnqvist & Rowe 2002b].

Arnqvist & Rowe [2002a] predicted that intersexual arms races will often lead to a stalemate, with increases in male armaments offset by increases in female defenses. When examining patterns across species, they therefore predicted a strong correlation between male arms and female defenses [Arnqvist & Rowe, 2002b]. However, antagonistic coevolution is expected to be dynamic. Thus, in rare circumstances throughout evolutionary history, one of the sexes will express traits involved in intersexual conflict to a greater degree than expected based on the trait in the other sex, perhaps due to varying ecological conditions. When differences in armaments and defenses exist, Arnqvist and Rowe [2002a] predicted that the sex with greater expression of the trait will win a greater proportion of mating interactions, as measured quantitatively by pre-mating and mating behaviors [see Gavrillets et al., 2001; also see Rice, 1996, for an experimental test of a similar process in fruit flies]. Thus, when females have the relative advantage, the average mating duration should decline, while it is predicted to increase when males possess the advantage.

In line with these predictions, Arnqvist and Rowe [2002a] found that variation in mating behavior across species was unrelated to the absolute level of armament, as expected if males and females have, in general, reached a stalemate in most lineages on the phylogeny. But relative degree of armament was able to account for significant variation in pre-mating struggles, male struggle success, female mating activity, and female mating rate. Thus, relative differences in morphological traits that function in intersexual conflict were correlated with the behavioral expression of intersexual conflict.

Arnqvist and Rowe [2002a] also examined the degree to which the behavioral and morphological variables were correlated with phylogeny [Gittleman & Kot, 1990; Blomberg & Garland, 2002]. Given that antagonistic coevolution produces cyclical evolutionary dynamics, with rapid, bidirectional changes in intersexual conflict, Arnqvist & Rowe [2002a] predicted that traits involved with intersexual conflict would show a weak correlation with phylogeny. Using a phylogenetic method that examines the association between a set of traits and a phylogenetic tree [Gittleman & Kot 1990], Arnqvist & Rowe [2002a] found that traits involved with intersexual conflict were generally uncorrelated with phylogeny. This result is consistent with periods of escalation and de-escalation occurring throughout the evolutionary history of a clade.

Comparison is also crucial for understanding differences in sexual selection among major mammalian clades, or even more broadly. For example, we know little about the costs of reproductive conflict at a physiological level in primates, although Reeder points out many physiological processes that may be involved with cryptic female choice. This physiological conflict can be costly to females in other taxa. In insects, for example, male products in seminal fluids may reduce the propensity for females to remate with another male at a later time [Eberhard, 1996], and, after cumulative doses,

these products can even reduce female survival [Rice, 1996]. As another example, comparison helps to place intersexual conflict in an ecological context. Thus, in water striders, the intensity of intersexual conflict varies within species according to population density, demography, food availability and predation pressure [reviewed in Rowe et al., 1994; see Strier regarding the demographic context of sexual selection in primates]. Indeed, these temporally varying ecological pressures may be partly responsible for the cyclical dynamics revealed in Arnqvist and Rowe's [2002a] comparative study across species.

Finally, we know little about the spatial distribution of intersexual conflict within species. Given the dynamic nature of the coevolutionary process at different geographical scales [Thompson, 1994], it seems reasonable to expect that patterns will vary among primate populations according to ecological differences, the evolutionary history of populations, and the opportunities for dispersal between populations that differ in patterns of intersexual conflict. Thus, for some of the better studied species of primates, it may be possible to investigate the dynamics of intersexual conflict within-species [Chapman et al., 2003], specifically by using a comparative approach that takes into account geographical and ecological proximity [e.g., Smouse & Long, 1992] rather than phylogeny.

