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Cover: A common langur with its young, in Ranthambhor, India. A special report on the debate over whether animals influence the sex of their offspring begins on page 63. Photograph by Günter Ziesler; Peter Arnold, Inc.
Can parents influence the sex of their offspring? New research indicates many creatures, including humans, do change the odds to favor Daughters or Sons.
"May you be blessed with eight sons." This traditional benediction at a Hindu marriage is symptomatic of a preference for sons deeply felt across much of the world. Soon after the new wife conceives, the marriage blessing is followed up by a second ceremony. Mantras are chanted so that if, by some mischance, the fetus is female, she can be magically transformed into a son. In the words of one ethnographer in India: "A daughter's birth makes even a philosophic man gloomy... whereas a son's birth is like sunrise in the abode of gods."

Today more than mantras are available to assist parents in their quest for the desired sex. For a brief period last year Americans could have purchased from certain drugstores "Gender Choice Child Selection Kits" for a mere $49.95. The kits contained directions, thermometers, and paraphernalia for monitoring vaginal mucus, all so as to determine the best moment for conceiving a son or a daughter. That was before the U.S. Food and Drug Administration decided that the implied claims of the packages, some of which were pink, some blue, had not been substantiated. All these kits should by now have been pulled from drugstore shelves.

More reliable than the kits are newly announced methods for separating sperm carrying the X chromosome from that bearing the Y. This high-tech approach, pioneered at the University of Tokyo, requires artificial insemination and, for that reason, may be less appealing to many prospective parents. It is also simply beyond the means of most people. Currently, the most widely practiced procedure for choosing the sex of offspring is prenatal sex determination followed by selective abortion. The British journal Nature recently published statistics, provided by a Bombay social worker, on abortions at Indian clinics: out of a sample of 8,000 abortions, 7,997 involved female fetuses. Nevertheless, nowhere is sex-selective abortion officially sanctioned. In fact, Maharashtra has just become the first state in India to ban prenatal sex determination for precisely this reason. In traditional societies, infanticide has always been the option of last resort. University of Colorado psychologist Leigh Minturn has estimated that sex-biased infanticide has characterized some 9 percent of the world's cultures, and more often than not, the unwanted sex has been female.

Infanticide and abortion are extreme measures. More often, the discrimination is more subtle. The little boy is

Worldwide, boy and girls are born in approximately equal numbers, but in many cultures, sons are preferred.

Photograph by Irving Penn © 1988 by The Condé Nast Publications Inc.
pampered and fed; the girl is more or less neglected. In cultures as far apart geographically as twentieth-century Lebanon and Ecuador, we find evidence that boys are suckled twice as long as girls, a pattern also documented for parts of medieval France. Only in a minority of the world’s cultures, many of them matrilineal gardening societies, do we find widespread sentiments leading to the preferential treatment of daughters.

Many reasons are offered to explain why sons are so desirable: their strength and potential contributions as laborers, warriors, or hunters; their role in perpetuating the family name or performing special rites when parents die; and the requirement in some societies that daughters, but not sons, bring expensive dowries to their marriage. But regardless of the reason, and totally apart from ethical considerations, the fact remains that the bias in favor of sons dates back many generations. The birth of a son or the birth of a daughter . . . on the outcome has hung many a mother’s reputation— and occasionally the fate of a nation. And this is precisely where the problem becomes an interesting one for evolutionary biologists. Here we have a species that produces notably costly offspring. Nine months of gestation at a cost of some 80,000 calories, followed by a potentially hazardous delivery, and after all this, the parents neglect or dispose of the baby. From an evolutionary point of view, this is puzzling inefficiency. Why hasn’t natural selection led to a race of parents who automatically produce the desired sex?

A survey of the planet’s life-forms suggests that the feat might be possible. For an assortment of fishes, reptiles, worms, and plants, sexual identity can be determined by something as seemingly simple as where on the beach a mother lumbers up to lay her eggs or where seeds happen to fall. In many turtle species, eggs in sunny spots develop into females; those in the shade, males—a rule of thumb that also holds for some orchids, which only produce female flowers in full light. The rule is reversed for many other species.

In at least one species of fish, sex is determined by a combination of genetic and environmental factors. David Conover and Stephen Heins, both of the Marine Sciences Research Center at the State University of New York at Stony Brook, studied the Atlantic silverside, a fish found as far north as the Canadian Provinces and as far south as Florida. They found that in southern populations, sex is determined by temperature: most offspring born early in the breeding season, when the water is relatively cool, are females; those born later, by which time the water has warmed up, are mostly males. Dividing things up this way may be adaptive: fish born early in the season have a longer time to grow, and being big appears to be more of an advantage to females than to males—large females are more fecund than small ones. At higher latitudes, sex is determined genetically, with temperature playing little or no role. This, too, seems to make sense: the further north the fish are, the shorter the growing and breeding seasons, and the shorter the breeding season, the less effect birth date—that is, early or late in the season—could have on body size.

In all these cases, the question can be asked, Is there truly anything adaptive going on, either for the individuals involved or for the population at large? According to Conover, for the silversides, the answer seems to be a relatively confident yes. The reptile situation is murkier. By laying her eggs in the sun, for example, does the American alligator “intend” to skew the sex ratio of her offspring (that is, the number of sons to the number of daughters) toward females? And if so, why? Or is the association an artifact of something else?

One group of organisms for which we have some answers to these sorts of questions are the haplodiploid insects—wasps, bees, and ants. In these insects, fertilized eggs develop into daughters, unfertilized eggs into males. And in many species of bees and wasps, the mother does indeed demonstrate exquisitely fine tuned control over the sex ratio of her progeny. At the time she mates, the female stashes the sperm away in special storage chambers within her
Warm American alligator eggs hatch as males; cool ones as females.

Unlike the radically skewed sex ratios of fig wasps, most mammalian and avian sex ratios at birth fall close to 50/50. In our own species, for example, between 102 and 106 little boys are born for every 100 little girls, roughly 51 percent males, a classically conservative mammalian sex ratio. (No one is certain why slightly more boys than girls are born, but it may be to compensate for the greater vulnerability of males and their higher mortality rates at all ages.) Traditionally, two reasons have been given to explain why this should be so. First, sex in mammals is chromosomally determined. The somatic cells of all females carry two X chromosomes, while those of males carry one X and one Y. The single gene recently found to determine maleness is almost always found on the Y chromosome. During meiosis, each egg receives one X chromosome, and each sperm receives either an X or a Y. The likelihood of an egg being fertilized by an X-bearing sperm, to become a daughter, or a Y-bearing sperm, to become a son, is thought to be as random as the flip of a coin. Also, once fertilization occurs, gender is for keeps, with none of the hanky-panky some fish are capable of—changing sex if size and circumstances are favorable. Chromosomal sex determination works similarly in birds, except the configurations are reversed: the females carry two types of sex chromosomes—known as Z and W—while males carry two Z chromosomes.

