

7 Empathy, Polyandry, and the Myth of the Coy Female

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Sexual selection theory (Bateman, 1948; Darwin, 1871; Trivers, 1972; Williams, 1966) is one of the crown jewels of the Darwinian approach basic to sociobiology. Yet so scintillating were some of the revelations offered by the theory, that they tended to outshine the rest of the wreath and to impede comprehension of the total design, in this instance, the intertwined, sometimes opposing, strategies and counter strategies of both sexes which together compose the social and reproductive behavior of the species. (Hrdy & Williams, 1983, p. 7)

But why did that happen, and how? And what processes led to the current destabilization of the model and reformulation of our thinking about sexual selection?

Introduction

For over three decades, a handful of partially true assumptions were permitted to shape the construction of general evolutionary theories about sexual selection. These theories of sexual selection presupposed the existence of a highly discriminating, sexually “coy,” female who was courted by sexually indiscriminating males. Assumptions underlying these stereotypes included, first, the idea that relative male contribution to offspring was small, second, that little variance exists in female reproductive success compared to the very great variance among males, and third, that fertilization was the only reason for females to mate. While appropriate in some contexts, these conditions are far from universal. Uncritical acceptance of such assumptions has greatly hampered our understanding of animal breeding systems particularly, perhaps, those of primates.

These assumptions have only begun to be revised in the last decade, as researchers began to consider the way Darwinian selection operates on females as well as males. This paper traces the shift away from the stereotype of female as sexually passive and discriminating to current models in which females are seen to play an active role in managing sexual consortships that go beyond traditional “mate choice.” It is impossible to understand this history without taking into account the background, including

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the gender, of the researchers involved. Serious consideration is given to the possibility that the empathy for other females subjectively felt by women researchers may have been instrumental in expanding the scope of sexual selection theory.

Anisogamy and the Bateman Paradigm

In one of the more curious inconsistencies in modern evolutionary biology, a theoretical formulation about the basic nature of males and females has persisted for over three decades, from 1948 until recently, despite the accumulation of abundant openly available evidence contradicting it. This is the presumption basic to many contemporary versions of sexual selection theory that males are ardent and sexually indiscriminating while females are sexually restrained and reluctant to mate. My aims in this paper will be to examine this stereotype of “the coy female,” to trace its route of entry into modern evolutionary thinking and to examine some of the processes that are only now, in the last decade, causing us to rethink this erroneous corollary to a body of theory (Darwin, 1871) that has otherwise been widely substantiated. In the course of this examination, I will speculate about the role that empathy and identification by researchers with same-sex individuals may have played in this strange saga.

Obviously, the initial dichotomy between actively courting, promiscuous males and passively choosing, monandrous females dates back to Victorian times. “The males are almost always the wooers,” Darwin wrote in 1871, and he was very clear in his own writings that the main activity of females was to choose the single best suitor from among these wooers. As he wrote in *The Descent of Man and Selection in Relation to Sex* (1871), “It is shown by various facts, given hereafter, and by the results fairly attributable to sexual selection, that the female, though comparatively passive, generally exerts some choice and accepts one male in preference to the others.” However the particular form in which these ideas were incorporated into modern and ostensibly more “empirical” versions of post-Darwinian evolutionary thought derived from a 1948 paper about animals by a distinguished plant geneticist, Angus John Bateman.

Like so much in genetics, Bateman’s ideas about the workings of nature were based primarily on experiments with *Drosophila*, the minuscule flies that materialize in the vicinity of rotting fruit. Among the merits of fruitflies rarely appreciated by housekeepers are the myriad of small genetic differences that determine a fruitfly’s looks. Bred over generations in a laboratory, distinctive strains of *Drosophila* sporting odd-colored eyes, various bristles, peculiar crenulations here and there, grotesquely shaped eyes, and so forth can be produced by scientists, and these markers are put to use in tracing genealogies.

Bateman obtained various lots of differently decorated *Drosophila* all belonging to the one species, *Drosophila melanogaster*. He housed three to five flies of each sex in glass containers and allowed them to breed. On the basis of 64 such experiments, he found

(by counting the offspring bearing their parents' peculiar genetic trademarks) that while 21% of his males failed to fertilize any female, only 4% of his females failed to produce offspring.

A highly successful male, he found, could produce nearly three times as many offspring as the most successful female. Furthermore, the difference between the most successful and the least successful male, what is called the *variance* in male reproductive success, was always far greater than the variance among females. Building upon these findings, Bateman constructed the centerpiece to his paradigm: whereas a male could always gain by mating just one more time, and hence benefit from a nature that made him indiscriminately eager to mate, a female, already breeding near capacity after just one copulation, could gain little from multiple mating and should be quite uninterested in mating more than once or twice.

From these 64 experiments with *Drosophila*, Bateman extrapolated to nature at large: selection pressures brought about by competition among same-sexed individuals for representation in the gene pools of succeeding generations would almost always operate more strongly upon the male than upon the female. This asymmetry in breeding potential would lead to a nearly universal dichotomy in the sexual nature of the male and female:

One would therefore expect to find in all but a few very primitive organisms . . . that males would show greater intra-sexual selection than females. This would explain why . . . there is nearly always a combination of an indiscriminating eagerness in the males and a discriminating passivity in the females. Even in a derived monogamous species (e.g. man) this sex difference might be expected to persist as a rule. (Bateman, 1948, p. 365)

This dichotomy was uncritically incorporated into modern thinking about sexual selection. In his classic 1972 essay on "Parental Investment and Sexual Selection," Harvard biologist Robert Trivers acknowledged Bateman's paper as "the key reference" (provided him, as it happens by one of the major evolutionary biologists of our time, and Trivers' main mentor at Harvard, Ernst Mayr). Trivers' essay on parental investment, carrying with it Bateman's model, was to become the second most widely cited paper in all of sociobiology, after Hamilton's 1964 paper on kin selection.

Expanding on Bateman's original formulation, Trivers argued that whichever sex invests least in offspring will compete to mate with the sex investing most. At the root of this generalization concerning the sexually discriminating female (apart from Victorian ideology at large) is the fact of anisogamy (gametes unequal in size) and the perceived need for a female to protect her already substantial investment in each maternal gamete; she is under selective pressure to select the best available male to fertilize it. The male, by contrast, produces myriad gametes (sperm), which are assumed to be physiologically cheap to produce (note, however, that costs to males of competing for females are rarely factored in), and he disseminates them indiscriminately.

Two central themes in contemporary sociobiology then derive directly from Bateman. The first theme is the dichotomy between the “nurturing female,” who invests very much more per offspring than males, and “the competitive male,” who invests little or nothing beyond sperm but who actively competes for access to any additional female (see for example Daly & Margo Wilson,¹ 1983, pp. 78–79; Trivers, 1985, p. 207). As Trivers noted in his summary of Bateman’s experiments with *Drosophila*, “A female’s reproductive success did not increase much, if any, after the first copulation and not at all after the second; most females were uninterested in copulating more than once or twice” (1972, p. 138). And so it was that “coyness” came to be the single most commonly mentioned attribute of females in the literature on sociobiology. Unlike the male, who, if he makes a mistake can move on to another female, the female’s investment was initially considered to be so great that she was constrained from aborting a bad bet and attempting to conceive again. (Criticisms and recent revisions of the notion are discussed later in the section, “The Females Who Forgot to be Coy.”) In this respect, contemporary theory remains fairly faithful to Darwin’s original (1871) two-part definition of sexual selection. The first part of the theory predicts competition between males for mates; the second, female choice of the best competitor.

The second main sociobiological theme to derive from Bateman is not explicitly discussed in Darwin but is certainly implicit in much that Darwin wrote (or more precisely, did not write) about females. This is the notion that female investment is already so large that it can not be increased and the idea that most females are already breeding close to capacity. If this were so, the variance in female reproductive success would be small, making one female virtually interchangeable with another. A logical corollary of this notion is the incorrect conclusion that selection operates primarily on males.

The conviction that intrasexual selection will weigh heavily upon males while scarcely affecting females was explicitly stated by Bateman, but also appears in implicit form in the writings of contemporary sociobiologists (Daly & Margo Wilson, 1983, Chapter 5; Wilson, 1978, p. 125). It is undeniable that males have the capacity to inseminate multiple females while females (except in species such as those squirrels, fish, insects, and cats, where several fathers can sire a single brood) are inseminated—at most—once each breeding period. But a difficulty arises when the occasionally true assumption that females are not competing among themselves to get fertilized is then interpreted to mean that there will be reduced within-sex competition among females generally (e.g., Freedman, 1979, p. 33).