Simulation Models of Antagonistic Coevolution

A second means to investigate antagonistic coevolution is by using theoretical modeling, in particular, through computer simulation of an agent-based model, in which individuals (agents) interact over a series of moves to obtain some goal [Kohler & Gumerman, 2000]. There are two main advantages to studying antagonistic coevolution with an agent-based model. First, by handling multiple parameters of interest, an agent-based model can provide more flexibility than analytical approaches, such as game theory, in which multiple players and multiple variables can quickly spiral beyond understanding. Second, simulation is better able to reveal cycles of coevolutionary dynamics that occur in complex systems, whereas analytical approaches tend to focus on identifying equilibria. As discussed above, phylogenetic approaches suggest that antagonistic coevolution is a dynamic process in biological systems, yet it is difficult to study these processes directly.

One promising simulation approach is based on genetic algorithms (GA). Use of GA occurs within an agent-based model, in which individual entities compete with one another in rounds of the simulation to earn points based on parameters set by the user. Behavior of each individual is determined by "chromosomes," usually composed of a series of discrete values (e.g., 0's and 1's) that are translated by algorithm into particular behavioral actions, including responses to the actions of other individuals in the simulated population. For example, GA's have been used to study the evolution of cooperation in the Prisoner's Dilemma [Axelrod, 1987]. In this application, individual agents started off with random values corresponding to cooperation or defection (chromosomes consisting of C's and D's), with behavior determined based on the last three rounds of interaction with another individual in the simulation. Points were assigned based on a standard Prisoner's Dilemma scoring matrix, and agents that scored higher

points at the end of the simulation were better represented in the next round of simulation, in effect leaving a greater number of “offspring.” Variation was produced through mutation (changing, at random, C’s to D’s, and vice versa) and recombination (two relatively successful individuals exchanged a randomly-determined portion of their chromosomes). After starting with random strategies, Axelrod [1987] found that a strategy that resembled tit-for-tat [Axelrod & Hamilton, 1981] had evolved by the end of most simulations.

To illustrate the application of an agent-based model to antagonistic coevolution, I constructed a GA that addresses the question: How can a female entice a male to mate, given that other females in the group may be cycling and mating effort is costly for males? In a group of 18 “females” and 6 “males,” each individual was given two chromosomes that determined their interactions with other individuals during the course of the simulation. Chromosome 1 coded female swelling size in relation to the timing of ovulation, with swelling size ranging from 1 to 24 (coded as a binary variable using strings of 0’s and 1’s). All females began the simulation with chromosomal configurations such that a relatively small swelling (size 4) indicated the day of ovulation, but, otherwise, females exhibited the smallest possible swelling (size 1). Thus, rather than start with random values, as in the approach discussed above for the Prisoner’s Dilemma, I am making use of phylogenetic information to set the “ancestral state” of a small, precise swelling [Nunn, 1999a]. The simulation, therefore, investigates the process of evolution during shifts from single-male (with discrete, small signals of ovulation) to multimale-multifemale mating systems, which are characterized in real primates by a greater diversity of ovulatory signals [Nunn, 1999a; van Schaik et al., 1999]. Importantly, swellings larger than size 4 produce costs that are proportional to the size of the swelling. These costs were translated into a lower probability that a female conceives.

Chromosome 2 coded male behavior in relation to swelling size and also determined the probability that a male commits infanticide, based on the length of time that has passed since he last mated with a female. Males began with a preference for swellings of size 4. As in the chase-away model [Holland & Rice, 1998], at the start of the simulation they possessed a pre-existing bias for swellings that exceed this ancestral value. Three male behaviors were possible in relation to female swelling size. Males could ignore a cycling female, they could consort with the female for an entire day and prevent other males from mating with her (ancestral condition for swelling size >4), or they could mate opportunistically with the female and, therefore, possibly mate with other females on that same day. The costs of consorting were proportional to the number of other males in the population that were interested in mating with the female. Individuals were scored based on the number of offspring that survived to independence after a period of gestation and lactation, during which infanticide can occur. Individuals with higher scores contributed more offspring to the next generation of the simulation, and mutation and recombination occurred among these individuals.

