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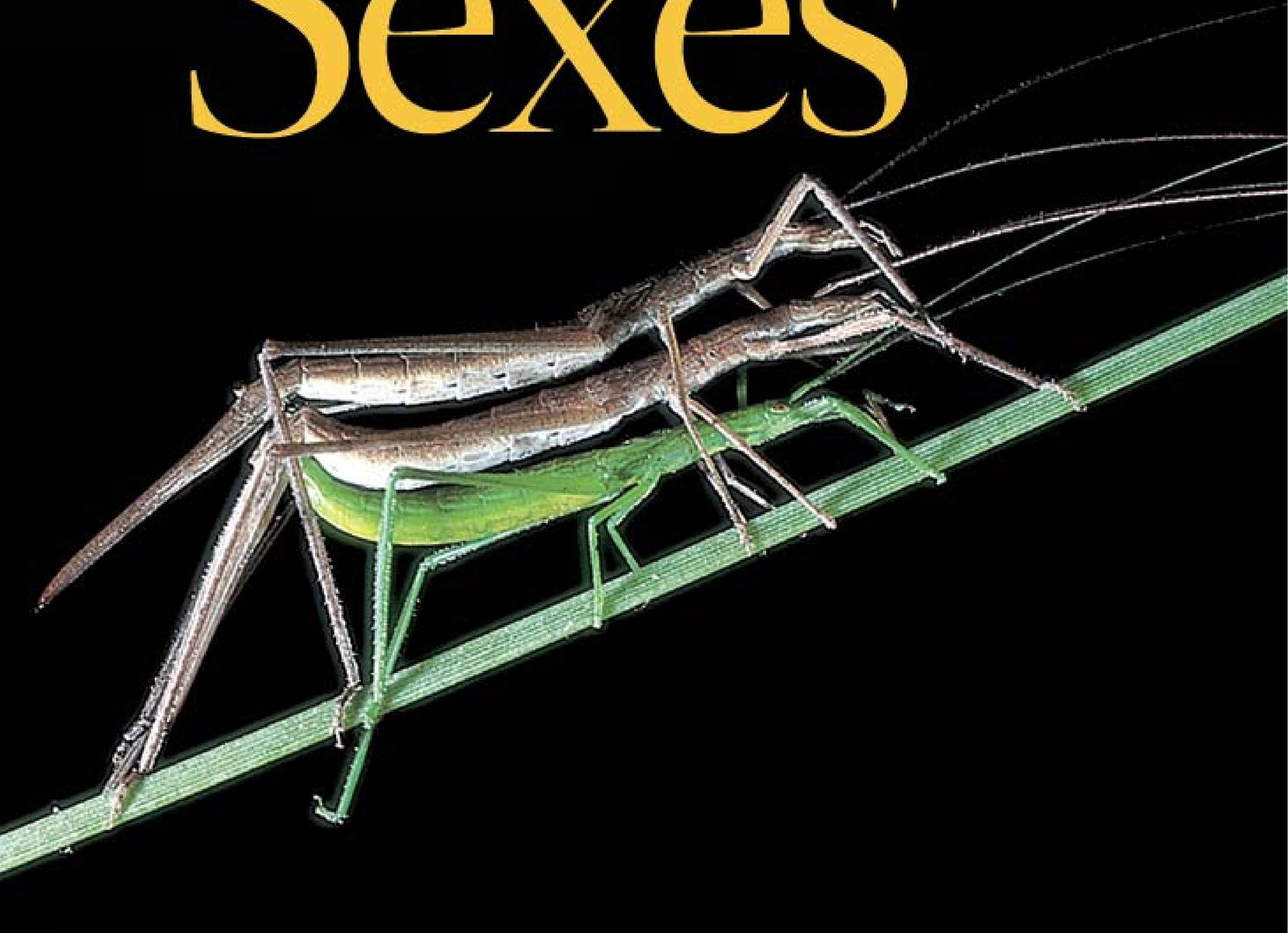
Battle of the Sexes



BATTLE OF THE SEXES

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As any nature lover knows, males and females of the same species commonly diverge in appearance and behavior—a reflection of their differing roles in reproduction. Take, for example, the brilliantly hued male peacock and his relatively drab counterpart, or the promiscuous sage grouse male and discriminating female.