Until about 1980—and even occasionally after that—some theoreticians were writing about females as though each one was relatively identical in both her reproductive potential and in her realization of that potential. This erroneous generalization led some workers (perhaps especially those whose training was not in evolutionary biology per se) to the erroneous and patently non-Darwinian conclusion that females are

not subject to selection pressure at all and the idea that competition among males is somehow more critical because “leaving offspring is at stake” (Carol Cronin, 1980, p. 302; see also Virginia Abernethy, 1978, p. 132). To make an unfortunate situation worse, the close conformity between these notions and post-Victorian popular prejudice meant that ideas about competitive, promiscuous men and choosy women were selectively picked up in popular writing about sociobiology. An article in *Playboy Magazine* celebrating “Darwin and the Double Standard” (Morris, 1979) comes most vividly to mind, but there were many others.

The Females Who Forgot to Be Coy

Field studies of a number of animal groups provide abundant examples of females who, unlike Bateman’s *Drosophila*, ardently seek to mate more than once or twice. Furthermore, fertilization by the best male can scarcely be viewed as their universal goal since in many of these cases females were not ovulating or else were actually pregnant at the time they solicit males.

It has been known for years (among some circles) that female birds were less than chaste, especially since 1975 when Bray, Kennelly, and Guarino demonstrated that when the “master” of the blackbird harem was vasectomized, his females nevertheless conceived (see also Lumpkin, 1983). Evelyn Shaw and Joan Darling (1985) review some of this literature on “promiscuous” females, particularly for marine organisms. Among shiner perch, for example, a female who is not currently producing eggs will nevertheless court and mate with numbers of males, collecting from each male sperm that are then stored in the female’s ovaries till seasonal conditions promote ovulation. Female cats, including leopards, lions, and pumas are notorious for their frequency of matings. A lioness may mate 100 times a day with multiple partners over a 6–7-day period each time she is in estrus (Eaton, 1976). Best known of all, perhaps, are such primate examples as savanna baboons, where females initiate multiple brief consortships, or chimpanzees, where females alternate between prolonged consortships with one male and communal mating with all males in the vicinity (DeVore, 1965; Hausfater, 1975; Caroline Tutin, 1975). However, only since 1979 or so has female promiscuity been a subject of much theoretical interest (see for example Alatalo, Lundberg, & Stahlbrandt, 1982; Sandy Andelman, in press; Gladstone, 1979; Sarah Blaffer Hrdy, 1979; Susan Lumpkin, 1983; Meredith Small, forthcoming; R. Smith, 1984; Wirtz, 1983), largely I believe because theoretically the phenomenon should not have existed and therefore there was little theoretical infrastructure for studying it, certainly not the sort of study that could lead to a PhD (or a job).

In terms of the order Primates, evidence has been building since the 1960s that females in a variety of prosimian, monkey, and ape species were managing their own reproductive careers so as actively to solicit and mate with a number of different males,

both males within their (supposed) breeding unit and those outside it. As theoretical interest increased, so has the quality of the data.

But before turning to such evidence, it is first critical to put sex in perspective. To correct the stereotype of “coyness,” I emphasize female sexual activity but, as always in such debates, reality exists in a plane distinct from that predefined by the debate. In this case, reality is hours and hours, sometimes months and months, of existence where sexual behavior is not even an issue, hours where animals are walking, feeding, resting, grooming. Among baboons (as in some human societies) months pass when a pregnant or lactating mother engages in no sexual behavior at all. The same is generally true for langurs, except that females under particular conditions possess a *capacity* to solicit and copulate with males even if pregnant or lactating, and they sometimes do so. At such times, the patterning of sexual receptivity among langurs could not be easily distinguished from that of a modern woman. The same could be said for the relatively noncyclical, semicontinuous, situation-dependent receptivity of a marmoset or tamarin.

With this qualification in mind—that is the low frequencies of sexual behavior in the lives of *all* mammals, who for the most part are doing other things—let’s consider the tamarins.

Tamarins are tiny South American monkeys, long thought to be monogamous. Indeed, in captivity, tamarins do breed best when a single female is paired with one mate. Add a second female and the presence of the dominant female suppresses ovulation in the subordinate. (The consequences of adding a second male to the cage are unknown, since such an addition was thought to violate good management practices.) Nevertheless, in the recent (and first) long-term study of individually marked tamarins in the wild, Anne Wilson Goldizen discovered that given the option, supposedly monogamous saddle-backed tamarins (*Saguinus fuscicollis*) will mate with several adult males, each of whom subsequently help to care for her twin offspring in an arrangement more nearly “polyandrous” than monogamous (Goldizen & Terborgh, forthcoming). Furthermore the presence of additional males, and their assistance in rearing young may be critical for offspring survival.) One of the ironies here, pointed out in another context by Janet Sayers (1982), is that females are thus presumed to commit what is known in sociobiology as a *Concorde fallacy*; that is, pouring good money after bad. Although in other contexts (e.g., Dawkins, 1976) it has been argued that creatures are selected to cut bait rather than commit Concorde fallacies, mothers were somehow excluded from this reasoning (however, see Trivers, 1985, p. 268, for a specific acknowledgement and correction of the error). I happen to believe that the resolution to this contradiction lies in recognizing that gamete producers and mothers do indeed “cut bait” far more often than is generally realized, and that skipped ovulations, spontaneous abortion, and abandonment of young by mothers are fairly routine events in nature. That is, the reasoning about the Concorde fallacy is right enough, but our

thinking about the commitment of mothers to nurture no matter what has been faulty.)

Indeed, on the basis of what I believe today (cf. Hrdy, 1981, p. 59), I would argue that a polyandrous component² is at the core of the breeding systems of most troop-dwelling primates: females mate with many males, each of whom may contribute a little bit toward the survival of offspring. Barbary macaques provide the most extreme example (Taub, 1980), but the very well-studied savanna baboons also yield a similar, if more moderate, pattern. David Stein (1981) and Jeanne Altmann (1980) studied the complex interactions between adult males and infants. They found that (as suggested years ago by Tim Ransom and Bonnie Ransom, 1972) former, or sometimes future, consorts of the mother develop special relationships with that female's infant, carrying it in times of danger and protecting it from conspecifics, possibly creating enhanced feeding opportunities for the infant. These relationships are made possible by the mother's frequent proximity to males with whom she has special relationships and by the fact that the infant itself comes to trust these males and seek them out; more is at issue than simply male predilections. Altmann aptly refers to such males as *god-fathers*. Infants, then, are often the focal-point of elaborate male-female-infant relationships, relationships that are often initiated by the females themselves (Barbara Smuts, 1985).

Even species such as Hanuman langurs, blue monkeys, or redtail monkeys, all primates traditionally thought to have "monandrous" or "uni-male" breeding systems, are far more promiscuous than that designation implies. Indeed, mating with outsiders is so common under certain circumstances as to throw the whole notion of one-male breeding units into question (Cords, 1984; Tsingalia & Thelma Rowell, 1984). My own first glimpse of a langur, the species I was to spend nearly 10 years studying intermittently, was of a female near the Great Indian Desert in Rajasthan moving rapidly through a steep granite canyon, moving away from her natal group to approach and solicit males in an all-male band. At the time, I had no context for interpreting behavior that merely seemed strange and incomprehensible to my Harvard-trained eyes. Only in time, did I come to realize that such wandering and such seemingly "wanton" behavior were recurring events in the lives of langurs.

In at least three different sets of circumstances female langurs solicit males other than their so-called *harem-leaders*: first, when males from nomadic all-male bands temporarily join a breeding troop; second, when *females* leave their natal troops to travel temporarily with all-male bands and mate with males there; and third, when a female for reasons unknown to any one, simply takes a shine to the resident male of a neighboring troop (Hrdy 1977; Moore 1985; filmed in Hrdy, Hrdy, & Bishop, 1977). It may be to abet langurs in such projects that nature has provided them attributes characteristic of relatively few mammals. A female langur exhibits no visible sign when she is in estrus other than to present to a male and to shudder her head. When she encounters strange males, she has the capacity to shift from cyclical receptivity (that is, a bout of

heat every 28 days) into a state of semicontinuous receptivity that can last for weeks. Monkeys with similar capacities include vervets, several of the guenons, and gelada baboons, to mention only a few (reviewed in Hrdy & Whitten, 1986).

A number of questions are raised by these examples. First, just exactly why might females bother to be other than coy, that is why should they actively seek out partners including males outside of their apparent breeding units (mate “promiscuously,” seek “excess” copulations, beyond what are necessary for fertilization)? Second, why should this vast category of behaviors be, until recently, so generally ignored by evolutionary theorists? As John Maynard Smith noted, in the context of mobbing behavior by birds, “behavior so widespread, so constant, and so apparently dangerous calls for a functional explanation” (1984, p. 294).