The large number of parameters, as well as strong frequency-dependent selection, produced a remarkably wide range of results, but several interesting patterns emerged. Swelling size increased rapidly in the simulations (Figure 2a). In general, the increase in

swelling size at the time of ovulation corresponded to male preference for larger swellings: when females produced relatively larger swellings at the time of ovulation, males generally preferred larger swellings (values greater than 0 in Figure 2b & 2c). However, this coevolutionary pattern was not consistent in all generations of the simulation, and the end results often differed among runs of the simulation. In Figure 2c, for example, the shaded rectangle indicates one of several time periods when mean swelling size at the time of ovulation increased, but male preference for large swellings actually decreased, eventually leading to a preference for small swellings. One plausible explanation for such a pattern is that the costs of producing a larger swelling reduced the probability that a female with a large swelling would conceive, making it advantageous for males to prefer females with smaller swellings at ovulation. It is also remarkable that in some rounds of the simulation, swelling size indicated ovulation prominently (Figure 2c, with swelling size larger at ovulation), while in others the difference in swelling size throughout the cycle was slight (Figure 2b, swelling size was only slightly larger at first and became negative in later generations, ending with ovulation indicated by a smaller swelling).

I also compared output from five runs of the simulation when infanticide was allowed, to five runs when infanticide was eliminated by setting the probability of infanticide equal to zero. Consistent with the hypothesis that intersexual conflict produces cycles of coevolutionary change, infanticide tended to produce situations in which male and female interests were more often misaligned, as indicated, for example, when males expressed greater interest in larger swellings but ovulation was associated with smaller swellings. Thus, Figure 2d shows that when infanticide was allowed, the proportion of time that male behavior and female signals were mismatched increased ($F_{1,148}=7.15$, $P=0.008$, two-tailed; see figure legend for details of analysis).

In summary, the simulation results in Figure 2 reveal several interesting patterns relevant to antagonistic coevolution in primates. First, male interest and female signals will tend to coevolve, but not always (Figure 2b & 2c). Second, coevolution can be cyclical, with major changes occurring at some times, but relatively more stable periods at others (e.g., generations 160-250 in Figure 2c). Third, intersexual conflict can increase this cyclicity, with a corresponding decline in the coevolution of female ovulatory signals and male responses to these signals. Finally, an important point to re-emphasize is that agent-based modeling focuses on dynamics rather than equilibria [Kohler, 2000]. Although general patterns, such as the one shown in Figure 2d, can be revealed by simulations, understanding the dynamics of such patterns, as revealed in Figure 2a-2c, will often provide additional insights.

How can we link the output from simulations, such as the one described here, to empirical patterns in the real world? One approach is to generate competing situations in the simulations (e.g., by varying the relative risk of infanticide [Figure 2d]), identify consistent differences in the output for these different parameters, and then test whether populations of real primates differ in the way predicted by the model. With strong statistical support for the similarity of real-world and simulated data, it will be possible to make inferences about coevolutionary processes taking place in primate populations. An important step in this research will involve spatially-explicit simulation mod-