The second major constraint thought to discourage birds and mammals from specializing in a favorite sex is explained by the time-honored axiom of population genetics known as Fisher’s theorem of the sex ratio. Mathematician Ronald Fisher reasoned that so long as producing sons and daughters requires equivalent amounts of parental resources, so long as outbreeding prevails (that is, so long as brothers do not routinely breed with sisters), and so long as all individuals have the same chance to breed, then equal numbers of sons and daughters should be produced.

To better understand Fisher’s insight, imagine a population in which certain parents started to specialize in producing offspring of a particular sex—say, sons. When these offspring mature and seek to breed, they will find themselves in a world with many more males than females. Too bad for them. Whereas all females will be able to breed, only a portion of males will find a mate. Too bad for their parents, too, since on average, parents specializing in sons will be penalized by having fewer grandchildren, while parents producing daughters will be rewarded, at least temporarily. Over time, natural selection favors female
specialists, with the predictable outcome: a glut of daughters. Once again the pendulum will swing back toward son producers. And on it goes, with the pendulum swinging first to daughters, then to sons. The outcome? A population with more or less equal numbers of sons and daughters.

Fisher's model helps to explain why one-to-one sex ratios should be so common among many animals. But alter the critical underlying variables—for example, step up inbreeding—and the rules of the game change. This is just what seems to have happened to some little lemmings of the north.

The wood lemming of northern Europe and the varying lemming, which ranges from Canada to Siberia, have evolved a wasplike capacity to dramatically bias the sex ratio of their offspring. In the lemmings' case, the skew is always toward daughters. Three to four times as many females as males are born in the population, with some individual mothers producing no sons at all. The lemmings' trick is accomplished by curious changes on the X chromosome. In the case of the wood lemming, a peculiarly "imperialistic" version of the X chromosome has evolved with the power to overwhelm the male-producing Y chromosome. Paired with one of these "super-X" chromosomes, a Y chromosome fails to express itself and the X-Y individual develops into a female.

Just why such chromosomal oddities have evolved in these lemmings and, so far as we know, in no other mammals remains a matter for debate. But as they tunnel through moss in the dark recesses of fir forests, feeding on red wortleberries and the bark of juniper trees, these lemmings are subject to the vagaries of good and bad years, and a consensus is emerging that the boom-or-bust population cycles characteristic of these small arctic mammals play a role. According to this interpretation, lemmings in a "bust" year would find themselves scarce, isolated in pockets where brothers would have little choice but to mate with their sisters. The same local mate competition that led mother fig wasps to produce ten daughters for every son may at some point in the past have also favored the one-in-a-million wood lemming carrying the aberrant super-X chromosome.

Most other mammals, however, have never been subject to such inbred conditions, and current wisdom still rates mammals and birds as resolutely committed to more-or-less equal production of sons and daughters. Yet recently, biologists have been turning up instances of sex ratio at birth (or shortly after) significantly different from the expected 1/1. At issue are not the striking biases found in fig wasps, but more subtle biases on

**Manipulating Mothers**

The jewel wasp is a consummate artist at controlling the sex of its offspring. Found throughout the world, this small parasitic wasp (at 3 millimeters, it is smaller than a fruit fly) delivers a lethal sting and then lays its eggs in the pupae of various species of blowfly. Typically, from twenty to forty young wasps develop on each host. The wasps mate immediately upon emerging from the host pupa, and mated females then disperse in search of new fly pupae in which to deposit their own eggs. The pupae relished by the wasps are usually found under carcasses or in bird nests. Despite the deliberate human sensibility—rather repulsive circumstances under which it lays its eggs, I have found the reproductive affairs of this little wasp to be intriguing.

Male jewel wasps have short wings and cannot fly. Since the wasps mate right after emergence, brothers and sisters sometimes have only one other to mate with. Such inbreeding occurs, for example, when all the wasps emerging from one bird nest or carcass are produced by a lone female. At other times, many females will parasitize the same nest or the many blowfly pupae patchily distributed under a carcass, and then mating is spread among many females.

Impressively, the jewel wasp can alter the sex ratio of her progeny depending on how many other females have discovered the same patch of potential hosts. When by herself, a female will produce about 85 percent daughters, with just enough sons to inseminate all her daughters and thus with a minimum of energy wasted on sons competing with one another. When she finds herself in the company of other egg-laying females, however, she changes her tactics dramatically. Now, she needs more sons to compete with males of other families, so she shifts the sex ratio of her offspring closer to 50/50.

Sometimes two females lay their eggs in the very same blowfly pupa. If that pupa is some distance away from any others, then mating competition will be restricted to the offspring of those two females. In that case, the first wasp to find such a host lays about 85 percent daughters, as expected. However, if the second female encounters the pupa within a day or two, she can detect that it has already been attacked. She accomplishes this by "tasting" chemical changes in the host with her stinger, which is also a complicated sensory organ. If she "decides" to insert a single egg into the host, it will be a son. Because of the many daughters laid by the first female, the second female's son will un-
doubtlessly have many mating opportunities. (Eggs laid within two days of each other routinely emerge as adults at the same time.) If, however, she "decides" to lay many eggs, she will produce both sons and daughters. The more eggs she lays, the more she will bias her own production toward daughters.

Understanding the intricacies of the jewel wasp's ability to manipulate the sex ratio of its offspring is challenge enough. Complicating the picture is a recently discovered assemblage of "parasitic" genetic factors within the species that can usurp and undermine this ability. These parasitic genes (both inherited microorganisms and "renegade" chromosomes have been found) promote their own transmission by distorting the wasp's sex ratio. One of these genes—known as the paternal sex ratio element—is carried by about 10 percent of jewel wasps and causes the female to produce all males, whether or not she has fertilized some of her eggs. (In wasps and other haplodiploid organisms, only fertilized eggs develop into females.) Males carrying the paternal sex ratio element transmit it through their sperm to eggs during fertilization. Normally these eggs would develop into females, but instead the paternal sex ratio element somehow destroys the paternal chromosomes in the egg, thus converting a diploid female into a haploid male. This amazing accomplishment is evolutionarily advantageous for the paternal sex ratio element since—unlike all other known parasitic genes—it is transmitted through males but not through females. In contrast, it is decidedly detrimental to the rest of the father's genome. Such a gene can also cause problems for the whole population since an all male population will obviously go extinct. This system of birds parasitized by flies parasitized by wasps parasitized by genetic elements makes poignant Jonathan Swift's famous quote:

So, Nat’ralists observe, a Flea
Hath smaller Fleas that on him prey;
And these have smaller fleas to bite ‘em
And so proceed ad infinitum

John H. Werren

Female jewel wasp on fly pupa
Sonny Side Up—or Down

Many egg-laying reptiles are of special interest to sex ratio theory because the incubation temperature of the egg determines whether it will hatch as male or female. Temperature-dependent sex determination first gained recognition through the work of Claude Pieau in France during the 1970s. Pieau studied two species of European turtles, but scientists around the world have since investigated the phenomenon in many other reptiles. The early studies were in the laboratory; more recent work in the field has confirmed the temperature effect in nature.