To be fair, it should be acknowledged that mobbing behavior in birds is more stereotyped than sexual behavior in wild cats or monkeys, and it can be more systematically studied. Nevertheless, at issue here are behaviors exhibited by the majority of species in the order primates, the best studied order of animals in the world, and the order specifically included by Bateman in his extrapolation from coyness in arthropods to coyness in anthropoids. Furthermore, females engaged in such “promiscuous matings” entail obvious risks ranging from retaliatory attacks by males, venereal disease, the energetic costs of multiple solicitations, predation risks from leaving the troop, all the way to the risk of lost investment by a male consort who has been selected to avoid investing in other males’ offspring (Trivers, 1972). In retrospect, one really does have to wonder why it was nearly 1980 before promiscuity among females attracted more than cursory theoretical interest.

Once the initial conceptual block was overcome (and I will argue in the last section that the contributions of women researchers was critical to this phase, at least in primatology), once it was recognized that oh yes, females mate promiscuously and this is a most curious and fascinating phenomenon, the question began to be vigorously pursued. (Note though that the focus of this paper is on male-centered theoretical formulations, readers should be aware that there are other issues here, such as the gap between theoreticians and fieldworkers, which I do not discuss.)

In my opinion, no conscious effort was ever made to leave out female sides to stories. The Bateman paradigm was very useful, indeed theoretically quite powerful, in explaining such phenomena as male promiscuity. But, although the theory was useful in explaining male behavior, by definition (i.e., *sexual selection* refers to competition between one sex for *access* to the other sex) it excluded much within-sex reproductive competition among females, which was not over fertilizations per se but which also did not fall neatly into the realm of the survival-related phenomena normally considered as due to natural selection. (The evolution of sexual swellings might be an example of a phenomenon that fell between definitional cracks and hence went unexplained until recently [Clutton-Brock & Harvey, 1976; Hrdy, 1981].) To understand

female promiscuity, for example, we first needed to recognize the limitations of sexual selection theory and then needed to construct a new theoretical base for explaining selection pressures on females.

The realization that male–male competition and female choice explains only a small part of the evolution of breeding systems has led to much new work (e.g., Wasser, 1983, and work reviewed therein). We now have, for example, no fewer than six different models to explain how females might benefit from mating with different males (see Smith, R., 1984, for a recent review).

These hypotheses, most of them published in 1979 or later, can be divided into two categories, first those postulating genetic benefits for the offspring of sexually assertive mothers, and second, those postulating nongenetic benefits for either the female herself or her progeny. All but one of these (the oldest, “prostitution hypothesis”) was arrived at by considering the world from a female’s point of view.

Whereas all the hypotheses specifying genetic benefits predict that the female should be fertile when she solicits various male partners (except in those species where females have the capacity to store sperm), this condition is not required for the nongenetic hypotheses. It should be noted, too, that only functional explanations for multiple matings are listed. The idea that females simply “enjoy” sex begs the question of why females in a genus such as *Drosophila* do not appear highly motivated to mate repeatedly, while females in other species apparently are so motivated and have evolved specific physiological apparatus making promiscuity more likely (e.g., a clitoris, a capacity for orgasm brought about by prolonged or multiple sources of stimulation, a capacity to expand receptivity beyond the period of ovulation, and so forth; see Hrdy, 1981, Chapter 7 for discussion). Nevertheless, the possibility persists that promiscuous behaviors arise as endocrinological accidents or perhaps that females have orgasms simply because males do (Symons, 1979), and it is worth remembering that an act of faith is involved in assuming that there is any function at all. (I mention this qualifier because I am not interested in arguing a point that can not currently be resolved.)

Assuming that promiscuous behaviors and the physiological paraphernalia leading to them have evolved, four hypotheses are predicated on genetic benefits for the offspring of sexually assertive mothers: (a) the “fertility backup hypothesis,” which assumes that females will need sperm from a number of males to assure conception (Meredith Small, forthcoming; Smith, R., 1984); (b) “the inferior cuckold hypothesis,” in which a female paired with an inferior mate surreptitiously solicits genetically superior males when conception is likely (e.g., Benshoof & Thornhill, 1979); (c) “the diverse paternity” hypothesis, whereby females confronted with unpredictable fluctuations in the environment produce clutches sired by multiple partners to diversity paternity of offspring produced over a lifetime (Parker, 1970; Williams, 1975); or (d) in a somewhat obscure twist of the preceding, females in species where litters can have

more than one father alter the degree of relatedness between sibs and maternal half-sibs by collecting sperm from several fathers (Davies & Boersma, 1984).

The remaining explanations are predicated on nongenetic benefits for females and do not assume the existence of either genetic differences between males or the existence of female capacities to detect them: (e) the “prostitution” hypothesis, whereby females are thought to exchange sexual access for resources, enhanced status, etc.—the oldest of all the explanations (first proposed by Sir Solly Zuckerman, 1932, recently restated by Symons, 1979; see also, Nancy Burley & Symanski, 1981, for discussion); (f) the “therapeutic hypothesis” that multiple matings and resulting orgasm are physiologically beneficial to females or make conception more likely (Mary Jane Sherfey, 1973); (g) the “keep ‘em around” hypothesis whereby females (with the connivance of dominant males in the group) solicit subordinate males to discourage these disadvantaged animals from leaving the group (Stacey, 1982); and (h) the “manipulation hypothesis,” suggesting that females mate with a number of males in order to confuse information available to males about paternity and thereby extract investment in, or tolerance for, their infants from different males (Hrdy, D. B., 1979; Stacey, 1982).

It is this last hypothesis that I now want to focus on, not because that hypothesis is inherently any better than others, but because I know the most about it and about the assumptions that needed to be changed before it could be dreamed up.

The “manipulation hypothesis,” first conceived in relation to monkeys, grew out of a dawning awareness that, first of all, individual females could do a great deal that would affect the survival of their offspring, and second, that males, far from mere dispensers of sperm, were critical features on the landscape where infants died or survived. That is, females were more political, males more nurturing (or at least not neutral), than some earlier versions of sexual selection theory would lead us to suppose.

A Female Is Not a Female Is Not a Female

To his credit, A. J. Bateman was a very empirical scientist. He was at pains to measure “actual” and not just “potential” genetic contribution made by parents. Not for him the practice—still prevalent in primatology several decades later—of counting up some male’s copulations and calling them *reproductive success*. Bateman counted offspring actually produced. And, in a genus such as *Drosophila*, where infant mortality is probably fairly random and a stretch of bad weather accounts for far more deaths than a spate of bad parenting, the assumption that one mother is equivalent to another mother is probably not farfetched. Such factors as the social status of the mother, her body size, her expertise in child-rearing, or the protection and care elicited from other animals may indeed make little difference. But what if he had been studying monkeys or even somebody’s favorite fish? Even for *Drosophila* conditions exist in which females benefit from multiple copulations. In a series of experiments with *Dro-*

sophila pseudoobscura, Turner and Anderson (1983) have shown that the number of offspring that survive to maturity was significantly higher for females allowed to mate for longer periods and with more partners than for females isolated from males after brief mating periods. This effect was most pronounced in laboratory groups that were nutritionally stressed.

The female coho salmon buries her eggs in nests, which she guards for as long as she lives. Females fight over the best nest sites, and about one out of three times, a female will usurp another female's nest and destroy her eggs. Females vary greatly in size, and their differing dimensions may be translated into different degrees of fecundity. A big female may produce more than three times as many eggs as a small one. Differences in the survival of eggs to hatching lead to even greater variance in female reproductive success; there may be as much as a 30-fold difference in number of surviving offspring (Van den Berghe, 1984).

But the mother salmon only breed once; consider an iteroparous monkey mother who, although she produces only one or two infants at a time, breeds over many years and who, like a macaque or baboon, may inherit her feeding range and troop rank from her mother at birth. These legacies will affect her reproductive output and will, in turn, pass to her own daughters. Males of course enter this system, and vary among themselves, but in most instances they are transients, breeding briefly, and indeed, possibly living shorter lives on average than females. Take the extreme example of the gelada baboon who has only one chance for controlling access to a small "harem" of females (who by the way have about as much to do with controlling the male, as he does in controlling them). The male gelada baboon breeds in his unit for several years before another male enters, pushing him into forced retirement. The former "harem-leader" lingers on in the troop, but as a celibate watcher, possibly babysitting, but breeding no more (Dunbar, 1984). It is a tale of the tortoise and the hare. After the male hare is dismissed, the female tortoise breeds on year after year.