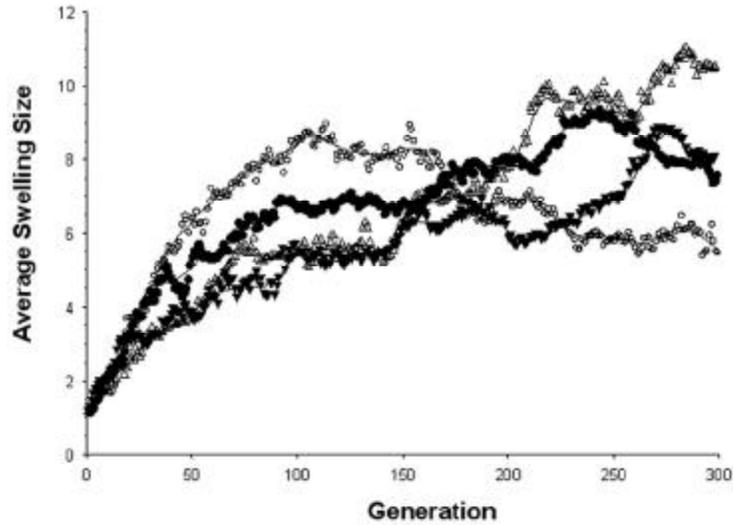


Figure 2a. Simulation of Female Swellings and Male Interest Using a Genetic Algorithm. The computer program was written in MATLAB (vers. 6.5, Natick, Massachusetts). Plot shows average swelling size over four runs of the simulation, starting from the initial condition in which females exhibit a small swelling at the time of ovulation (size 4), but no swelling at other times in the cycle. Each run of the simulation is shown with a different symbol. Because swellings can range in size from 1 to 24, the expected median under random drift is 12.5. Swelling size increases throughout the simulation, but in all generations remains below the expected median, indicating selection against extremely large swellings.

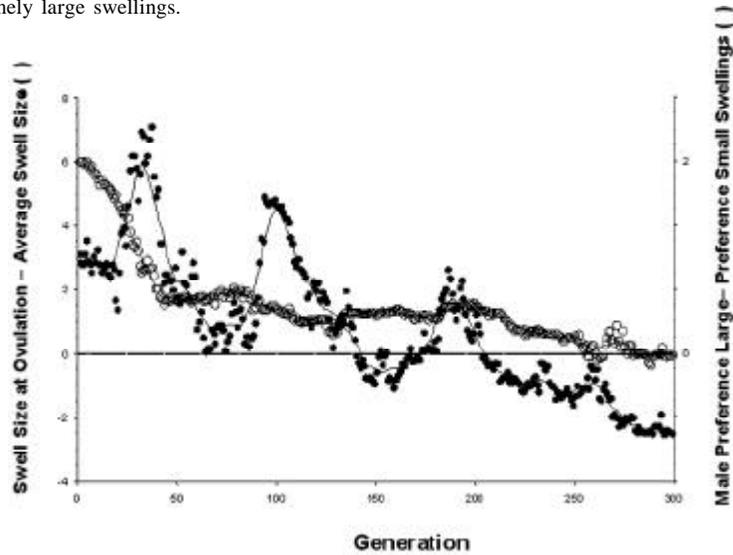


Figure 2b. In this run of the simulation, swelling size at ovulation relative to other times declines as the simulation proceeds, but it shows a cyclical pattern. Thus, in the final generations, females indicate ovulation with a smaller swelling, as compared to swelling size at other times in the cycle. Male interest in large swellings shows a correlated decline.

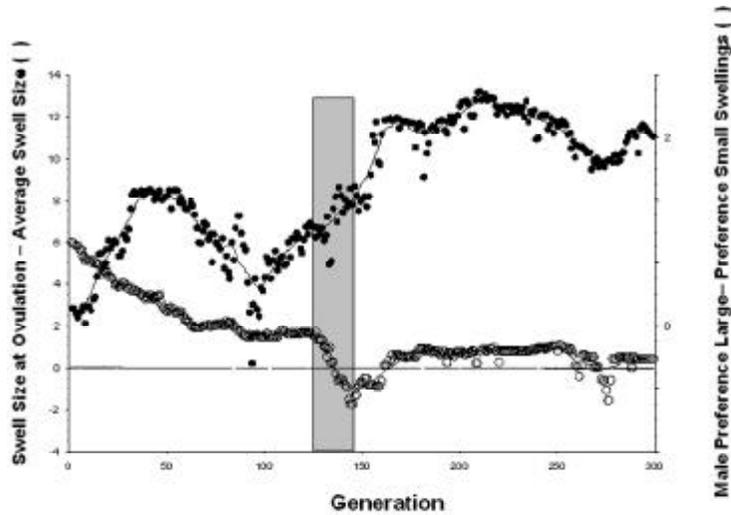


Figure 2c. This run of the simulation showed a pattern opposite to that shown in panel b, with swelling size at ovulation increasing relative to average swelling size. The shaded bar indicates one of several time periods when relative swelling size at ovulation increases, but male interest in large swellings decreases. Male interest scores show a later dip that corresponds to a decline in relative swelling size, but ovulation is still indicated with a larger swelling.