Unlike birds and mammals, only some species of reptiles carry chromosomes directly involved in the genetic determination of gender; many others do not. So far, all of the reptiles known to have temperature-dependent sex determination are alike in lacking sex chromosomes. The particular effect that temperature has on the sex ratio, however, differs markedly among these species. In many
crocodilians, such as the American alligator, and in some lizards, high temperatures produce males and low temperatures produce females. The pattern is reversed in many turtles. A more complicated pattern occurs in several turtles and at least one crocodilian, where females develop at high and low extremes and males develop at intermediate temperatures. Finally, in some turtles, lizards, and snakes, temperature has no apparent effect on sex determination. Presumably, the many reptile species that do have sex chromosomes would fall into this category, but only a few of those species have been studied in this regard.

Also, unlike birds and mammals, most reptiles do not incubate their eggs or care for their young. Some crocodilians, such as the American alligator, construct mounds of rotting vegetation in which their eggs are laid and then briefly tended, but most reptile mothers simply bury their eggs in the ground and abandon them.

Nevertheless, the mother’s action can play a decisive role in determining the sexual fate of her little embryos, since it is up to her to “decide” just where to lay the eggs. An alligator that builds her nest in a wet (hence cool) marsh will produce many more daughters than one that builds on an elevated (warm) levee. Freshwater turtle mothers may select sunny or shady nesting spots; these microclimatic differences can result in offspring sex ratios ranging from all female to all male.

The effect of temperature can even be felt in a single nest. The common snapping turtle typically lays thirty to fifty eggs per nest, each egg being shaped like a one-inch Ping-Pong ball. With so many eggs piled on top of one another in the nest, the bottommost eggs may be 10 cm below those on the top and may incubate at a significantly cooler temperature. The sex ratio thus sometimes varies within the nest, for example, with all females developing in the top eggs and all males in the bottom.

Is there any advantage in having sex determined by temperature rather than by sex chromosomes? We do not know yet, but one model currently under study suggests that an individual’s incubation temperature affects its fitness later in life, that is, how successful it will be in producing offspring of its own. To take an extreme case, if heat rendered all males sterile, then natural selection would favor the evolution of a temperature-dependent sex determination that caused all embryos developing at high temperatures to be female. Work is under way in several research laboratories to see whether the temperature effect is, in fact, tied to reproductive fitness, but scientists still have a long way to go before they will be able to fully understand the adaptive significance of this unusual mechanism of sex determination.

James J. Bull

the order of four of one sex to six of the other. In an effort to capture these elusive trends, a body of work somewhere between knowledge and sheer speculation has arrived at center stage. Inspired by a considerable degree by Hamilton’s suggestion twenty years ago that different circumstances might select for different mixes of sons and daughters, sex ratio research has become one of the fastest-growing, most talked about, most exciting, and most speculative areas in all of evolutionary biology. There are many like myself who are convinced one day, skeptical the next. Sometimes I am certain that skewed sex ratios exist and that they must have some adaptive significance; then I begin to worry that we are all simply carried away, caught in the scientific equivalent of seventeenth-century Dutch tulipmania, when a whole nation was swept into bidding for an obscure, practically useless, but pretty Turkish flower bulb. All this sound and fury, one of the hottest Ph.D. topics going—surely it signifies something. Or does it?

Let us begin with Morris Gosling and the mystery of the missing coypu. Coypu, or nutria, are aquatic, guinea-pig-like creatures native to South America. Because of their luxurious fur, coypu have been exported to fur farms around the world. As prolific as they proved to be footloose, descendants of escaped coypu have also become something of a pest. To deal with the problem, Britain’s Ministry of Agriculture set up the Coypu Research Laboratory to control them. Enter zoologist Gosling, enlisted to help trap the coypu from the marshlands of eastern England.

As a scientist, Gosling was not content merely to eliminate his quarry; he wanted to know what was going on inside them. So he dissected 5,853 female coypu. Of these, 1,485 had embryos old enough to count and to sex. Examining them, Gosling made a curious discovery. As he studied small litters (those with no more than four embryos), he noticed that many contained mostly male embryos, while remarkably few small litters were predominantly female. After additional investigation—in which he compared young females with old and small litters with large—he came to the conclusion that his findings could be plausibly explained in only one way: mother coypu were somehow selectively aborting small, mostly female litters. Furthermore, the fatter and healthier the female, the more likely her body was to terminate such a pregnancy.

Why, Gosling wondered, should such a seemingly counterproductive process go on? Not long after Gosling presented his preliminary findings, another British zoologist was puzzling over fifteen years worth of data on the reproductive ecology of red deer on the isle of Rhum,
Among red deer, socially dominant mothers in good condition produce more sons, such as these stags, than daughters.

Off Scotland, Tim Clutton-Brock, of the University of Cambridge, and his colleagues had found that year after year, the socially dominant mothers in the best physical condition were producing more sons than daughters. (For an earlier report on this study, see Natural History, November 1982.) Furthermore, these same mothers were likely to have more grandchildren by their sons than by their daughters. During this same period, low-ranking mothers (presumed to be in worse shape) were giving birth to more daughters than sons. And although the subordinate mothers generally had fewer grandchildren than did dominant females, what grandchildren they did have were more apt to have been born to their daughters than sired by their sons. All in all, mothers seemed to adjust their probability of producing a son or a daughter in line with their own condition, and Clutton-Brock suspected that the overproduction of sons by dominant females and their underproduction by subordinate ones was adaptive, with each mother bearing the sex more likely to provide her with the most grandchildren.

If the full story be told, neither Clutton-Brock nor Gosling had simply out-of-the-blue happened to look at sex ratios in relation to the mother's condition. Both were aware of a controversial, even notorious, paper published in Science some years before. In 1973, biologist Robert Trivers and mathematician Dan Willard—both still graduate students when they did the work—audaciously proposed that there ought to be situations in which natural selection should favor biased sex ratios, rather than 50/50. Sometimes, parents ought to be able to adjust the energy and resources that they poured into the production of offspring so as to produce more of the sex most likely to translate that parental investment into subsequent reproductive success.

Implicit in Trivers and Willard's hypothesis was the far-ranging and general proposition that parents should bias investment according to the number of grandchildren they could expect to have from their sons as compared with their daughters. But the original model they spelled out was a very specific one. Their idea was that mothers in good condition should favor sons; those in poor condition, daughters. This state of affairs ought to hold for creatures satisfying two criteria. One, the mother's rank or condition must affect the breeding potential of her offspring. Two, sons in good condition must have the potential to sire more offspring than comparably healthy daughters could produce. The latter criterion certainly applies to red deer, coyu, and other polygynous species, in which a successful male may impregnate many females, quickly outstripping even the most fertile of females.

Supposedly, a high-ranking, especially fit mother has greater access to food and is free from harassment by other group members. Her son, fast growing and well nourished, should be bigger and stronger than the average male, well equipped to compete in the free-for-all contest for mates. Such a male, the argument runs, should sire a larger than average number of offspring, providing his mother with greater than average numbers of grandchildren.

At the other end of the scale, a low-ranking mother, harassed and underfed, could at best produce a scrawny son, who would have very few, if any, opportunities to
breed. For this mother, the conservative strategy would be to favor daughters, which regardless of their condition would be likely to produce at least a few offspring. Just exactly how this bias in favor of daughters might be brought about remains a mystery, but Trivers thought the most likely explanation was greater fetal mortality for males when the mother was stressed during pregnancy.