Although we do not yet have data on the lifetime reproductive success of males or females from any species of wild primate, I will be surprised if the variance among males exceeds the variance among females by as much as traditionally thought in species such as Japanese or rhesus macaques or gelada baboons. In the most polyandrous species, such as tamarins, variance in the reproductive success of twin-producing females may actually be greater than that for males. If we carry out our calculations over generations, remembering that every male, however wildly reproductively successful, has a mother and a grandmother (e.g., see Hartung, in press) differences in the degree of variance between the two sexes grow even smaller, though extremes of variance in reproductive success will of course crop up one generation sooner for fathers than for mothers.

The anisogamy paradigm of Bateman offered powerful insights into the selective pressures that operate on males; for many mammals, selection weighs heaviest on

males in competition with other males for access to females. In addition, Bateman provided the framework that eventually led to an understanding of why males tend to compete for mates while females compete for resources. But the Bateman and the anisogamy paradigm also led us to overlook the full range of possible sources of variance in female reproductive success; not only variance arising from female–female competition over resources to translate into large gametes, but also variance arising from other factors as well. Not all females conceive. In some cases, such as marmosets, the presence of the dominant female suppresses ovulation in her subordinates. Some offspring, once conceived, are not carried to term. Among the factors leading to spontaneous abortion in baboons may be harassment by other females or the arrival of strange males (Mori & Dunbar, in press; Wasser & Barash, 1984). And of course, offspring once born need not survive. If born to a low-ranking toque macaque mother, a juvenile daughter may die of starvation, or if born to a mother chimp who for some reason is incapacitated, an offspring may be killed by a higher-ranking female. Having survived, a maturing female howler monkey may nevertheless find herself unable to join a breeding group and never have a chance to reproduce. A mother's condition, her competitive abilities, and her maternal skills are all very much at issue in the case of creatures such as primates. Yet, as amazing as it sounds, only relatively recently have primatologists begun to examine behaviors other than direct mother–infant interactions that affect the fates of infants (for elaboration see Hrdy, 1981; Small, 1984). Not the least among the variables affecting their survival is the role played by males, and the capacity of females to influence this male performance.

Male Involvement with Infants

Even for *Drosophila* it was a mistake to imagine that male investment never went further than chromosomes. Recent research makes it clear that, as in various butterflies and cockroaches, male fruitflies may sometimes transmit along with their sperm essential nutrients that otherwise would be in short supply (Markow & Ankney, 1984). When assumptions about minimal male involvement are extrapolated to species such as primates, however, far more than underestimation of male involvement is at stake. I would argue that it is not only ill-advised but impossible to understand primate breeding systems without taking into account the role of males in determining the survival or demise of infants.

There is probably no order of mammals in which male involvement with infants is more varied, more complex, or more crucial than among primates. About 10% of all mammalian genera exhibit some form of direct male care, that is the male carries the infant or provisions it. Among primates, however, the percentage of genera with direct, positive (if also sometimes infrequent) interactions between males and infants is roughly four times that, the highest figure reported for any order of mammals (Devra

Kleiman & Malcolm, 1981; Vogt, 1984). Conversely, infanticide has been reported for over 15 different species of primates belonging to 8 genera and is probably widespread among apes and monkeys (Hausfater & Hrdy, 1984). Indeed, some male care is probably a direct outgrowth of the need by males to protect infants from other males (Busse & Hamilton, 1981). Yet, oddly, after two decades of intensive study of wild primates, we are only now beginning to scratch the surface of the rich interactions that exist between infants and adult males, which seem to have such critical repercussions for infant survival (see Hrdy, 1976; and especially, Taub, 1984a, 1984b). Effects of these relationships for infants after they grow up have rarely been investigated, although several researchers have recently suggested the possibility that fathers among gibbons and orangutans may play a role in helping their sons to set up or defend territories (MacKinnon, 1978; Tilson, 1981). These cases are of special importance because apart from intervention by brothers or by fathers in adopting an orphan (among gorillas and chimpanzees) direct, "maternal-like" care of infants by males is not typically seen among apes. But, the fact that parental investment by males does not take the same form as investment by females does not lessen its importance for offspring or its cost to the parent. My focus here is on primates, but I believe I could make many of the same points if I were a student of amphibians or fish in which male care is very common. One critical role of males is to protect immatures from distantly related conspecifics. It has long been assumed that one reason for male care among these species was the greater certainty of paternity permitted in species with external fertilization (i.e., the male can *know* which eggs he fertilized). But surely among these groups, as among primates, there has been selection on females to manipulate this situation.

The main exception to a general pattern of ignoring interactions between males and infants was of course the study of male care among monogamous primates. It has been known for over 200 years, ever since a zoologist-illustrator named George Edwards decided to watch the behavior of pet marmosets in a London garden, that among certain species of New World monkeys males contributed direct care for infants that equalled or exceeded that given by females (Edwards, 1758). Mothers among marmosets and tamarins typically give birth to twins, as often as twice a year, and to ease the female in her staggering reproductive burden the male carries the infant at all times except when the mother is actually suckling it. It was assumed that monogamy and male confidence of paternity was essential for the evolution of such care (Kleiman, 1977), and at the same time, it was assumed that monogamy among primates must be fairly rare (e.g., see Symons, 1979, or virtually any textbook on physical anthropology prior to 1981).

Recent findings, however, make it necessary to revise this picture. First of all, monogamy among primates turns out to be rather more frequent than previously believed (either obligate or facultative monogamy can be documented for some 17–20% of extant primates) and, second, male care turns out to be far more extensive than previously

thought and not necessarily confined to monogamous species (Hrdy, 1981). Whereas, previously, it was assumed that monogamy and male certainty of paternity facilitated the evolution of male care, it now seems appropriate to consider the alternative possibility, whether the extraordinary capacity of male primates to look out for the fates of infants did not in some way pre-adapt members of this order for the sort of close, long-term relationships between males and females that, under some ecological circumstances, leads to monogamy! Either scenario could be true. The point is that on the basis of present knowledge there is no reason to view male care as a restricted or specialized phenomenon. In sum, though it remains true that mothers among virtually all primates devote more time and/or energy to rearing infants than do males, males nonetheless play a more varied and critical role in infant survival than is generally realized.

Male–infant interactions are weakly developed among prosimians, and in these primitive primates, male care more or less (but not completely) coincides with monogamy (Vogt, 1984). Direct male care occurs in 7 out of 17 genera, including one of the most primitive of all lemurs, the nest-building ruffed lemur (*Lemur variegatus*), where the male diligently tends the nest while the mother forages (personal communication from Patricia Wright). Among New World monkeys, 12 of 16 genera (Vogt, 1984) or, calculated differently, 50% of all species (Wright, 1984) exhibit direct male care, often with the male as the primary caretaker. That is, shortly after birth, an adult male—often with the help of various immatures in the group or other males—will take the infant, carry it (or them, in the frequent case of twins) on his back, share food with infants, either adult males or juveniles may catch beetles to feed them, or assist them by cracking the casing of tough fruit.

The role of males as primary caretakers for single (nontwin) infants is very richly developed among the night monkeys, *Aotus trivirgatus*. These small, monogamously mated, South American monkeys are the only nocturnal higher primate. Because of the difficulty in watching them, their behavior in the wild has gone virtually undocumented until detailed behavioral studies were undertaken by Patricia Wright using an image intensifier and other gear to allow her to work at night. Combining her observations of captive *Aotus* with field observations, a picture emerges in which the male is primary caretaker (in terms of carrying the infant) from the infant's first day of life, although the mother, of course, still is providing physiologically very costly milk. Based on captive observations, the mother carried the infant 33% of the time during the first week of life, the male 51%, and a juvenile group member 15%. In the wild, the infant was still being carried by the male at 4 months of age, although "weaning" tantrums were seen, as the male would try to push the infant off his back. By 5 months, the infant was relatively independent of either parent (Patricia Wright, 1984).

There is little question that there is an association between monogamy and extensive male care. Nevertheless, this does not mean that the evolution of male care is precluded

by situations in which females mate with more than one male, as discussed for the case of savannah baboons.

Recent research on male–infant relations among baboons reveals that during their first week of life infant baboons at Amboseli spend about a third of their daylight hours within 5 feet of an adult male, often, but not always, a former sexual consort of the mother. This level of proximity was maintained throughout the first 7 weeks and then dropped sharply. At the same time, the amount of time infants spend in actual contact with an adult male, which is never much, is rising from 1% in the first week to 3% by the eighth week. During their first half-year of life, infants spend .5% of their time connected with an adult male, a low figure (Stein, 1984). Averaging together data from a number of different baboon field studies, David Taub calculates that a male–infant interaction takes place only about once every 19 hours (or, adjusting for the number of males in a multi-male troop, one interaction per male every 344 hours). However, Taub concurs with Busse and Hamilton (1981) and others, that the proximity of these males may be crucial for infant survival, particularly critical for discouraging attacks on the infant either by incoming males, unfamiliar with the infant’s mother or, as suggested by Wasser (1983) for forestalling harassment by female troop members belonging to competing matriline. That is, when the cost of care is fairly low (the male need only remain in the vicinity of the infant but can engage in other activities) and when it is rendered nonexclusively to several infants (e.g., to the offspring of each of the male’s special female friends), male care certainly does occur in nonmonogamous systems. What is offered may not be “quantity” time, but it may well be “quality” time—“quality” in a very real sense: enhancing infant survival.