This exclusive online issue explores that divide through a collection of especially fascinating case studies. Uncover the invisible charms of the Little Yellow butterfly, whose males and females are identical in color to the human eye but quite different to that of the insect, thanks to the male's ultraviolet adornments. Learn how a female guppy selects her mate from a school of competing males (hint: copycatting seems to play a role). Consider katydid courtship, unusual in that the male is the choosy one, carefully considering his options before bestowing on his bride a precious nuptial gift. And then there's the prairie vole, whose pheromones appear to orchestrate a reproductive strategy rarely seen in mammals: monogamy.

Eighteenth-century naturalists interpreted plant reproductive biology through the lens of human sexuality and social customs of the day, as an article in this issue recounts. It is surely tempting in our modern era to take the reverse tack: look to other organisms to gain insight into gender differences and social organization in our own species. Studies of the bonobo, for one, raise the possibility that rather than being male-centered, early human societies were female-centered. In any event, men and women almost certainly played different roles in evolutionary history and may thus have been subjected to varying selective pressures. According to our final article, this could help explain alleged cognitive differences between the sexes today.--*The Editors*

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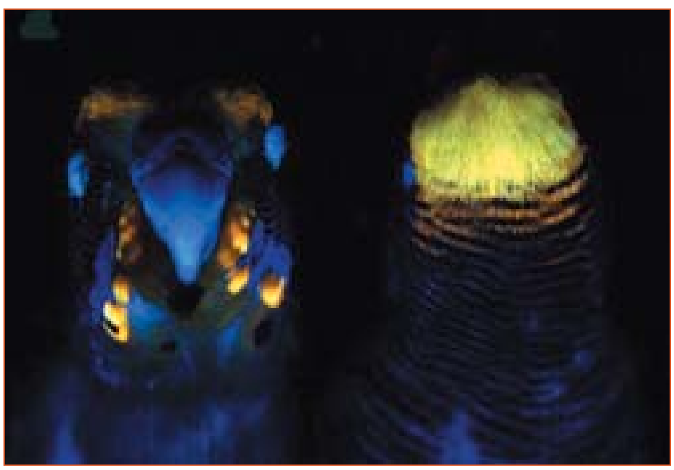
BATTLE OF THE SEXES IN BRIEF

Wimps Win in Cockroach Romance

Sometimes it pays to be a wimp—at least if you're a male cockroach. According to a study of the Tanzanian roach *Nauphoeta cinerea* published in the March 7, 2001 *Proceedings of the Royal Society*, females prefer low-ranking males to dominant ones any day. Trysts with weaklings, it seems, leave the females roaches in better shape than do encounters with more aggressive males. Yet when females do land a wimp (the high-ranking males do their best to thwart these couplings), they produce fewer sons. This, Allen Moore of the University of Manchester and his colleagues suggest, is the cost of the females' opting for safer sex.

Roaches aren't the only creatures in which females choose subordinate males. Previous studies have documented this preference in about a dozen species, including certain birds and salamanders. Exactly why the female roaches have fewer sons as a result of this choice, however, is a mystery. Paradoxically, producing fewer sons might actually maximize reproductive fitness: with fewer males in the next generation, the sons of these females with eyes for wimps might be more successful in themselves finding mates.—*Kate Wong*

Fluorescent Feathers Elicit Parrot Amour


SCIENCE

Fluorescent colors come and go on the fashion runways, but parrots always consider the glow a must-have. Indeed, the results of a new study, published in the January 7, 2002 *Science*,suggest that the birds look for feather fluorescence when choosing their mates.