If you buy the underlying assumptions, the Trivers-Willard hypothesis is compellingly logical. But does anything like it occur in nature? Gosling’s answer, like Clutton-Brock’s, was yes. His interpretation of the coyote data is vintage Trivers-Willard. “Young females in better than average physical condition . . . abort small litters of predominantly female embryos . . . Large litters and small, predominantly male litters are retained,” he wrote in 1986. “Neonate size is positively correlated with female condition (and body size). The differences in body size at birth are carried through to adult size. These data are consistent with the hypothesis that when females are in above-average condition, it would pay them to invest preferentially in offspring of the sex whose chances of future RS [reproductive success] will benefit most.”

Yet many others remained far from convinced. For some, the reality of chromosomal sex determination simply ruled out the possibility that the wild Triversian dream could be true. For others, the idea that a mother’s condition could affect the sex of her offspring was outlandish. Many would have agreed with Harvard biologist Steve Austad as he recounted his own first reaction: “I wanted to finish off that notion once and for all.” With co-worker Mel Sunquist, Austad set about doing just that with a particularly elegant set of field experiments.
on opossums. No one could have been more surprised than they were by the results: better fed opossum mothers did indeed produce bigger babies, and those babies were indeed disproportionately male. This is when Austad switched from skeptic to the ranks of the converted.

Meg Symington's conversion took a different form. Symington, then a Ph.D. candidate at Princeton University, was studying spider monkeys in the rain forest of the Manu National Park in Peru. There she stood one day several years ago, head back, straining her eyes to peer through the heavy mists that hover over the park each rainy season. With the rains had come a peak of births in the population of monkeys she was following, and Symington was struggling for a glimpse of a new baby's genitalia in order to sex it correctly. Not that she wondered much. It was bound to be female, like all of the other births. Back at camp, she joked out loud: "Another female!"

But there was a visitor in camp that night, a young Dutch scientist, Carel Van Schaik, with a more than passing interest in sex ratio research. The visitor asked Symington the inevitable question: "But why should they all be female?" It was as if one of the Dutchman's countrymen from the seventeenth century, during the heyday of tulipmania, had just inquired of his neighbor if he had invested yet in the fabulous Turkish bulb that was going to make the people of Holland so rich. Symington was hooked.

Primateologists had long been aware that spider monkeys lived in hierarchical groups that contained mostly females. Some suggested that the males just lived elsewhere; others argued that males were more likely to die. No one seriously entertained the belief that more females were born. But by now, Symington had ceased to be blase about the run of female births in her sample. As she pored over her birth records, an answer emerged. It wasn't every spider monkey female that produced daughters, just the low-ranking ones.

Out of forty-six infants born between 1981 and 1986, twelve were male, thirty-two female, and two could not be accurately sexed. All of the twenty-one infants born to her lowest-ranking females were female. The probability that such a specialization in daughters could have occurred by chance was a staggering 1 in 10,000. Middle- and higher-ranking females produced equal numbers of sons and daughters. The highest-ranking females may have had a tendency to produce sons, but the sample size was too small to say for sure—six of eight were male. What was clear was that the dominant females who mothered these rare sons cared for them more, nursing them for a longer period than they suckled their daughters.

Why should this be? Was the answer linked to the

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**More Sons For Plump Possoms**

An entire litter of newborn opossums weighs less than a dime and fits comfortably in a teaspoon, and although they are capable of using their forelimbs to crawl the inch and a half from vagina to pouch, the little marsupial babies are virtual embryos—hairless, deaf, and blind, with little more than buds where their hind limbs and tails will eventually be. Because opossum young move to an external pouch at such an early age, they are ideal for experimentally examining how the condition of the mother might affect the number, size, and sex ratio of her offspring.

Over the course of two years, we radio collared forty virgin female South American, or common, opossums at Hato Masaguaral, a cattle ranch and biological field station in central Venezuela. The basic design of our experiment was simple: we left twenty of the radio-collared females alone; we offered supplemental food to the other twenty. In principle, this is an easy task. The animals can be traced to their daytime sleeping dens by the signal from their radio collars. Then at dusk, just before they emerge, food (in this case, the cheapest sort of smelly bait—sardines) is placed near the mouths of their dens. Every month, we recaptured all animals in order to count, sex, and measure the young in their pouches. In practice, the labor involved—ours and that of our field assistants—turned out to be immense, mainly because the Venezuelan savanna becomes flooded, mucky, and impassable to vehicles during the opossums' breeding season, and making matters worse, the dens are widely spaced.

Our results were clear-cut. First, females given extra food did invest more in reproduction. Litter size itself remained constant, but the individual young of food-supplemented mothers were larger at every stage of development than young from the controls. By the time the young opossums began to leave the comfort of the pouch, those whose mothers had dined on sardines were 50 percent larger than those whose mothers had not been so pampered.

Second, while both males and females within a litter experienced a similar increase in size when the mother was fed extra food, the additional size was especially beneficial to the males. During the breeding season, males fight vigor-
ously for the single mating each female allows during her reproductive cycle, and larger males usually win the fights. Female reproduction, on the other hand, was not affected by body size. We also found that supplementing the mother's food promoted the survival of newly independent young of both sexes, but again males gained more: female survival increased by 16 percent, while that of the males rose by nearly 30 percent.

Our third result concerned sex ratios. The Trivers-Willard hypothesis predicts that our food-supplemented females should produce an excess of sons, because high-quality sons—able to outsurvive and outcompete other males and impregnate numerous females—will pass along more of their mothers' genes to the next generation than will high-quality daughters, whose reproductive output is limited by the number of young they can themselves bear. This is precisely what we found. Food-supplemented females produced nearly 1.4 sons for each daughter, while the control females produced an equal number of sons and daughters.

This striking result led us to reexamine information we had gathered over the years on elderly females. Aged opossums—those in their second reproductive year—often develop cataracts, lose weight, have smaller ovaries, bear fewer litters, and wean fewer offspring than when they were young. Because these females are in comparatively poor condition, unable to produce high-quality offspring, we expected they might bear an excess of daughters, which would be likely to find mates regardless of their condition. And in fact, they did, producing nearly 1.8 daughters for each son. Thus, depending on their physical condition, opossums are capable of biasing the sex ratio of their young in either direction.

Steven N. Austad and Mel E. Sunquist
Boys Will Be Boys—or Girls

Many fishes lead conventional sex lives: the gender of their offspring is fixed for life at fertilization, and they produce equal numbers of male and female young. But many others display a dazzling diversity of sex determination. For some species, environmental factors, such as temperature, determine whether young will be born male or female. Some species consist only of females, perfectly capable of producing their daughters without benefit of males, while others are simultaneous hermaphrodites, each individual producing eggs and sperm at the same time. Yet others change sex during their adult lives: some start off as females and later shift to males, while others do just the opposite.