Yet, even these caveats can be dispensed with in the unusual case of the polyandrous tamarin species (*Saguinus fuscicollis*) studied by Goldizen. The female mates with several males and each of them subsequently helps rear the infant. Indeed, preliminary data from Goldizen’s continuing research suggests that infants with several male caretakers are more likely to survive than infants born in small groups with only one adult male. Here, then, is both quality and quantity time, combined in a nonmonogamous breeding system, a system where males have a probability but no certainty of paternity. If we pause for a moment and consider the tamarin case from the male’s point of view, the system Goldizen reports almost certainly derived initially from a monogamous one in which males were indeed caring for offspring likely to be their own. Only after such a system was established could a female have plausibly manipulated the situation to enlist the aid of two helpers.

Assuming that primate males do indeed remember the identity of past consorts and that they respond differentially to the offspring of familiar and unfamiliar females, females would derive obvious benefits from mating with more than one male. A researcher with this model in mind has quite different expectations about female

behavior than one expecting females to save themselves in order to mate with the best available male. The resulting research questions will be very different.

The Role of Women Researchers

When generalizations persist for decades after evidence invalidating them is also known, can there be much doubt that some bias was involved? We were predisposed to imagine males as ardent, females as coy; males as polygynists, females monandrous. How else could the *Drosophila* to primate extrapolation have entered modern evolutionary thinking unchallenged?

Assuming, then, this bias, a preconstituted reality in which males played central roles, what factors motivated researchers to revise invalid assumptions? What changes in the last decade brought about the new focus on female reproductive strategies and, with it, the recognition that certain assumptions and corollaries of the Bateman paradigm, and especially female monandry, were seriously limited and even, if applied universally, quite wrong.

The fact that there is relatively less intrasexual selection for mates among females does not mean reduced intrasexual competition or reduced selection among females in other spheres of activity. To understand male–male competition for mates is to understand only a small part of what leads to the evolution of particular primate breeding systems. We need also consider the many sources of variance in female reproductive success, including a whole range of female behaviors not directly related to “mothering” that may have repercussions on the fates of their infants.

Polyandrous mating with multiple males, mating with males when conception is not possible—what from the males’ point of view might be termed “excessive” matings—can only be understood within this new framework, but it requires a whole new set of assumptions and research questions. As a result, sexual selection theory is currently in a state of flux; it is being rethought as actively as any area in evolutionary biology. What processes contributed to this destabilization of a long-held paradigm? And in particular, what led us to rethink the myth of the coy or monandrous female?

Improved methodologies and longer studies would not by themselves have led us to revise the myth of the coy female, simply because the relevant information about “female promiscuity” was already in hand long before researchers began to ask why females might be mating with more than one male. Indeed, at least one writer, working in a framework well outside of primatology and evolutionary biology, picked up on the reports of female promiscuity in baboons and chimpanzees at an early date (1966) and asked why it had evolved. This of course was the feminist psychiatrist Mary Jane Sherfey in her book, *The Evolution of Female Sexuality* (1973). Sherfey’s vision of the “sexually insatiable” female primate was generally ignored by primatologists and biologists both because of her ideological perspective and because her standards of evi-

dence were far from scientific. If her ideas were mentioned, it was typically with sarcasm and derision (Symons, 1979, pp. 76–77, 94, 262, 311). And, yet, it is important to note that however extreme her views (and scholarly balance was not Sherfey's strong point), they provided a valuable antidote to equally extreme ideas about universally coy females that were widely held by scientists within the academic mainstream of evolutionary biology. Elsewhere, I wrote about the various factors which caused us to recognize the importance of female dominance hierarchies in the lives of cercopithecine monkeys (Hrdy, 1984). Changes in methodology (e.g., focal animal sampling of all individuals in a group) and the emergence of long-term studies played critical roles in revising male-centered models of primate social organization. In that case as well, some of the relevant information was available long before we decided it was significant (e.g., the detailed Japanese studies indicating matrilineal inheritance of rank, Kawai, 1958; Kawamura, 1958). But, in the “coy female” case, I don't think that the duration of the studies or the field methods made as much difference as the particular research questions being asked. Ultimately, however, long-term studies are going to be very important for testing the various hypotheses to explain why females mate with multiple males.

New or better data alone did not change the framework in which we asked questions; rather, I believe, something motivational changed. Among the factors leading to a reevaluation of the myth of the coy female, the role of women researchers must be reconsidered. That is, I seriously question whether it could have been just chance or just historical sequence that caused a small group of primatologists in the 1960s, who happened to be mostly male, to focus on male–male competition and on the number of matings males obtained, while a subsequent group of researchers, including many women (beginning in the 1970s), started to shift the focus to female behaviors having long-term consequences for the fates of infants (reviewed in Hrdy & Williams, 1983).

In this paper, I deliberately included first names whenever the work of a woman was cited. I did this to emphasize just how many women are currently working specifically in this area. Even a casual inspection reveals that women are disproportionately represented among primatologists compared to their representation in science generally. For example, in 1984, just over a third of the members (36%) of the American Society of Primatologists were women.³ As we reconstruct the journey from Bateman (1948) to the recognition that the adjectives *coy* and *female* are something less than synonymous, it seems clear that the insights of women are implicated at every stage along the way and that their involvement exceeds their representation in the field. Having said this, I need to remind readers that as history my account here is biased by a conscious focus on contributions by women. A broader treatment would also have to describe the pioneering research on long-term male–female relations by T. M. Ransom and Robert Seyfarth and the extensive studies of male–infant relations by Mason, Mitchell, Redican, Stein, Taub, and others (see Taub, 1984a, 1984b, for reviews). I am

acutely aware that my treatment here is biased both by my particular purpose (discussing the role of empathy by females for other females in causing us to revise old assumptions) and by my own involvement in the transition of primatology from the study of primate “behavior” to the study of primate “sociobiology.” Hence, I leave to someone else the task of writing a balanced history of primatology in this period (e.g., see Alison Jolly, 1985).

The contributions of women researchers can be interpreted in several ways. Perhaps, women are simply better observers. As Louis Leakey used to say in an effort to justify his all-too-evident preference for women researchers, “You can send a man and a woman to church, but it is the woman who will be able to tell you what everyone had on” (personal communication, 1970). Or perhaps women are by temperament more pragmatic or more empirical, less open to theoretical bias. A difficulty with both ideas, of course, is that a few women were present in primatology in the 1960s, and both sexes participated in perpetuating myths about monkeys living in male-centered societies, where the primary activities of females had to do with mothering (e.g., Jane Goodall, 1971 or Phyllis Jay, 1963; but see Jane Lancaster, 1975; and Thelma Rowell, 1972, for exceptions). Women seemed just as vulnerable to bias as men.

If the presence of women was a constant but our ideas changed, perhaps, as Donna Haraway (1976) likes to remind us, the interpretations of primatologists simply mirror ideological phases in the history of the Western world. Indeed, it is disconcerting to note that primatologists are beginning to find politically motivated females and nurturing males at roughly the same time that a woman runs for vice president of the United States and Garry Trudeau starts to poke fun at “caring males” in his cartoons.

Or, perhaps, as Thelma Rowell (1984) suggested it was easier “for females to empathize with females, and . . . empathy is a covertly accepted aspect of primate studies” (p. 16). Perhaps, the insights were there all along but it took longer to challenge and correct male-centered paradigms because the perceptions of women fieldworkers lacked the authority of male theorists.

In *A Feeling for the Organism*, Evelyn Fox Keller (1983) hints at the possibility that women biologists may have some special sensibility concerning the creatures that they study, an ability to enter into the lives of their subjects—a suggestion that maize geneticist Barbara McClintock, the subject of her biography, would surely deny. Among other things, such a singular “gift” for women might be thought to confine women to particular areas of science or to diminish their accomplishments. That is, as primatologist Linda Fedigan wrote recently,

I do admit to some misgivings about the wider implications of female empathy. Rowell may be correct about our sense of identification with other female primates, but I well remember my dismay when, having put many hours of effort into learning to identify the individual female monkeys of a large group, my ability was dismissed as being inherent in my sex by a respected and senior male colleague. (p. 308)

To put Fedigan's concern in perspective one needs to realize that in conversations with primatologists and, indeed, among ethologists generally, it is fairly commonplace to hear it said that women seem better able than men to learn to individually identify large numbers of animals. In a now legendary study, the seemingly incredible capacity of British ornithologist Dafila Scott to identify and remember hundreds of unmarked swans was tested by a male colleague. Indeed, it is occasionally suggested that the difficulty men have learning individuals is one reason why more men go into the ecological side of primatology.