Fluorescent pigments appear to glow because they absorb and reemit ultraviolet light at longer wavelengths. Such pigments decorate the crown and cheek feathers of budgerigar birds, commonly known as budgies. (In the image at the right, short-wavelength illumination reveals the budgies' fluorescent markings.) But whether the fluorescence serves a specific purpose or is merely a by-product of the birds' brilliant coloring has remained somewhat of a mystery. To answer that question, Kathryn E. Arnold of the University of Glasgow and her colleagues devised a clever experiment. They gave budgies of both sexes their choice of two birds of the opposite sex, one of which retained its fluorescent plumage and the other of which had its glow snuffed with sunblock. Both males and females, the researchers found, showed a strong sexual preference for the fluorescent birds.

The team also considered the bird's visual apparatus and determined that the fluorescent yellow feathers are ideally placed for chromatic detection by another lovelorn budgie. "These findings show that the fluorescent plumage of parrots is an adapted sexual signal, rather than a by-product of plumage pigmentation," the investigators conclude. "Given the elaborate biochemical pathway by which fluorescent pigments are produced, they may be costly and thereby honest indicators of individual quality."—*Kate Wong*

Bile Acid Key to Lamprey Love

When female sea lampreys look for suitable mates, a male's bile acid may be his most attractive feature, according to new research. During spawning season, these eel-like, parasitic fish migrate from open waters to streams, where males build themselves nests. Once they settle in, the males secrete a bilious love potion capable of attracting mates from afar. Although researchers have long suspected some kind of chemical communication between aquatic animals, this is the first evidence of water-released pheromones with long-range potency. These insights, detailed in the April 5, 2002 *Science*, suggest novel possibilities for managing lamprey populations in regions such as the Great Lakes, where the parasitic fish have decimated local populations of salmon and trout.

Weiming Li of Michigan State University and his colleagues spent two years distilling a relatively tiny sample of the chemical secreted by male lampreys from more than a ton of water. They designed a simple experiment in which ovulated female lampreys placed in a watery maze could swim into one of two rooms. Each time a pheromone-releasing male swam upstream from one of the rooms, the female inevitably searched out the source of the bile, neglecting the regular water next door. The females exhibited nearly as much interest when the researchers treated the water in that same area with the purified pheromone compound, thus proving the viability of the sample. In contrast, the presence of a nonfertile male in one room had no effect on female choice.

Detailed chemical analysis of the compound also enabled Li's group to track the pheromone's probable source and pathway within the male. The bile acid most likely originates in the lamprey's liver. From there it travels through the bloodstream to the animal's gills, which secrete the pheromone into the water, allowing it to flow downstream to expectant females. Li says that this new understanding of the lamprey mating process could be used to manipulate fish populations in an environmentally friendly manner.—*Greg Mone*

COURTESY EMORY UNIVERSITY

Gene Linked to Lasting Love in Voles

The manipulation of a single gene is enough to cure the wandering eye of a meadow vole. According to a report published in the June 17, 2004 *Nature*, gene therapy that increases levels of a specific protein in the brain turned the promiscuous creatures into monogamous mates.

Previous research with captive male prairie voles, which form lifelong bonds with a single partner, indicated that the animals had high levels of vasopressin receptors in the ventral pallidum, a brain region closely associated with the reward system. In contrast, captive male meadow voles, which often take multiple partners throughout their lives, lacked vasopressin receptors. In the new work, Miranda M. Lim of Emory University and her colleagues inserted a gene that encodes for the vasopressin receptor protein directly into the brains of male meadow voles. The researchers then observed the animals' behavior as they were introduced to a variety of potential partners. They found that meadow voles treated with gene therapy acted more like their prairie vole counterparts—they spent more time huddling near their original companion. According to study co-author Larry J. Young of Emory University, the results provide evidence "in a comparatively simple animal model that changes in the activity of a single gene profoundly can change a fundamental social behavior of animals within a species."