Sex change is especially common among coral reef fishes, where the direction of change and the sex ratio of a population often reflect the mating system. Where large males can completely monopolize the females, there is no advantage in being a small male. In this situation, all fish are born as females, and most remain so for their entire lives. Only the oldest and largest fish change sex to function as males. When females cannot be monopolized, the sex ratio of the population is more evenly divided. In still other species and situations, large females appear to have some advantage over males; then, the sex change is from male to female.

A good example of sex change can be found in the Caribbean bluehead wrasse, a common coral reef fish that I have studied for the last fifteen years. All reefs contain spots especially favorable to spawning. On small reefs, a few dominant males can easily control these sites and thus the females that gather at them to release their eggs. Small males are out of luck, so nearly all individuals spend their entire lives as females. On large reefs, however, where there are more wrasse and more good spawning sites, the big males lose control of the situation, and smaller males are able to join in group mating. There, many more individuals spend part of their lives as males, and the sex ratio approaches 50/50.

Other studies have shown that sex change, and the resultant sex ratio, among some reef fishes is socially controlled and that individuals can change sex quickly to take advantage of a new situation. The Pacific cleaner wrasse lives in harems consisting of a single male and several females. When the male is removed, the largest female immediately begins to transform herself into a male and is producing sperm within a week. In contrast, among the brightly colored, monogamous anemonefish, if the female of a pair dies, her mate changes sex, while a smaller juvenile in the vicinity matures to become the new male.

Simultaneous hermaphrodites have somewhat different concerns. These fish, while able to produce eggs and sperm, generally mate with other individuals. The question for the females is somewhat different: whether to let the male suck out sperm from her body, to fertilize his; or to mate with another male and have spermatophores from another species. Some small females choose not to mate all, but each species has its own ratio.

Male bluehead wrasse and two females eating a sea urchin
them is whether to make mostly eggs, mostly sperm, or something in between. Eric Fischer and Chris Petersen of the University of Washington have shown that this option, too, depends on the social system. In monogamous species, both partners devote most of their energy to egg production, making just enough sperm to fertilize their mate’s eggs. In species that live and mate in larger social groups, the smaller fish produce nearly all eggs, while the largest, dominant individual produces mostly sperm and mates with all the subordinates, saving energy for controlling his harem rather than for making eggs.

Robert R. Warner

unusual social system of spider monkeys? Symington wondered. For most monkeys, the rule is for females to remain in their natal area, close to home, close to mother, living in “female-bonded social groups.” The males migrate, looking for breeding opportunities elsewhere. But in spider monkeys, and a very few other species—red colobus monkeys (Natural History, September 1981), howler monkeys (Natural History, August 1984), and two apes (the gorilla and the chimpanzee)—the females move and the males stay behind among their relatives.

Symington proposed that unlike most monkey mothers, high-ranking spider monkey mothers would therefore be in a position to help their sons achieve a similar high rank, and with it the sexual perquisites that many high-ranking male mammals possess in polygynous species. Symington cautions that we do not yet know that a positive relation exists between a male spider monkey’s rank and his later reproductive success, but she speculates it might.

Well and good for spider monkeys, deer, and coyops, which all appear to fit the original Trivers-Willard model, but what about species where there are other, equally potent variables? In some species, for example, offspring of one sex stick around the den or nest in order to help their parents rear the next generation. If they could, wouldn’t mothers do well to produce more of the accommodating sex? James Malcolm, of California’s University of Redlands, has postulated just such goings-on to explain male-biased sex ratios among African wild dogs. Typically, the females migrate, while males stay on in the pack and help raise more pups. The male helpers’ contribution is substantial—they provide as much meat to the pups, for example, as the fathers do.

Not all stay-at-home offspring are helpful, however, and in some species, these homebodies are actually forced into competition with their mother and siblings for finite local resources. Mothers faced with this situation should—again, if they could—avoid such competition by producing more of the sex showing the good grace to leave home. The type case for this particular sex ratio permutation was provided by a shy, nocturnal prosimian known as the thick-tailed bush baby. About the size of a squirrel and looking a bit like a caricature of a saucer-eyed, short-legged cat, these bush babies of East and South Africa survive catch as catch can. During the wet, warm season in nearly temperate southern Africa, they cock their batlike membranous ears to detect the rustle or whoosh of their insect prey or they hang on to tree trunks, often upside down, to lick up the sugary gum that drips into fissures in the bark. During the dry, colder months, moths, beetles, and the like disappear from the forest and the bush babies rely heavily on the gum. This
gum is rich in carbohydrates and calcium, but each little well typically yields only enough for three to four minutes of licking; after that, the animal must move on to another site. In winter especially, when the cold gum oozes slowly, it may be hours before enough has collected to make a return visit worthwhile.

Thick-tailed bush babies live in neighborhoods of loosely bonded animals of both sexes, which forage and sleep in overlapping home ranges. The ranges of females are smaller than those of males, and daughters remain in their natal ranges longer than males do, sometimes long after they reach maturity. Mothers tolerate their own daughters but may drive away other females. Intruders are especially unwelcome in the wintertime, when many females are pregnant and the gum is in scarce supply.

At the time field biologist Anne Clark first went to South Africa to study these bush babies, the general assumption was that a single big male would control an area inhabited by a number of females. Thus she was delighted when the first animal she was able to live-trap, for the purpose of individually marking it, was just such a big male. She was equally crestfallen when she tripped and released her prize. She feared she might never catch another, at least not in her main study area. To her astonishment, she did. And then another. Indeed, all she ever seemed to catch were males. She was also surprised to note that in her year and a half in the field, almost all of the births she recorded (thirteen of seventeen) were also male, but her sample was too small to draw any conclusions.

Clark, now at Michigan State University’s Kellogg Biological Station, returned from Africa in a suspicious frame of mind. She sent a questionnaire to all of the institutions in the world that were breeding bush babies in captivity or had collected them from the wild. Todd Olson, then a Ph.D. candidate at the University of London, contributed museum data on whole populations of bush baby specimens. The resultant sex ratios were wildly male biased — on the order of 130 to 177 males for every 100 females. By the time she received a visit from University of Utah sex ratio theorist Eric Charnov, Clark was ready to lay out her arguments. As she wrote later in *Science*, her explanation of the skewed sex ratio involved “a difference between male and female offspring in their use of local high-productivity areas which are essential for female reproduction.” If, indeed, daughters that remain near their natal ranges would have to compete for scarce resources with each other (and their mother), might not successive production of daughters cost the mothers more than producing sons would? Charnov listened and modeled Clark’s ideas mathematically. They worked. The term local resource competition was chosen in homage to William Hamilton and his concept of local mate competition, and it has been adopted by all subsequent researchers.

Since then, local resource competition has received support from far-flung quarters, as both an explanation and a predictor of sex ratio biases. Recently, Australian National University’s Alexander Cockburn reported that for *Antechinus*, a genus of mouse-like marsupials, there is an inverse correlation between the likelihood of mother—daughter competition and the proportion of daughters born to those mothers. In some *Antechinus* species, females produce a single litter of offspring and then die. In others, the mothers breed more than once and daughters stay close to home, even sharing their mother’s nest when the next breeding season rolls around. Mother and daughter are thus potential competitors, and apparently to avoid this, the long-lived mothers produce male-biased litters (see *Natural History*, March 1988).