Similarly, and I believe justifiably, women primatologists have worried about identifying too closely with the study of mothers and infants for fear that this area would become the "home economics" of primatology, a devalued women's domain within the discipline, or for fear that it would exacerbate the already common view that women study monkeys because it satisfies a deep-felt need to be around cuddly creatures.

Yet, suppose that there is some truth to the idea that women identified with same-sex subjects and allowed this identification to influence research focus? After all, isn't this what male primatologists, and many other ethologists as well, were doing throughout the 1960s and, occasionally, into the 1980s?

Even today, one can encounter lovely examples of what I call the *punch line phenomenon*, when a covert identification by researchers with same-sex individuals suddenly becomes overt in a last paragraph or emphatic comment. For example, in a seemingly impartial 1982 paper entitled, "Why Do Pied Flycatcher Females Mate with Already Mated Males?," the authors present data to show that females who mate with already mated males rear fewer offspring than female flycatchers who are the sole mates of males, regardless of the kind of territories they had to offer her. Surely, this modern, post-"coy female" paper, focused as it is upon the reproductive success of females, a paper essentially about female strategies, will not succumb to a male-centered perspective. Yet by the end of the paper, by some imperceptible process, the female has become object, the male protagonist: "Our conclusion is that polygamous pied flycatcher males deceive their secondary females" (p. 591) and the strategy works, according to the authors, because the females lack the time to check out whether the male already has a mate whose offspring he will invest in: "it pays for a pied flycatcher female to be fast rather than coy, and therefore *she* [italics mine] can be deceived. . . ."

My own work, before I began consciously to consider such matters, provides another example. The last line of *The Langurs of Abu: Female and Male Strategies of Reproduction* (1977), a book in which I scrupulously devoted equal space to both sexes, reads, "For generations, langur females have possessed the means to control their own destinies: caught in an evolutionary trap they have never been able to use them" (p. 309). I might as well have said *we*.

On a conversational level, few primatologists bother to deny this phenomenon. As a colleague remarked recently when the subject came up, "Of course I identify with them. I sometimes identify with female baboons more than I do with males of my own species." But why, we still need to ask, was the process of same-sex identification by women different in the 1970s and 1980s than in the early years of primatology?

I leave the general answers to such questions to social historians, who are more qualified than I to deal with them. At this point in the chapter, I abandon scholarship and attempt briefly to trace my own experiences as I remember them, particularly as they relate to the recognition of the active roles females were playing in the evolution of primate breeding systems.

Reminiscence

In 1970, as a first-year graduate student at Harvard, I began research on infanticidal behavior by males and ended, a decade later, almost entirely focused on the reproductive strategies of females. What processes were involved? Some months after starting my fieldwork in Rajasthan, India, I abandoned my original hypothesis (that infanticide was a response to crowding) and adopted an interpretation based on classical sexual selection theory: infanticide was an outcome of male–male competition for access to females. That is, males only killed infants when they (the males) invaded breeding units from outside; mothers whose infants were killed subsequently mated with the killer sooner than if the mothers had continued to lactate (Hrdy, 1974). By killing infants sired by other males, the usurpers increased their own opportunities to mate with fertile females.

The story was straightforward enough and in line with everything I had been taught at Harvard. But, there were loose ends, not the least of which was my growing emotional involvement with the plight of female langurs. Every 27 months, on average, some male was liable to show up and attempt to kill a female's infant, and increasingly, my identification was with the female victimized in this way, not with the male who, according to the sexual selection hypothesis, was thereby increasing his reproductive success. If infanticide really was an inherited male trait that could be elicited by particular conditions (as I believed was the case), why would females put up with this system? Why not refuse to breed with an infanticidal male and wait until a male without any genetic propensity for infanticide showed up? Consideration of this question led to many others related to the question of intrasexual competition among females generally (Hrdy, 1981).

First came an unconscious process of identification with the problems a female langur confronts followed by the formulation of conscious questions about how a female copes with them. This, in turn, led to the desire to collect data relevant to those questions. Once asked, the new questions and new observations forced reassessment of old

assumptions and led to still more questions. Even events I had seen many times before (e.g., females leaving their troops to solicit extratroup males) raised questions as they never had before.

If it was really true that females did not benefit from additional matings, why were female langurs taking such risks to solicit males outside their troop? Why would already pregnant females solicit and mate with males? What influence might such behavior have for the eventual fate of the female's offspring? What were the main sources of variance in female reproductive success and what role did nonreproductive sexuality play in all this? Why is situation-dependent receptivity, as opposed to strictly defined cyclical receptivity or estrus, so richly developed in the order primates? Where did the idea of the coy female ever come from anyway? These are the questions that preoccupied me since 1977 and all of them grow out of an ability to imagine females as active strategists.

Yet, identification with same-sex individuals in another primate species may not be quite so simple as it sounds. This history of primatology suggests that the nature of this identification was changing over time as the self-image of women researchers also changed. In my own case, changes in the way I looked at female langurs were linked to a dawning awareness of male–female power relationships in my own life, though “dawning” perhaps overstates the case.

It would be difficult to explain to an audience of political activists how intelligent human beings could be as politically unaware as many field biologists and primatologists are. Almost by definition, we are people who lead isolated lives and, by and large, avoid joining groups or movements. In addition, I was the sole woman in my cohort, since I was the first woman graduate student my particular advisor had taken on and only toward the end of the 1970s did I begin to read anything by feminist scholars like Carolyn Heilbrun and Jean Baker Miller. Each step in understanding what, for example, might be meant by a term like *androcentric* was embarked upon very slowly and dimly, sometimes resentfully, as some savage on the fringe of civilization might awkwardly rediscover the wheel. When I did encounter feminist writings, I was often put off by the poor quality of the scholarship. Sherfey's book is a case in point: highly original insights were imbedded in what seemed to me a confused and often erroneous matrix. Nevertheless, the notion of “solidarity” with other women and, indeed, the possibility that female primates generally might confront shared problems was beginning to stir and to raise explicit questions about male–female relations in the animals I studied. That is, there were two (possibly more) interconnected processes: an identification with other females among monkeys taking place at roughly the same time as a change in my definition of women and my ability to identify and articulate the problems women confront.

Such an admission raises special problems for primatologists. My discipline has the choice of either dismissing me as a particularly subjective member of the tribe or else

acknowledging that the tribe has some problems with objectivity. It is almost a cliché to mention now how male-biased the early animal behavior studies were (see Wasser, 1983). But, in the course of the last decade of revision, are we simply substituting a new set of biases for the old ones?

The feminist charge that most fields, including psychology, biology, and animal behavior, have been male-centered, is, I think, by now undeniable. Yet to me, the noteworthy and encouraging thing is how little resistance researchers in my own field have exhibited when biases are pointed out. Although I still sense in Britain a reluctance to admit that male bias was ever actually a problem, among primatologists in the United States it is now widely acknowledged, and this has to be a healthy sign. Indeed, in animal behavior and primatology, there has been something more like a small stampede by members of both sexes to study female reproductive strategies, as well as perhaps a rush to substitute a new set of biases for the old. (That is, among feminist scholars it is now permissible to say that males and females are different, provided one also stipulates that females are more cooperative, more nurturing, more supportive—not to mention equipped with unique moral sensibilities; among sociobiologists *kudos* accrue to the author of the most Machiavellian scenario conceivable.)