Of course, it's a big step from voles to people, but the researchers hope the results will contribute to a better understanding of how human attachments form. Such knowledge could inform treatment options for disorders such as autism, which disrupt a person's ability to form social bonds. "It is intriguing," says Young, "to consider that individual differences in vasopressin reception in humans might play a role in how differently people form relationships."—*Sarah Graham*

Male Songbird Responds to Mate Only When He's the Third Wheel

Like a stereotypical husband who pretends not to hear his wife berating him, some male songbirds show no signs of recognizing the call of their long-term mate in laboratory settings. But recent work with these animals finds that they can, in fact, differentiate their mate's voice but will react to it only in certain social situations.

Zebra finches are monogamous songbirds from Australia that fly in large flocks. As a result, couples routinely lose visual contact of each other and use calls to keep in touch. Whereas the female zebra finch clearly responds to the sound of her partner, the reciprocal behavior had not been observed in the male. Clémentine Vignal of Jean Monnet University in Saint-Etienne, France, and her colleagues acoustically analyzed the calls of seven female finches to see whether they had distinguishing characteristics. The results, published in the July 22, 2004 *Nature*, demonstrated significant variation in the songs of the female birds, implying that the males could in all likelihood identify their sweethearts if they put their minds to it.

To test this hypothesis, the researchers observed the reactions of male zebra finches while recordings of their mates were played back. Unlike previous setups in which the male was alone in a cage, the team placed other zebra finches nearby. As in previous experiments, the male made no display of recognition to his mate's voice in the company of either two males or a male and female who were not mates. Interestingly, however, when a mated couple was in the next cage, the male made it clear that he knew his mate's voice by nearly doubling the rate of his own calls.

Prior to this work, the ability to judge social context had been observed only in primates. "It really is a big finding because it shows that these birds can make social assessments like bigger-brained animals," remarks Christopher B. Sturdy of the University of Alberta, who authored an accompanying commentary. Sturdy suggests that the main function of the male's response is "to advertise that 'she's with me.'" But he is at a loss as to how to explain why the male does not have this advertising urge when in the presence of competitive suitors, because human analogies only go so far.—*Michael Schirber*

For Spiders, Familiarity Breeds Love


COURTESY OF THE *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES*

For a male wolf spider, approaching the wrong female with a romantic overture can be deadly: lady wolf spiders often cannibalize males that they don't want to mate with. Findings published online October 28, 2003 by the *Proceedings of the National Academy of Sciences USA* indicate that females of this species develop preferences for certain males based on early social interactions, a trait that is virtually nonexistent among invertebrates.

Among spiders, the wolf spider, *Schizocosa uetzi*, is unique because males can take on a variety of different looks, or phenotypes. Some have ornamental tufts of hair on their forelegs, and the exoskeleton comes in a variety of colors. Eileen Hebets of Cornell University introduced 81 sexually immature female wolf spiders to a variety of sexually mature males in the laboratory. Once the females were sexually mature and ready to take on a mate, Hebets again exposed them to a variety of male spiders. She found that females most often chose a mate of a familiar phenotype. In addition, those that had previously met more than one type of male were more likely to devour a suitor that was completely unfamiliar to them.

"Social experience influences mate choice," Hebets explains. "This shows that invertebrates have social recognition, and it can be maintained and remembered even through the molting process. These influences affect adult behavior and possibly the evolution of traits."—*Sarah Graham*

Fish Study Finds That Male Mate Choice Matters

Biologists generally agree that female choosiness drives the males of their species to ever-greater heights of showmanship, from having brighter feathers and more sprawling antlers to driving faster cars. Now, in a striking validation of the cosmetics and fashion industries, Trond Amundsen and Elisabet Forsgren at Sweden's Goteborg University demonstrate, at least in fish, that male choice matters too.