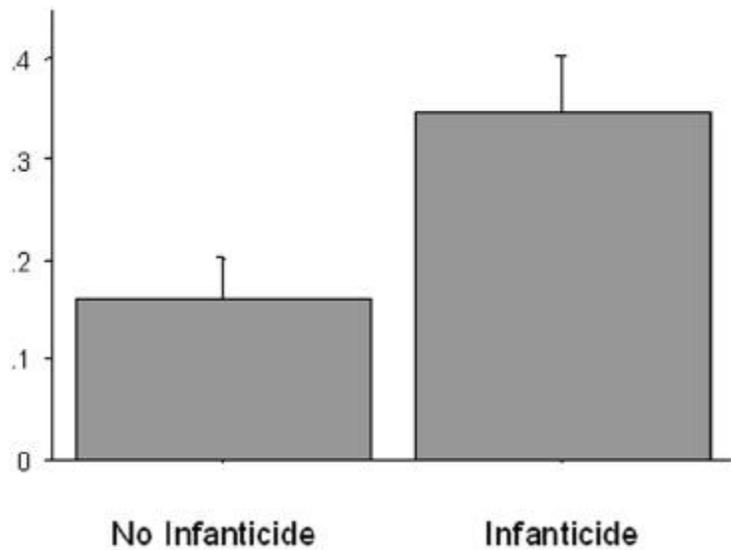


Figure 2d. Proportion of time that male and female signals are “mismatched,” with males preferring a larger swelling but females producing a smaller swelling at ovulation, or vice versa. Because data points are serially correlated, this analysis used data points separated by 20 generations, which reduces problems of pseudo-replication.

els of multiple social groups connected by gene flow (dispersal), rather than the focusing on a single group. Such a model is possible, but will take large amounts of computing power. For example, in the simulations described above, with 300 generations and 24 individuals, each simulation required approximately 90 minutes of processor time. Simulating 10 populations with, say, 100 groups each, and allowing for dispersal between groups, would require a different computing approach to be efficient (e.g., programming for parallel processors).

COMPARATIVE PRIMATE SOCIOECOLOGY

Socioecology has played a dominant role in understanding primate social systems, and comparison of multiple species forms the foundation of primate socioecology [Crook & Gartlan, 1966; Crook, 1970, 1972; Clutton-Brock & Harvey, 1977; Lee, 1999; Harcourt, 2001]. The standard socioecological model proposes that risks and resources determine the distribution of females in space and time [Emlen & Oring, 1977; Nunn, 1999b]. The resulting distribution of females influences the male competitive regime, with the primary goal of males in this model to maximize their number of copulations with potentially fertile females. Thus, the environment is viewed as determining female strategies, which then influence male strategies (Figure 3). As noted above, a major feature of comparative primate socioecology involves consideration of suites of variables, including life history traits, ecological traits, and social traits.

Several chapters in this volume adhere to this basic socioecological framework. For example, Heymann places his study within a socioecological context at the start of his chapter, while Hager discusses a variety of socioecological traits, such as dispersal and resource competition, that may drive patterns of reproductive skew [see also chapter by Robbins]. Thomsen et al. test hypotheses by using interspecific comparisons, while Bicca-Marques explicitly considers foraging behavior as related to sexual selection. Other chapters in this volume challenge the basic assumptions of the socioecological model in provocative ways that may lead to new insights. For example, Strier notes that the standard socioecological framework is turned upside-down when females transfer between groups. It certainly is true that female dispersal will be a major influence on adult sex ratios in this case. But such a pattern is also consistent with indirect mate choice, in which males defend access to resources to attract females [i.e., resource defense polygyny; Clutton-Brock, 1989]. In fact, this form of polygyny is considered to conform to basic expectations of the model in Figure 3 [Emlen & Oring, 1977]. Although resource defense polygyny is thought to be relatively rare among primates, a recent paper argued that this form of indirect mate defense has been understudied and is most likely to occur when females can transfer between social groups [Fashing, 2001].