But what if a daughter were to compete not with her mother but with other, unrelated females in a large group? Such females should be especially reluctant to share scarce resources with the interloper, with whom they have no genetic interests in common. Herein lies one of the more fascinating twists to the tangled collection of sex ratio research results.

When Trivers and Willard first proposed their hypothesis, they had in mind creatures, such as the red deer, where males are the gambling sex, the players who either win big or very possibly lose out altogether in the competition for mates. Little thought was given to the possibility that females’ reproductive abilities might also be quite variable and that in some species, the mother’s rank matters more to her daughters than to her sons. We now know, for example, that among baboons and macaques, females belong to powerful matriline and that rank—high or low—is passed from mother to daughter over several generations. In this system, sons disperse after adolescence while daughters stay at home, fitting into the hierarchy just under their mother. Females that defer to a high-ranking mother will one day, if they live long enough, defer to her daughters. (Social rank is not, however, inherited in any strictly genetic sense. Upsets occur, and when the opportunity arises, subordinates seize the chance to rebel and establish a new pecking order.)

Members of dominant matriline form lasting alliances to maintain their high status. The flip side of this, of course, is that some other matriline is usually being shortchanged. For some populations, low-ranking females eat and drink less well. They may produce fewer offspring, and those they produce are less likely to survive. High-ranking females have and abuse daughters born to lower-ranking females. According to University of California anthropologist Joan
Silk, the daughters of low-ranking bonnet macaque females are so severely harassed that few live. No wonder, she argues, that stressed females produce fewer daughters than sons and that after birth, they care less for their all-too-often doomed daughters than for their sons. The sons, at least, will soon emigrate, leaving behind the disadvantages of their mother’s low rank.

In two other studies of matrilineal cercopithecine monkeys—of rhesus macaques kept in a colony at Cambridge University in England and of wild baboons studied now for over sixteen years in Kenya’s Amboseli National Park—low-ranking females have produced more sons than daughters. In the eighty births at Amboseli reported by the University of Chicago’s Jeanne Altmann, the proportion of sons produced by low-ranking females was nearly twice as high as that produced by high-ranking females, results that could have occurred by chance fewer than five out of a hundred times. Furthermore, painstaking behavioral observations have confirmed that high-ranking baboon mothers care for their daughters longer than they do sons, and such daughters have a higher survival rate than sons. Most strikingly, sons born to low-ranking mothers fare better than do sons born to high-ranking mothers (see Natural History, September 1982).

Data from other sites raise the question of how widespread this pattern is. At one other site where Old World cercopithecine monkeys have been studied, high-ranking mothers were reported to produce significantly more sons. At four other sites, a mother’s rank had no effect. Such diversity of results has inspired heated discussions among primatologists. We do not yet know how general the Amboseli results will prove to be, but they are solid. And while the results run counter to the pattern first envisioned by Trivers and Willard (that is, overproduction of sons by high-ranking mothers), they may actually provide the sort of exception that confirms the larger rule: biases in sex ratio follow anticipated gains for parents in terms of numbers of grandchildren. In the case of Meg Symington’s spider monkeys—a population that conforms rather precisely to the Trivers-Willard model—the mother’s rank can directly influence her son’s success. But that same mother presumably has little influence on her daughters, since spider monkey females leave their natal group. Among the Amboseli baboons, however, it is sons who push off, passing forever from the maternal sphere of influence. As Jeanne Altmann points out, it is the stay-at-home daughters who stand to benefit most (or suffer least, as the case may be) from their mother’s rank and who will contribute to the future fortunes of her lineage.

The evidence appears to be mounting. Among our animal relations, mothers are better off having sons in some situations, daughters in others, depending on the social and ecological setting. And at least some of the time, some of these mothers appear capable of tilting toward the “sex of the hour.” Could anything comparable apply to our own species? Surely there cannot be any relation between human sex preferences and the sort of evolved propensity to bias sex ratios found in fig wasps and bush babies.

In fact, that possibility was very much on the minds of Trivers and Willard when they published their hypothesis and was another reason their paper was met with skepticism. While acknowledging the difficulties, Trivers and Willard nevertheless believed that their model could be applied to “humans differentiated on a socioeconomic scale, as long as the reproductive success of a male at the upper end of the scale exceeds his sister’s, while that of a female at the lower end of the scale exceeds her brother’s. A tendency for the female to marry a male whose socioeconomic status is higher than hers will, other things being equal, tend to bring about such a correlation, and there is evidence of such a bias in female choice in the United States.”
Trivers and Willard cited data indicating that wealthy Americans produce relatively more sons than daughters. Most scientists are more cautious on this point, and only a few would agree, on the basis of the data currently available, that parents give birth to disproportionately more sons or daughters depending on their socioeconomic status. Many would agree, however, that there is considerable discrimination in favor of one or the other sex after birth and that more often than not, sons are preferred. Indeed some anthropologists are now hard at work, attempting to use the logic of Trivers and Willard to explain nothing less than the origins of patriarchy. These efforts are concentrated on a small subset of human cultures: those highly stratified societies in which women by custom and as a matter of family honor are hypergamous, that is, marry up the social ladder. For it is in these highly stratified societies that parents have overcome the normally conservative human sex ratio, albeit at a high price: the selective neglect or even outright infanticide of daughters.

Such societies are exemplified by certain eighteenth- and nineteenth-century castes of northern India. Using a variety of historical materials, including records kept during the British campaign against infanticide, anthropologist Mildred Dickemann of California State University at Sonoma investigated female infanticide among the Rajputs, Sikhs, and other high-status groups. She found sex ratios as high as four little boys for every surviving little girl. In some high-status families, no daughter had been allowed to live for generations.

From the dusty census records emerged the cruel realities of life among these people, who found the means to create sex ratios as extreme as any in mammaldom, except perhaps those of the little wood lemming. Indeed the very name of one of the Sikh clans—Kuri Mar—means “daughter destroyers.” After eliminating their own daughters at birth, high-status families obtained wives for their sons from lower-ranking families within the same caste. These families competed among themselves to amass

**Daughters Dearest**

“How do you tell the sex of a chromosome? You pull down its genes.” The silliness of this riddle appeals to students of avian sex ratios because it conveys something of how difficult sexing young birds can be. Unlike many adult birds, male and female juveniles are almost always indistinguishable, and telling them apart usually requires either the surgical examination of the gonads or chromosomal analysis.

Red-cockaded woodpeckers are a striking reversal of the rule. In their very first plumage, males boast a bright medallion of red feathers that covers much of their crown—a badge that is clearly visible at all times—while females have solid black crowns. Once the males undergo their first, postjuvenile molt and enter adulthood, however, black feathers replace the red crown feathers. As a result, most of the time, adult males and females look exactly alike, with males’ red feathers—now small tufts, or cockades, on the sides of the crown—hidden by the black crown feathers that cover them. Only during aggressive interactions does the male raise his crown feathers and reveal his red cockade.