There are of course antidotes to the all-too-human element that plagues our efforts to study the natural world. Common sense in methodology is one. No one will ever again be permitted to make pronouncements about primate breeding systems after having studied only one sex or after watching only the conspicuous animals. A recognition of the sources of bias is another. If, for example, we suspect that identification with same-sex individuals goes on or that certain researchers identify with the dominant and others with the oppressed and so forth, we would do well to encourage multiple studies, restudies, and challenges to current theories by a broad array of observers. We would also do well to distinguish explicitly between what we know and what we know is only interpretation. But really (being generous) this is science as currently practiced: inefficient, biased, frustrating, replete with false starts and red herrings, but nevertheless responsive to criticism and self-correcting, and hence better than any of the other more unabashedly ideological programs currently being advocated.⁴

Acknowledgments

In the preface to her recent book *Mother Care: Other Care*, my colleague in behavioral biology Sandra Scarr (1984, p. xi) notes, “I wish I could thank all the wonderful graduate school professors who helped me to realize the joys of combining profession and motherhood; unfortunately there weren’t any at Harvard in the early 1960s.” A decade later, things at Harvard—at least in the biologically oriented part of Harvard that I encountered—had changed remarkably little. As I think back on those postgraduate years (my undergraduate experience at Harvard was a wonderful and very different

story), I can not recall a single moment's fear of success, but what I do distinctly recall was the painful perception that there were professors and fellow students (no women in those years) who acted as if *they* feared that I might succeed. Intellectually, it was a tremendously exciting environment, filled with stimulating and occasionally inspirational teachers and coworkers. It was also an environment that was socially and psychologically hostile to the professional aspirations of women. But there were exceptions, exceptions made all the more significant because they were rare. In particular, I remain deeply grateful to Ed Wilson for encouragement and for unfailing behind-the-scenes support (probably the best kind) offered not only to me, but to other women ethologists both younger and older than myself.

Writing now from an ecological niche so benign as to cause me to wonder if perhaps my zeal as a feminist won't now lapse as a consequence, it is a pleasure to acknowledge discussions with Leo Berenstain, Daniel Hrdy, Jon Marks, David Olmsted, Peter Rodman, and Judy Stamps, who read and gave me detailed criticisms of this paper. I also thank Jeanne Altmann, Alison Jolly, Jane Lancaster, Linda Partridge, Joannie Silk, Meredith Small, Barbara Smuts, and the Pats, Whitten and Wright, for valuable discussion, and thank Ruth Bleier and Erik Eckholm for inciting me to think along the lines that I do at the end of this paper. Not least, I thank Nancy McLaughlin for her assistance in preparing the manuscript.

Notes

1. In this chapter, I designate women researchers by spelling out their first names; the point of using this admittedly odd convention will become clear in the section on "The Role of Women Researchers."
2. For want of a better term, *polyandrous* is used here to refer to a female with more than one established mate. The term *promiscuous* will be used to refer to multiple, brief consortships, some of which may last longer. Whereas *polyandrous* is a poor term because it suggests some stable, institutionalized relationship, which is probably wrong for describing tamarins, *promiscuous* is also problematic. It implies a lack of selectivity among females, which may or may not be the case. Davies and Lundberg (1984, p. 898) have recently proposed using the term *polygnandry* to refer to "two or three males sharing access to two, three or four females." Such a term applies to Barbary macaques and might be a good one for the baboon situation except that there is not a 100% overlap in the females with which each male mates. Clearly, the terminology needs to be cleared up, but for the time being the important point is to emphasize the contrast between what we now know and the old stereotype of monandrous females selecting a single mate.
3. It should be noted however that membership in the ASP signals the *motivation* of women to join, since all one has to do is sign up and pay dues. Recognition and acceptance may be quite different. Contrast, for example, the position of women on editorial boards (4 of 40 on the *International Journal of Primatology* are women; 0 of 19 on the editorial board of the journal *Behavioral*

Ecology and Sociobiology). When we examine the prestigious roster of *elected* fellows of the Animal Behavior Society for 1985, 1 of 62 is a woman. All 19 autobiographical chapters in *Leaders in the Study of Animal Behavior* are by men.

4. Recent feminist programs advocating “conscious partiality” come to mind. If an unbiased knowledge is impossible, this argument runs, an explicitly biased, politically motivated approach is preferable to the illusion of impartial research.

References

Abernethy, V. (1978). Female hierarchy: An evolutionary perspective. In L. Tiger & H. Fowler (Eds.), *Female Hierarchies*. Chicago: Beresford Book Service.

Alatalo, R. V., Lundberg, A., & Stahlbrandt, K. (1982). Why do pied flycatcher females mate with already mated males. *Animal Behaviour*, 30, 585–593.

Altmann, J. (1980). *Baboon mothers and infants*. Cambridge: Harvard University Press.

Altmann, S. (Ed.). (1965). *Japanese monkeys: A collection of translations*. Edmonton, Canada: The editor.

Andelman, S. (forthcoming). Concealed ovulation and prolonged receptivity in vervet monkeys (*Cercopithecus aethiops*).

Bateman, A. J. (1948). Intra-sexual selection in drosophila. *Heredity*, 2, 349–368.

Benshoof, L., & Thornhill, R. (1979). The evolution of monogamy and concealed ovulation in humans. *Journal of Biological Structures*, 2, 95–106.

Bleier, R. (1984). *Science and gender*. Elmsford, NY: Pergamon.

Bray, O. E., Kennelly, J. J., & Guarino, J. L. (1975). Fertility of eggs produced on territories of vasectomized red-winged blackbirds. *Wilson Bulletin*, 87, no. 2, 187–195.

Burley, N., & Symanski, R. (1981). Women without: An evolutionary perspective on prostitution. In *The immoral landscape: Female prostitution in Western societies*. Toronto: Butterworth.

Busse, C., & Hamilton, W. J., III. (1981). Infant carrying by male chacma baboons. *Science*, 212, 1281–1283.

Clutton-Brock, T. H., & Harvey, P. (1976). Evolutionary rules and primate societies. In P. P. G. Bateson & R. A. Hinde (Eds.), *Growing points in ethology*. Cambridge: Cambridge University Press.

Cords, M. (1984). Mating patterns and social structure in redtail monkeys (*Cercopithecus ascanius*). *Zeitschrift für Tierpsychologie*, 64, 313–329.

Cronin, C. (1980). Dominance relations and females. In D. R. Omark, F. F. Strayer, and D. G. Freeman (Eds.), *Dominance relations*. New York: Garland Press.

Daly, M., & Wilson, M. (1983). *Sex, evolution and behavior*. Boston: Willard Grant Press.

- Darwin, C. (1871). *The descent of man and selection in relation to sex* (1887 edition). New York: D. Appleton and Co.
- Davies, E. M., & Boersma, P. D. (1984). Why lionesses copulate with more than one male. *The American Naturalist*, 123, no. 5, 594–611.
- Davies, N. B., & Lundberg, A. (1984). Food distribution and a variable mating system in the dunnock, *Prunella modularis*. *Journal of Animal Ecology*, 53, 895–912.
- Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.
- DeVore, I. (Ed.). (1965). *Primate behavior*. New York: Holt, Rinehart and Winston.
- Diamond, J. (1984). Theory and practice of extramarital sex. *Nature*, 312, 196.
- Dunbar, R. (1984). *Reproductive decisions: An economic analysis of gelada baboon social strategies*. Princeton, NJ: Princeton University Press.
- Eaton, R. (Ed.). (1976). *The world's cats II*. Seattle, WA: Feline Research Group, Woodland Park Zoo.
- Edwards, G. (1758). *Gleanings of Natural History* (Vol. 5). London: College of Physicians.
- Fedigan, L. (1984). Sex ratios and sex differences in primatology (book review of *Female primates*). *American Journal of Primatology*, 7, 305–308.
- Freedman, D. (1979). *Human sociobiology: A holistic approach*. New York: The Free Press.
- Fujioka, M., & Tamagishi, S. (1981). Extramarital and pair copulations in the cattle egret. *Auk*, 98, 134–144.
- Gladstone, D. (1979). Promiscuity in monogamous colonial birds. *The American Naturalist*, 114, no. 4, 545–557.
- Goldizen, A. W., & Terborgh, J. (in press). Cooperative polyandry and helping behavior in saddle-backed tamarins (*Saguinus fuscicollis*). Proceedings of the IXth Congress of the International Primatological Society. Cambridge: Cambridge University Press.
- Goodall, J. (1971). *In the shadow of man*. Boston: Houghton Mifflin.
- Haraway, D. (1976). The contest for primate nature: Daughters of man-the-hunter in the field. In M. Kann (Ed.), *The future of American democracy: Views from the left*. Philadelphia, PA: Temple University Press.
- Hartung, J. (in press). Matrilineal inheritance: New theory and analysis. *The Behavioral and Brain Sciences*.
- Hausfater, G. (1975). Dominance and reproduction in baboons (*Papio cynocephalus*). *Contributions to Primatology* (Vol. 7). Basel, Switzerland: S. Karger.
- Hausfater, G., & Hrdy, S. B. (Eds.). (1984). *Infanticide: Comparative and evolutionary perspectives*. New York: Aldine.

Hrdy, D. B. (1979). Integrated field study of the behavior, genetics and diseases of the Hanuman langur in Rajasthan, India. Proposal submitted to the National Science Foundation.

Hrdy, S. B. (1974). Male–male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatologica*, 22, 19–58.