Comparison is fundamental to socioecology, and several chapters in this volume take an explicitly comparative approach to investigate aspects of sexual selection. For example, Gerald compiled data on dichromatism for a wide range of primate species. The next step is to make sense of this variation by testing *a priori* hypotheses in a rigorous phylogenetic context [Nunn & Barton, 2001]. Only one chapter in this volume used phylogenetic comparative methods to test hypotheses. Thomson et al. applied

The Socioecological Model

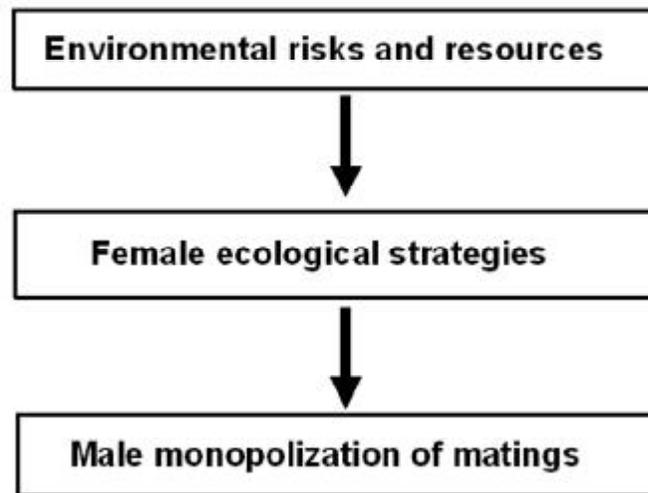


Figure 3. The Socioecological Model. In the standard socioecological model, risks and resources determine female ecological strategies, including their distribution in space and time (i.e., the timing of reproduction). The distribution of females then determines male strategies, particularly monopolization of fertile females.

methods based on independent contrasts [Felsenstein, 1985] to test the function of masturbation in nonhuman primates. It was unclear exactly how the method of independent contrasts was applied to the data analyzed by Thomson et al., as this method is more suitable for continuous data than for the discrete data analyzed by the authors [see Harvey & Pagel, 1991; Nunn & Barton, 2001]. Nonetheless, phylogeny is essential to the comparative approach that forms the basis for primate socioecology, for it is only through comparison that differences in social and mating systems come into sharp relief. Indeed, many features of primate socioecology are correlated with phylogeny [Di Fiori & Rendall, 1994].

When discussing comparative studies, it is important to remember that comparative studies are only one line of evidence that can be used to test hypotheses. Ultimately, the most will be gained by testing hypotheses using multiple lines of evidence that include comparative, observational, and experimental approaches. Particular levels of analyses are better suited for some questions than others; hence, for these questions, we will be faced with a preponderance of one kind of data. For example, Strier suggests that comparative evidence has been over-represented in studies of sexual selection. Whether or not this is true – for example, many field studies have been conducted on sexual selection in primates [e.g., Cords, 1984; Janson, 1984; Mitani,

1985b; Smuts, 1987; Pereira & Weiss, 1991; Soltis et al., 1997] – it is true that the demographic factors raised by Strier are best studied using population-level data. What is needed is a fuller appreciation of the extent to which field, laboratory, theory, and comparative research complement one another rather than compete for the status of the “best” test of a hypothesis. Indeed, at the most basic level these seemingly different approaches are inter-related. For example, rigorous comparative studies would be impossible without high quality information provided by field researchers. Theoretical research, such as the simulations discussed above, should be used to guide hypothesis generation at all levels.