Amundsen and Forsgren, who published their results in the october 16, 2004 *Proceedings of the National Academy of Sciences*, found that male two-spotted gobies stuck in a partitioned tank between two contrasting females—one with a bright yellow-orange belly, the other drab—spent twice as much time in the side of their chamber next to the flashier female, even if the color was markered on. They were also four times more likely to display their willingness to mate—by shivering up close to the female or undulating toward the nest—for the more brightly colored female fish. These results, the authors write, "suggest that the colorful belly of female two-spotted gobies has evolved, at least partly, as a response to male mate choice."

But male gobies aren't just interested in beauty. A female's color, which comes from carotenoids in her eggs and to a lesser extent her skin, may indicate to the male the quality of her eggs, the authors note. Males gobies are far outnumbered by females at the end of the mating season and nurture the eggs by themselves, so they have a strong incentive to recoup their investment by choosing a mate who produces eggs more likely to survive.

The authors point out that mate choice on the part of male animals is relatively widespread. For that reason, they write, "we suggest that more attention be directed at the largely unstudied phenomenon of female 'beauty' in fish and other animals." *—JR Minkel*

Female Antelopes Fight for Fine Mates

OURTESY OF THE *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES*

Humans aren't the only mammals with a swinging singles scene. Nine other species engage in a process known as lekking, whereby bachelor males congregate in certain areas during the mating season looking for love. And according to a report published June 25, 2002 in the *Proceedings of National Academy of Sciences*, females may be more aggressive about landing eligible males than previously thought.

Earlier work had shown that in bird species that engage in lekking, females often compete for preferred males. For mammals that form leks, however, scientists thought that factors other than mate choice attracted females to the party. Now the new study, conducted by Jacob Bro-Jørgensen of the Zoological Society of London, reveals that in the case of topi antelopes, leks actually have poorer food supplies, higher rates of predation and higher levels of harassment for females than surrounding areas do. But the opportunity to mate with desirable males, it seems, offsets these drawbacks. After two years of studying topi populations on the Serengeti and Masai Mara plains, Bro-Jørgenson reports that he witnessed competitive aggression between females (see image) over so-called central males, which tend to be larger and older and to have darker facemasks than their peers. In fact, some females even went so far as to disrupt matings that were already in progress. Bro-Jørgenson concludes that "the finding suggests that the forces leading to lek evolution in mammals and birds may be more similar than previously acknowledged." *—Sarah Graham*

Birds of Different Feathers Pair Together

For most animals, selecting a mate from a different species is risky business. More often than not, even if the offspring are viable, they cannot themselves reproduce, as in the classic case of mules. But findings described in the May 3, 2001 *Nature* reveal that some birds manage to avoid the costs of hybridization. In fact, such interspecies pairing can even be the female's best bet.

Ben Sheldon of the University of Oxford and his colleagues studied hybridization between two closely related species, pied flycatchers and collared flycatchers. Though males of the two species clearly differ in their plumage and songs, female collared flycatchers often pair with male pied flycatchers—far more often than would be expected by chance. At first glance, the mingling might seem fairly disastrous: first-generation female offspring are usually completely sterile. On closer inspection, however, the team found several mechanisms that cancel out the detrimental effects of mixing.

For one thing, if a collared female breeds late in the season, choosing a pied male can actually be advantageous because the "heterospecific" pair will produce more fledglings than a pure collared pair would, owing to interspecies differences in peak performance timing. Second, mixed-species pairs produce more males—which suffer fewer effects from hybridization than females—thus favoring the sturdier sex. Lastly, Sheldon's team found that in a number of cases, although collared females had formed pair bonds with pied males, collared males had actually sired the offspring. Dennis Hasselquist of Lund University suggests in a commentary accompanying the *Nature* report that perhaps the females cuckold the pied males because they provide better territories. (For their part, the males don't appear to be particularly discriminating. "Males have little mate choice," Hasselquist told *Nature Science Update*, "if they get a female, they're very happy.")