These distinctive traits enabled me and my colleague Mike Lennartz to discover another extraordinary fact about red-cockaded woodpeckers: in the populations we studied, almost two sons are fledged for every daughter. In most birds, the ratio of male to female young is close to 1/1, reflecting Fisher’s rule that because the reproductive value of sons and daughters is equal, total investment in the two should be the same. Thus, if Fisher’s rule holds for red-cockaded woodpeckers, sons—the abundant sex—should be somehow individually less expensive for parents to produce than daughters—the rare sex. We investigated how this might have come about.

Sons and daughters are the same size. They grow at the same rate and fledge at the same ages, so differences in size and development do not explain how red-cockaded woodpecker sons might be less costly than daughters. Daughters leave home months before sons, so, if anything, daughters should be less expensive to raise.

The key seems to lie in the birds’ distinctive social behavior. Red-cockaded woodpeckers are one of the few North American birds with a cooperative nesting system in which nonbreeding individuals help. The helpers at the nest, almost always adult sons of one or both of the breeding adults, incubate, guard, and feed the young.

The helping habit is explained most readily by the limited habitat available for breeding, which may also account for the species’ presence on the endangered species list. Red-cockaded woodpeckers are found only in the few remaining southern forests with stands of mature living pines. Groups of these birds excavate deep nesting and roosting cavities in the trunks of mature trees infected with “red heart,” a fungal disease that softens the heartwood. Thus,
a dowry large enough to win a place among the elite for their daughters. Parents who managed to marry their daughters into elite households as the wives of the well-to-do might well not have any granddaughters (for these would most likely be eliminated at birth), but their grandsons would enjoy a greater than average likelihood of surviving and reproducing. Among high-status families, harem polygyny and concubinage were common. Sons born to these families would thus be likely to sire many more children than any daughter—were she allowed to live—could bear. As for the sons of low-ranking families, few had any opportunity to marry.

The big difference between the Rajput and Sikh parents and the little wood lemmings, of course, is that the people were consciously calculating the costs of rearing male and female offspring. People in India discuss at length the size of the dowry that will be needed to marry a daughter into a family with status equivalent to, or higher than, her own. Family honor is on their minds, as well as benefits in terms of prestige to be won—or lost—for a child who marries advantageously—or fails to.

More than a century ago, when a landholder from Uttar Pradesh was asked whether privileged people such as himself were still killing their daughters, he answered simply that of course they were: “The father who preserves a daughter will never live to see her suitably married [and] the family into which she does marry will perish or be ruined.”

The concern of parents—rich and poor—went beyond immediate questions of family honor or the labor potential, of sons versus daughters; they had in mind the very survival of the lineage. For as Dickemann explains, these people lived in an ecologically perilous world. Recurrent famines and disease routinely culled the dispossessed. Lineages blinked on and off in a dark and forbidding landscape. Even among landholding families able to maintain their prestige and their property, only the most fortunate would survive for many generations. By more enlightened standards, the suitable nest sites are scarce, and breeding opportunities are few. All of which encourages adult sons to stay at home and—while waiting for their own opportunity to breed—help with the nesting attempts of their parents or sometimes of brothers who have ascended to breeding status.

On average, more young birds fledge from nests with helpers than from those without. Therefore, while raising sons and daughters to fledging may seem equally expensive, a son may return some of the parents’ investment by helping them raise yet more offspring. This may reduce his own net cost and may have led, over evolutionary time, to a population sex ratio that favors sons.

At the level of the individual, the story has additional wrinkles. Breeding females sometimes move from one colony to another. When a female makes such a move and begins to breed in her new home, she either does so without any help at all or she may receive help at the nest from unrelated males, generally the sons of her new mate. In either case, the first few clutches of such a female are almost always biased toward sons. However, after she has produced enough sons so that they become her helpers, she begins producing more daughters. It seems that the female’s first need is to assure her own genetic representation in the colony, and since red-cockaded woodpecker males tend to remain at home and wait for a chance to breed there, sons are the best way to accomplish this. The production of daughters, which will almost certainly leave and breed elsewhere, must wait until this requirement can be satisfied.

*Patricia Adair Gowaty*
Why are the babies of low-ranking black-faced black spider monkeys almost always females?

"strategies of heirship" worked out centuries ago by these turbaned warriors in their walled Rajasthani villages may seem inestimably cruel, but given the rules of the game, their calculations were shrewd ones.

Similar ends were apparently pursued by upper-class parents in medieval Portugal, although the means to the end were more refined. As the intriguing ramifications of the Trivers-Willard hypothesis began filtering through to the social sciences, James Boone, a young anthropologist from the University of New Mexico, was finding some striking marriage patterns in the medieval Portuguese genealogies he was studying. Boone had laboriously taken data from a compendium of family histories called the Pedigra Lusitana and translated it all into his computer so that he could analyze demographic trends for various social strata: royalty and other titled elites, the bureaucrats who surrounded the royal court, the landed gentry, and soldiers. Unfortunately, but as usual, no written records existed for the poorest, laboring classes.

For the two hundred years between 1380 and 1580, Boone traced the fates of sons and daughters from the various social classes. The graphs he came up with would have been strangely familiar to Trivers, now at the University of California at Santa Cruz. At the highest ranks, men were more likely than women to marry. Why so many elite women never married was simple enough. At any given point in time, between 10 and 40 percent of them were being sent to convents. And the elite women who did marry produced fewer recognized children than did their brothers at the same social level. At the lowest ranks for which records exist—soldiers—the opposite was the case: daughters were more likely to marry and have children. (Bastard children were rarely recorded at any social level.)

When Trivers and Willard first hypothesized that in some situations mammalian parents should sometimes have the ability to manipulate the sex ratio of their offspring before birth, many biologists dismissed the idea as just one more step in the misguided quest for adaptive explanations for what are in fact accidental or coincidental phenomena. Trivers himself was more philosophic. I remember him saying, "Even if I’m wrong, it will take them years to find out." That much at least has turned out to be prophetic. Certainly, no one could have guessed just how many and how diverse would be the multitude of scientists swept up into this wild and woolly world of sex ratio research.
Authors

Sarah Blaffer Hrdy (page 63) is a professor of anthropology at the University of California at Davis. Her work and writings have long touched on how offspring fare in the high-stakes game of reproduction that primate parents play. Her research topics have ranged from infanticide in Hanuman langurs (an Indian species she studied between 1971 and 1979) to last will and testaments in Sacramento County. Hrdy lectured on the topic of sex ratios at the third T. C. Schneiria Conference, held in 1985 at the American Museum of Natural History. A common thread in all her work has been her interest in understanding how and why parents may invest more in sons or daughters—at birth and afterward. Currently, Hrdy is writing about such matters on a Guggenheim fellowship. Her previous publications include several books: *The Langurs of Abu: Female and Male Strategies of Reproduction* (Cambridge: Harvard University Press, 1977); *The Woman That Never Evolved* (Cambridge: Harvard University Press, 1983); and *Infanticide: Comparative and Evolutionary Perspectives*, coedited with Glen Hausfater (New York: Aldine Publishing Co., 1984). Scientific papers on sex ratios are too numerous to mention, but for readers wishing to delve more deeply into the topic, Hrdy suggests chapter 11 of Robert Trivers's book *Social Evolution* (Menlo Park: The Benjamin-Cummings Publishing Co., 1985). She also recommends the more technical *The Theory of Sex Allocation*, by Eric L. Charnov (Princeton: Princeton University Press, 1982).