CONCLUSIONS AND PROSPECTS

As noted by Shahnoor and Jones, studies of primate sexual selection have increased markedly in the last three decades. Despite increased attention, however, some aspects of sexual selection are well-documented in primates, whereas others are under-represented. For example, in Table 6.A of Andersson [1994], which reviews studies of sexual selection in relation to quantitative characters, no primates are listed as having traits demonstrated to be involved in female choice. Compare this to birds in the same table! A critical issue for future research is to identify whether this gap is biologically interesting because it is real (i.e., female choice for quantitative characters is rare in primates compared to other animals) or because the topic has been studied insufficiently in primates. If the pattern is real, it may result from intense male intrasexual competition and intersexual conflict in primates, which may have limited opportunities for female choice. Or, perhaps the long-term relationships of primates have reduced the need for indicators of quality (Figure 4)?

Competition among females is fundamental to most models of primate socioecology [Wrangham, 1980; van Schaik, 1989; Sterck et al., 1997]. Thus, it is not surprising to see chapters on female intrasexual competition in a book about primates, and it should not be surprising that primatologists have investigated many interesting questions involving female-female competition as it relates to sexual selection [Watson; Saltzman; Vervaecke et al.; Reeder; Heymann]. Nonetheless, important work remains in the study of female mating competition. For example, Domb and Pagel [2001] proposed that female mating competition can account for the evolution of exaggerated sexual swellings in female primates [Pagel, 1994]. However, Zinner et al. [2002] noted that Domb & Pagel [2001] investigated only one of three levels at which sexual swellings may play a role in primate societies. First, swellings may reveal variation in the probability of ovulation over the course of a female’s cycle [Nunn, 1999a]. Second, swellings may indicate variation across cycles in a single female; in some cycles, a female may be more likely to ovulate than in other cycles [e.g., M. Emery, personal communication]. Finally, swellings may indicate differences in quality among females [Pagel, 1994], as tested by Domb & Pagel [2001]. Teasing apart these different hypotheses first requires clarifying the problem using theory, and second, finding an appropriate model system in which hormonal, behavioral and morphological data can be acquired in sufficient quantity and quality to discriminate among the hypotheses [Zinner et al., 2002].



Figure 4. The extravagant pelage and color of male and female golden lion tamarins (*Leontopithecus rosalia*) may function in social or sexual signaling. However, intersexual and intrasexual communication that may have evolved by sexual selection, social selection, and/or sexual conflict remains undemonstrated in this and numerous other primate species. (Photo by Jeffrey French).

Communication is an important product of sexual selection, resulting, for example, in the elaborate plumage of the peacock, or the parallel walk of red deer. As noted with the evolution of sexual swellings, much remains to be learned about communication that occurs in the context of primate sexual selection. Great opportunities exist for understanding these patterns in a phylogenetic context. For example, in the case of exaggerated sexual swellings, it is interesting that a typically female trait apparently has been co-opted for use by male primates – juvenile red colobus males exhibit a pseudo swelling [Wickler, 1967; Kuhn, 1972], while adult male hamadryas baboons also reveal a large red patch of skin on their rumps, producing a visual display with similarities to female sexual swellings [Dixson, 1998]. The functions of this male trait likely differ in the different mating and social systems in which it is found.

Female sexual behavior has emerged as the primary counterstrategy used by females to reduce the costs imposed by sexual selection [Hrdy & Whitten, 1987; Dixson, 1998; van Schaik et al., 1999]. As examples, mating promiscuity is thought to reduce the risk of infanticide [Hrdy & Whitten, 1987; van Schaik et al., 1999], mating synchrony has been proposed to reduce the ability of a single male to defend access to a group of females, resulting in multi-male groups [Nunn, 1999b] to reduce infanticide or predation risk [van Schaik & Hörstermann, 1994], and orgasm may function in sperm retention [see Reeder]. Patterns of estrous synchrony are likely to be important for future studies of primate sexual selection. For example, if female intrasexual competition for mates proves to be important, it should be revealed with increased asynchrony of female cycling, as demonstrated quantitatively for ring-tailed lemurs [Pereira, 1991]. In contrast, however, estrous synchrony is reported more often in the literature than asynchrony, and mainly in captive studies [e.g., Wallis, 1985; French & Stribley, 1987; Zinner et al., 1994].