The new results show that vertebrates may have evolved sophisticated mechanisms to balance out the negative consequence of hybridization, Hasselquist notes. "Such mechanisms might evolve rapidly in a location where two related species overlap," he writes. "Alternatively, it is possible that these mechanisms did not evolve to cope with hybridization, but rather are a side effect of existing female preferences." *—Kate Wong*

Mating Lizards Play a Game of Rock-Paper-Scissors

Not all lizards within one species look or behave the same way—especially when it comes to mating. Among side-blotched lizards (*Uta stansburiana*), males court their mates according to their own throat-colors, or morphs: Blue-throated males territorially guard their mates to get a shot at reproductive success; orange-throated males aggressively invade the territory of other males in search of females; and yellow-throated males sneak onto other males' turf, often by acting like females themselves.

Scientists have long assumed that these tactics must balance each other out to be evolutionarily stable. After all, if the approach of one type of lizard always won, only that type would be found in the next generation. For side-splotched lizards, the model researchers have used is the game of rock-paper-scissors. Just as a rock crushes—and so beats—scissors in the game, orange-throated lizards out-compete the less aggressive blue-throated males; just as scissors cut paper, protective blue-throated lizards win against sneaky yellow-throated males; and as paper covers a rock, the yellow-throated lizards are successful against roving orange-throated males.

Rock-paper-scissors makes for a convenient model, but until now, its predictions had not been tested. Barry Sinervo of the University of California, Santa Cruz and Kelly Zamudio of the University of California, Berkeley report in the December 5, 2000 issue of the *Proceedings of the National Academy of Sciences* that they have accomplished just that. They collected DNA samples from 96 females, 131 putative sires and 458 offspring among a population of lizards living in California during the 1992 breeding season, and ran several different rounds of paternity testing. As expected, they found no significant difference in the total numbers of offspring produced by each male type. "During the 1992 breeding season, each morph successfully used a different tactic to exploit weaknesses of another strategy and a morph's success depended on the close proximity of a vulnerable alternative strategy," the authors write. "Frequency-dependent selection arising from local competition can promote conditions that favor each morph, and thus preserve all three strategies of the rock-paper-scissors cycle in the long term." *—Kristin Leutwyler*

JOHN TOOKER

Wasps Tamper with Plant Chemistry to Woo Mates

A tiny wasp no bigger than a flea can change the chemistry of plants to help it land a mate, according to a new study. Results published online November 2, 2002 by the *Proceedings of the National Academy of Sciences* suggest that the gall wasp (*Antistrophus rufus*) alters the ratio of compounds within a plant's stem to attract members of the opposite sex.

Gall wasp larvae spend nine to 10 months developing within live plant stems that protect and nourish them. The presence of the wasps gives the plants a signature scent. John F. Tooker of the University of Illinois at Urbana-Champaign and his colleagues found that adult males, which emerge first, rely on olfaction to locate potential partners still encased in plant stems. Specifically, the males sniff out telltale differences in the ratio of two forms of so-called alpha pinenes and beta pinenes emanating from the plant. "If males find a stem with a 50-50 ratio they will move on," Tooker says. "If they find a stem with a 70-30 or a 100-0 ratio, they likely will stay and find females emerging from it." The wasps also demonstrated a preference for the same species of plant in which they matured. According to study co-author Lawrence Hanks, the findings show "that insects can influence plants for their own needs, using a substitute for sex pheromones." *—Sarah Graham*

Ticking Biological Clock Drives Female Cockroaches to Lower Standards

When it comes to reproduction, human females aren't the only ones to hear the tick-tock of their biological clocks. According to a report published in the July 24, 2001 *Proceedings of the National Academy of Sciences*, aging female cockroaches face similar pressure. In response, the study shows, female roaches beyond optimal mating age lower their standards, demanding far less courtship from suitors than younger counterparts.