Hrdy, S. B. (1976). The care and exploitation of nonhuman primates by conspecifics other than the mother. *Advances in the Study of Behavior*, VI, 101–158.

Hrdy, S. B. (1977). *The langurs of Abu: Female and male strategies of reproduction*. Cambridge: Harvard University Press.

Hrdy, S. B. (1979). Infanticide among animals: A review, classification and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology*, 1, 3–40.

Hrdy, S. B. (1981). *The woman that never evolved*. Cambridge: Harvard University Press.

Hrdy, S. B. (1984). Introduction: Female reproductive strategies. In M. Small, (Ed.), *Female primates: Studies by women primatologists*. New York: Alan Liss.

Hrdy, S. B., Hrdy, D. B., & Bishop, J. (1977). *Stolen copulations*. 16 mm color film. Peabody Museum.

Hrdy, S. B., & Whitten, P. (1986). The patterning of sexual activity. In D. Cheney, R. Seyfarth, B. Smuts, R. Wrangham, & T. Struhsaker (Eds.), *Primate societies*. Chicago: University of Chicago Press.

Hrdy, S. B., & Williams, G. C. (1983). Behavioral biology and the double standard. In S. K. Wasser (Ed.), *Social behavior of female vertebrates*. New York: Academic Press.

Jay, P. (1963). The female primate. In S. Farber & R. Wilson (Eds.), *The potential of woman*. New York: McGraw-Hill.

Jolly, A. (1985). *The evolution of primate behavior*. New York: Macmillan.

Kawai, M. (1958). On the system of social ranks in a natural troop of Japanese monkeys: I. Basic rank and dependent rank. *Primates*, 1–2, 111–130.

Kawamura, S. (1958). Matriarchal social ranks in the Minoo-B troop: A study of the rank system of Japanese monkeys. *Primates*, 1–2, 149–156.

Keller, E. F. (1983). *A feeling for the organism: The life and work of Barbara McClintock*. New York: W. H. Freeman.

Kleiman, D. (1977). Monogamy in mammals. *Quarterly Review of Biology*, 52, 39–69.

Kleiman, D., & Malcolm, J. (1981). The evolution of male parental investment in mammals. In D. J. Gubernick & P. H. Klopfer (Eds.), *Parental care in mammals*. New York: Plenum Press.

Koyama, N. (1967). On dominance rank and kinship of a wild Japanese monkey in Arashiyama. *Primates*, 8, 189–216.

Lamb, M. (1984). Observational studies of father-child relationships in humans. In D. Taub (Ed.), *Primate paternalism*. New York: Van Nostrand Reinhold.

- Lancaster, J. (1975). *Primate behavior and the emergence of human culture*. New York: Holt, Rinehart and Winston.
- Lott, D. (1981). Sexual behavior and intersexual strategies in American Bison. *Zeitschrift für Tierpsychologie*, *56*, 97–114.
- Lumpkin, S. (1983). Female manipulation of male avoidance of cuckoldry behavior in the ring dove. In S. C. Wasser (Ed.), *The social behavior of female vertebrates*. New York: Academic Press.
- MacKinnon, J. (1978). *The ape within us*. New York: Holt, Rinehart and Winston.
- Markow, T. A., & Ankney, P. F. (1984). *Drosophila* males contribute to oogenesis in a multiple mating species. *Nature*, *224*, 302–303.
- Moore, J. (1985). Demography and sociality in primates. Doctoral dissertation, Harvard University. Cambridge.
- Mori, U., & Dunbar, R. I. M. (in press). Changes in the reproductive condition of female gelada baboons following the takeover of one-male units. *Zeitschrift für Tierpsychologie*.
- Morris, S. (1979, August). Darwin and the double standard. *Playboy Magazine*.
- Parker, G. A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biological Review*, *45*, 525–567.
- Ransom, T., & Ransom, B. (1971). Adult-male–infant interactions among baboons (*Papio anubis*). *Folia Primatologica*, *16*, 179–195.
- Rowell, T. (1972). *Social behaviour of monkeys*. Baltimore, MD: Penguin Books.
- Rowell, T. (1984). Introduction: Mothers, infants and adolescents. In M. Small (Ed.), *Female primates*. New York: Alan Liss.
- Sayers, J. (1982). *Biological politics*. London: Tavistock.
- Scarr, S. (1984). *Mother care: Other care*. New York: Basic Books.
- Seyfarth, R. (1978). Social relationships between adult male and female baboons, part 2: Behavior throughout the female reproductive cycle. *Behaviour*, *64*, nos. 3–4, 227–247.
- Shaw, E., & Darling, J. (1985). *Female strategies*. New York: Walker.
- Sherfey, M. J. (1973). *The evolution of female sexuality* (first published 1966). New York: Vintage Books.
- Small, M. (Ed.). (1984). *Female primates*. New York: Alan Liss.
- Small, M. (Forthcoming). Primate female sexual behavior and conception: Is there really sperm to spare?
- Smith, J. M. (1984). Optimization theory in evolution. In E. Sober (Ed.), *Conceptual issues in evolutionary biology*. Cambridge, MA: The MIT Press.

- Smith, R. (1984). Sperm competition. In *Sperm competition and the evolution of animal mating systems*. New York: Academic Press.
- Smuts, B. B. (1985). *Sex and friendship in baboons*. New York: Aldine Publishing Co.
- Stacey, P. B. (1982). Female promiscuity and male reproductive success in social birds and mammals. *The American Naturalist*, 120, no. 1, 51–64.
- Stein, D. (1981). The nature and function of social interactions between infant and adult male yellow baboons (*Papio cynocephalus*). Doctoral dissertation, University of Chicago.
- Stein, D. (1984). Ontogeny of infant–adult male relationships during the first year of life for yellow baboons (*Papio cynocephalus*). In D. Taub (Ed.), *Primate paternalism*. New York: Van Nostrand Reinhold.
- Symons, D. (1979). *The evolution of human sexuality*. Oxford: Oxford University Press.
- Taub, D. (1980). Female choice and mating strategies among wild Barbary macaques (*Macaca sylvana*). In D. Lindburg (Ed.), *The macaques*. New York: Van Nostrand Reinhold.
- Taub, D. (1984a). Male–infant interactions in baboons and macaques: A critique and reevaluation. Paper presented at the American Zoological Society Meetings, Philadelphia, PA.
- Taub, D. (1984b). *Primate paternalism*. New York: Van Nostrand Reinhold.
- Tiger, L. (1977). The possible biological origins of sexual discrimination. In D. W. Brothwell (Ed.), *Biosocial man*. London: The Eugenics Society.
- Tilson, R. (1981). Family formation strategies of Kloss' gibbons. *Folia Primatologica*, 35, 259–287.
- Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man*. Chicago: Aldine.
- Trivers, R. L. (1985). *Social evolution*. Menlo Park, CA: Benjamin/Cummings.
- Tsingalia, H. M., & Rowell, T. E. (1984). The behaviour of adult male blue monkeys. *Zeitschrift für Tierpsychologie*, 64, 253–268.
- Turner, M. E., & Anderson, W. W. (1983). Multiple mating and female fitness in *Drosophila pseudoobscura*. *Evolution*, 37, no. 4, 714–723.
- Tutin, C. (1975). Sexual behaviour and mating patterns in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). Doctoral dissertation submitted to the University of Edinburgh, Edinburgh.
- Van den Berghe, E. (1984). Female competition, parental care, and reproductive success in salmon. Paper presented at Animal Behavior Society Meetings, Cheney, Washington, August 13–17.
- Vogt, J. (1984). Interactions between adult males and infants in prosimians and New World monkeys. In D. Taub (Ed.), *Primate paternalism*. New York: Van Nostrand Reinhold.
- Wasser, S. C. (Ed.). (1983). *The social behavior of female vertebrates*. New York: Academic Press.

Wasser, S. C., & Barash, D. (1984). Reproductive suppression among female mammals. *Quarterly Review of Biology*, 513–538.

Williams, G. C. (1966). *Adaptation and natural selection*. Princeton, NJ: Princeton University Press.

Williams, G. C. (1975). *Sex and evolution*. Princeton, NJ: Princeton University Press.

Wilson, E. O. (1978). *On human nature*. Cambridge: Harvard University Press.

Wirtz, P. (1983). Multiple copulations in the Waterbuck. *Zeitschrift für Tierpsychologie*, 61, 78–82.

Wright, P. (1984). Biparental care in *Aotus trivirgatus* and *Callicebus molloch*. In M. Small (Ed.), *Female primates*. New York: Alan Liss.

Zuckerman, Sir S. (1932). *The social life of monkeys and apes*. London: Butler and Turner, Ltd.