In future research, genetic data may provide a wealth of information for better understanding patterns of sexual selection in primates. For example, studies of genetic variation, as coded in MHC loci, may reveal important mate choice patterns in free-

ranging nonhuman primates. Genetic variation also contains the signature of intersexual conflict in the rapid evolution of reproductive proteins [Swanson & Vacquier, 2002]. Genetic data is becoming increasingly available (e.g. GenBank, <http://www.ncbi.nlm.nih.gov/>), providing potentially exciting integration of primatology with the bioinformatics revolution.

Finally, new theoretical approaches are needed to reinvigorate the study of sexual selection in primates. I provided an example using GA to investigate reproductive signaling in the context of intersexual conflict. Although other analytical and simulation approaches are available [Maynard Smith, 1982; Hammerstein & Parker, 1987; te Boekhorst & Hogeweg, 1994], GA could be used to investigate many of the questions raised in this volume, including alternative reproductive strategies [Jones & Agoramoorthy; Setchell], infanticide [Crockett; Palombit], and female mating competition [Saltzman; Vervaecke et al.; Heymann]. Consider, for example, reproductive skew [Hager]. In the GA described above, six males competed for access to 18 fertile females. Hence, the expected proportion of reproduction by the top two males is 33% if reproduction is spread evenly among individuals (no skew). The simulation output reveals striking skew among males, however, with the top two males responsible for 55.5% of reproduction on average across all generations. This observed value is significantly larger than expected ($t_{14}=10.7$, $P<0.0001$, using only every 20 data points to reduce pseudo-replication and a one-tailed test because the pattern, by definition, can only go toward more skew when comparing the two most successful males to average expected reproduction of all males). Females exhibit less striking reproductive skew (observed=13%, expected=11%), although results approached significance in a one-tailed test ($t_{14}=1.70$, $P=0.055$).

In conclusion, primatology is often viewed as a poor stepchild to evolutionary biology, but is this the case? As discussed above, studies of primates have prompted theoretical and empirical investigation of sexual selection in other systems, particularly studies of sperm competition [Harcourt et al., 1981, 1995], genitalic variation [Dixson, 1987; 1998, Dixson & Mundy, 1994], and intersexual conflict [Smuts & Smuts, 1993]. However, this chapter also revealed that primatology tends to lag behind other fields when new conceptual frameworks emerge, for example in studies of reproductive skew [Hager], the physiological mechanisms underlying cryptic female choice [Reeder], and recent advances in understanding intersexual conflict [Chapman et al., 2003]. In addition to the detailed studies of sexual selection in primates, the exciting aspects of this volume are the new directions that are provided as roadmaps for future research. With detailed information on behavioral variation at multiple sites, primatologists are uniquely positioned to make advances in understanding geographical variation in antagonistic coevolution and its relationship to ecological factors. We are also well-positioned to explore patterns of reproductive skew in male and female primates, and laboratory research is likely to reveal interesting patterns of cryptic female choice and its underlying mechanisms [Reeder]. Finally, and more fundamentally, future research is likely to reveal the factors that influence mate choice and patterns of female mating competition, both of which are critical for better understanding patterns of primate sexual selection.

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Dr. Charles Nunn studies mammalian social evolution, which he pursues using phylogenetic comparative methods, theoretical modeling, and field work. His current research focuses on the socio-ecological correlates of “disease risk” in mammals and the consequences of parasites for mammalian mating and social systems, including sexual selection. Charlie also studies the methods used to examine trait evolution in an explicitly phylogenetic context. He is in the Section of Evolution and Ecology at University of California, Davis.