A popular model of mate choice holds that females should choose mates based on their own reproductive quality. In other words, dishy females in their prime should hold out for the most desirable males, whereas females of low reproductive quality must be less discriminating. This theory, study authors Patricia J. Moore and Allen J. Moore of the University of Manchester note, considers reproductive quality as an intrinsic value of the female. But what happens when a female's reproductive quality changes over time?

To address the question, the Moores studied *Nauphoeta cinerea*, a cockroach that, like humans, has reproductive cycles and gives live birth. The scientists measured female choosiness by the amount of wooing required from males before mating. Their findings fit neatly with predictions: older females, which have decreased reproductive potential owing to age-related changes in their reproductive systems, were less selective than younger females. "As females age past an optimal breeding period, the cost of mating preferences increased rapidly if preferences delayed mating," the authors conclude.

Males, in contrast, did not exhibit changes in their courtship and mating behavior as a function of female age. "Under our experimental conditions, perhaps males were unable to assess female age and reproductive quality," the researchers write, "or that the cost of passing up even a poor mating opportunity was greater than the investment in time and sperm production." Or they just weren't that picky. *—Kate Wong*

Male Pregnancy May Spur Seahorse Speciation

COURTESY OF THE *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES*

No one could accuse a seahorse of being a hands-off father. That's because males are the ones that carry the young. Now findings published online May 7, 2003 by the *Proceedings of the National Academy of Sciences* suggest that male pregnancy not only takes the load off female seahorses, it can also drive the development of new species.

Prevailing theory holds that new species arise primarily because geographic barriers halt the flow of genes between different populations. But a number of recent theoretical studies have suggested that so-called sympatric speciation can occur, in which different populations originate in one geographical area, but do not interbreed. In the new work, Adam G. Jones of the Georgia Institute and his colleagues studied seahorses off the coast of Perth, Australia, in which the female deposits her eggs in a male's brood pouch and he fertilizes and carries the eggs until they hatch. Using genetic analyses the researchers confirmed that the creatures tend to choose mates of a similar size (a selection process known as assortative mating). This way, neither female eggs nor male pouch space is wasted. Notes Jones, "in seahorses assortative mating appears to be a consequence of male pregnancy and monogamy."

The researchers then devised a computer model to test whether this mating regime could lead to reproductive isolation and subsequent speciation. They determined that if environmental conditions favor either very small or very large body sizes as opposed to intermediate ones, new species may arise in just tens or hundreds of generations as a result of assortative mating. Male pregnancy, the authors thus conclude, "represents an unusual form of parental care with extraordinary evolutionary consequences." *—Sarah Graham*

originally published in July 1998

Mating Strategies in Butterflies

Butterflies meet, woo and win their mates using seductive signals and clever strategies honed by evolution

by Ronald L. Rutowski

As any postpubescent human knows, interest in potential mating partners is heavily influenced by sensory cues. A glimpse of lustrous hair or of piercing eyes can suddenly cause a man to be smitten with a woman, or she with him. The detection of a provocative scent or a sensuous touch may also kindle desire.

Grace Kelly's or Errol Flynn's obvious charms notwithstanding, an unbiased observer might find butterflies far more sensually appealing than humans. Perhaps unsurprisingly then, visual and other sensory cues also appear to govern these tiny creatures' decisions about mates. At stake is nothing less than the opportunity to produce offspring carrying an individual's genes through time.

Although Charles Darwin knew nothing of genes, he knew a great deal about sex (Gregor Mendel's work was not rediscovered until the early 1900s). Darwin first argued in 1871 that species tend to evolve attributes and behaviors that enhance courtship—and thus reproductive success. Some traits might render an individual more attractive to the opposite sex, whereas others might enable triumph over competing suitors. He specifically pondered butterflies when proposing this theory of sexual selection, largely because of the insects' vivid markings, which he felt might be influential in mate choice. "Their colours and elegant patterns are arranged and exhibited as if for display," he wrote in *The Descent of Man, and Selection in Relation to Sex*. "Hence I am led to suppose that the females generally prefer, or are most excited by the more brilliant males."