For years, reports in the scientific literature have suggested that among reptiles, gender is determined by incubation temperature. While on a postdoctoral fellowship in genetics at the University of Wisconsin, James J. Bull (page 70) decided to look into the matter. He began by marking turtle nests along the Mississippi River, noting the temperature at each nest, and waiting to see what hatched out. He also conducted parallel studies in the laboratory. His work convinced him that environmental sex determination was indeed going on, and later, at the University of Sussex, he began to write up his thoughts on the subject. The result, in 1983, was a book: *The Evolution of Sex Determining Mechanisms* (Menlo Park: The Benjamin-Cummings Publishing Co.). Bull, now an associate professor at the University of Texas at Austin, plans to investigate the physiology and molecular biology of sex determination in vertebrates.
Although John H. Werren (page 68) knew as a beginning Ph.D. candidate that he wanted to concentrate on theoretical questions pertaining to sex ratios, he "floundered about" for the first three years in search of a good study animal. But as soon as the jewel wasp was brought to his attention, he was off and running. After receiving his degree, however, Werren spent four years in the Army to fulfill an ROTC obligation incurred as an undergraduate. For three of those years, he was in a U.S. Army public health lab in Germany, gaining on-the-job training as a bacteriologist. This training stood him in good stead when he returned to his research, for—as he was to discover—jewel wasps carry many inherited microorganisms, some of which may affect sex ratios and the genetic structure of populations. For more on sex ratio manipulation by wasps and bees, see Werren's article in the July/August 1987 issue of Bioscience. Now an assistant professor of biology at the University of Rochester, Werren also has a long-range interest in the use of some of the world's 100,000 species of parasitic wasps to control insect pests.
Authors, continued

Steven N. Austad (page 74) graduated from college with a degree in English literature. But after three years of training lions, tigers, and other large animals for the movie industry in Hollywood, he returned to school to study science and is now an assistant professor in Harvard's Department of Organismic and Evolutionary Biology. Austad, above, was first forced to pay attention to opossums when they began interfering with coauthor Mel E. Sunquist's efforts to live-trap crab-eating foxes and ocelots in Venezuela. Austad and Sunquist decided to take advantage of the opossums' irritating habit of repeatedly getting caught in the traps and asked how they could make use of these animals. Austad says, "The sex ratio hypothesis jumped right out at us." Austad's current research—on aging, sexual selection, and sociality—involves him with a wide range of creatures: spiders, flour beetles, and tropical wrens, as well as the ever-useful opossum (about which he wrote in the February 1988 issue of Scientific American). Sunquist, below at right, a wildlife ecologist at the University of Florida in Gainesville, is continuing his research on the reproductive strategies of opossums, but he, too, studies a diversity of animals, most of them distinctly more carnivorous than opossums. He has researched ocelots in Venezuela; tigers, leopards, and sloth bears in Nepal; and snow leopards in Pakistan. Sunquist and his wife, Fiona, have a book, Tiger Moon, coming out this spring from the University of Chicago Press.

When Robert R. Warner (page 76), then a Ph.D. candidate at Scripps Institution of Oceanography, heard in 1970 that some fishes could change sex, he was hooked. He chose sex change in fishes as the topic of his thesis, and has been studying this and other aspects of fish biology ever since. Four years ago, he summed up many of his findings on mating behavior and hermaphroditism in coral reef fishes in American Scientist (vol. 72, pp. 128–36). A professor of marine ecology at the University of California at Santa Barbara, Warner is now investigating such questions as why some fishes take care of their young and others do not. Pursuing his research subjects takes him to such enviable places as Saint Croix, Corsica, the Galápagos, and Panama's San Blas Islands. He likes to bring his family along on extended stays in the field for "it's the best way to get to know both the fishes and my sons." In his spare time, Warner enjoys fishing and collecting banana stickers.

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At first, red-cockaded woodpeckers were a bit of a digression for Patricia Adair Gowaty (page 80). For the past decade, most of her research attention has been devoted to eastern bluebirds. Studying these “bluebirds of happiness” in South Carolina, Gowaty found striking amounts of fighting going on: males against males; females against females. Much of the aggression seemed to revolve around the species’ dependence on cavities for breeding. A female without a cavity to call her own may dump her eggs in a rival’s nest (see “Bluebird Belligerence,” Natural History, June 1985). At present, Gowaty is investigating the various mechanisms—behavioral and ecological—that may have evolved to thwart attempts at egg dumping. She is also interested in what determines when and why bluebirds leave their territories. In the future, Gowaty, a visiting associate professor of biological sciences at Clemson University, hopes to continue her woodpecker studies, with a view toward learning more about which possible behavioral and demographic factors lead to skewed sex ratios in this species. When not following the affairs of woodpeckers and bluebirds, she pursues a strong interest in politics, especially how it is affected by gender.

Günter Ziesler (page 110) has photographed wildlife in many exotic locales, but he came upon the ethereal scene depicted in “The Natural Moment” on his home ground in the Bavarian Alps, where mute swans are year-round residents. He used a Nikon FE-2 with a 80–100-mm zoom lens to photograph the birds nesting on Schwansee, or Swan Lake, just below the two fabulous mountain castles built by King Ludwig II of Bavaria. As a boy, Ziesler was fascinated by his grandfather’s cigarette cards depicting Mount Kilimanjaro and African wildlife. Widely traveled in Europe, South America, India, and parts of Asia, Ziesler realized a lifelong dream when he spent a full year photographing in Kenya in 1981. The results can be seen in his book *Safari* (New York: Facts on File, 1984), with text by Angelika Hofer. His work also illustrates Valnik Thapar’s *Tiger: Portrait of a Predator* (New York: Facts on File, 1986).

A third-year student at Cornell University’s New York State College of Veterinary Medicine, Steven A. Ososky (page 50) got his chance to work with the endangered Florida panther last summer, when he served as assistant to Melody Roelke, veterinarian for the Florida Panther Project. His first, “life-changing” experience with field conservation had come the year before he started vet school, when a Harvard University Travelling Fellowship enabled him to journey to Kenya, Tanzania, and Rwanda to observe wildlife species in their natural habitats and to examine conservation problems from a variety of perspectives. That led to the next summer’s work studying heat regulation in elephants in Kenya’s Tsavo East National Park and ultimately to his decision to spend at least part of his future career on projects involving the reintroduction of captive-bred animals into the wild, and managed breeding schemes integrating captive and wild stock. When not in the field, the lecture hall, or the clinic, Ososky—painted above with a cheetah—enjoys camping, photography, scuba diving, and racquetball. For anyone interested in understanding why we must try to preserve endangered species, he says that *Extinction: The Causes and Consequences of the Disappearance of Species*, by Paul and Anne Ehrlich (New York: Random House, 1981) is mandatory reading.