Recent experimental work with butterflies has borne out Darwin's suspicions of more than a century ago. Color is now known to spark sexual interest for some species in the butterfly world, as do other sensory signals that were beyond Darwin's human perception. But the creatures are more discerning than this observation might suggest. Ostentatious coloration or scent may do more than attract attention. Appearance and aroma may be shorthand notations of their bearer's health and heartiness.

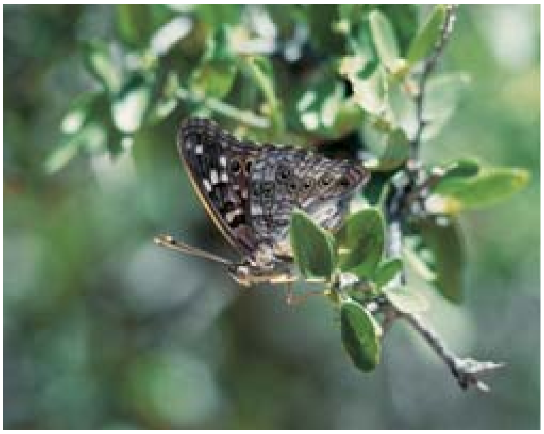
Color Cues

The clearest evidence for the role of color in sexual attraction among butterflies comes from studies of species in which males and females have distinctly different appearances. Obviously, to mate successfully, individuals must be able to determine whether other conspecific butterflies are of their own or of the opposite sex. The rest, it can be argued, is fine-tuning.

A gorgeous butterfly species whose males and females differ in color is the Little Yellow, *Eurema lisa*. Both sexes appear an identical yellow to the human eye, the shade being produced by pigments in the tiny scales that cover the butterflies' translucent wings. Males and females look quite different to butterflies, however, which perceive light at wavelengths beyond the human visible range and into the ultraviolet. Yellow wing scales on the upper surface of the males' wings reflect ultraviolet light, and those of females do not.

On encountering a female, a Little Yellow male flutters about her briefly before landing and attempting to copulate. On confronting another male, he speeds away and continues his search. These simple behaviors allowed me to develop a test for the cues males use to recognize females. I first glued Little Yellow wings to cards and presented them to males. Males landed on, and even attempted to copulate with, female wings. But male study subjects paid scant attention to male wings similarly mounted.

The next phase of the experiment showed that color was responsible for this choice. I prepared a card with two sets of male wings. A quartz slide that transmits both visible and ultraviolet light covered one set of wings, and a filter that blocks ultraviolet wavelengths overlaid the other. Males now attempted to



PHOTOGRAPHS BY RONALD L. RUTOWSKI

HIGHLY SYSTEMATIC APPROACH for finding mates is adopted by Empress Leilia (*Asterocampa leilia*) males: they stake out the hackberry trees where females are likely to appear newly emerged from the pupal stage or later to lay eggs. Early in the morning males perch on the ground in a sunny spot where they can both keep a lookout and warm up (*above*). Eventually they move into the trees (*right, top* and *bottom*)—to exactly the typical height of the flight of the females.

mate with the male wings under the filter—wings that appeared to be female. The late Robert E. Silberglied and Orley R. "Chip" Taylor, Jr., now at the University of Kansas, got similar results in their study of the Orange Sulphur (*Colias eurytheme*). This species displays a sexual difference in ultraviolet reflectance similar to that in the Little Yellow, and after a male's ultraviolet reflectance is obliterated other males treat him like a female.

Color also can influence mate recognition by females. My research group at Arizona State University took advantage of a dense population of a species known as the Checkered White, *Pontia protodice,* in a rural area near Phoenix to study this phenomenon. We focused on a well-known tendency among virgin females (as well as those who have not mated recently) to approach and chase males occasionally.

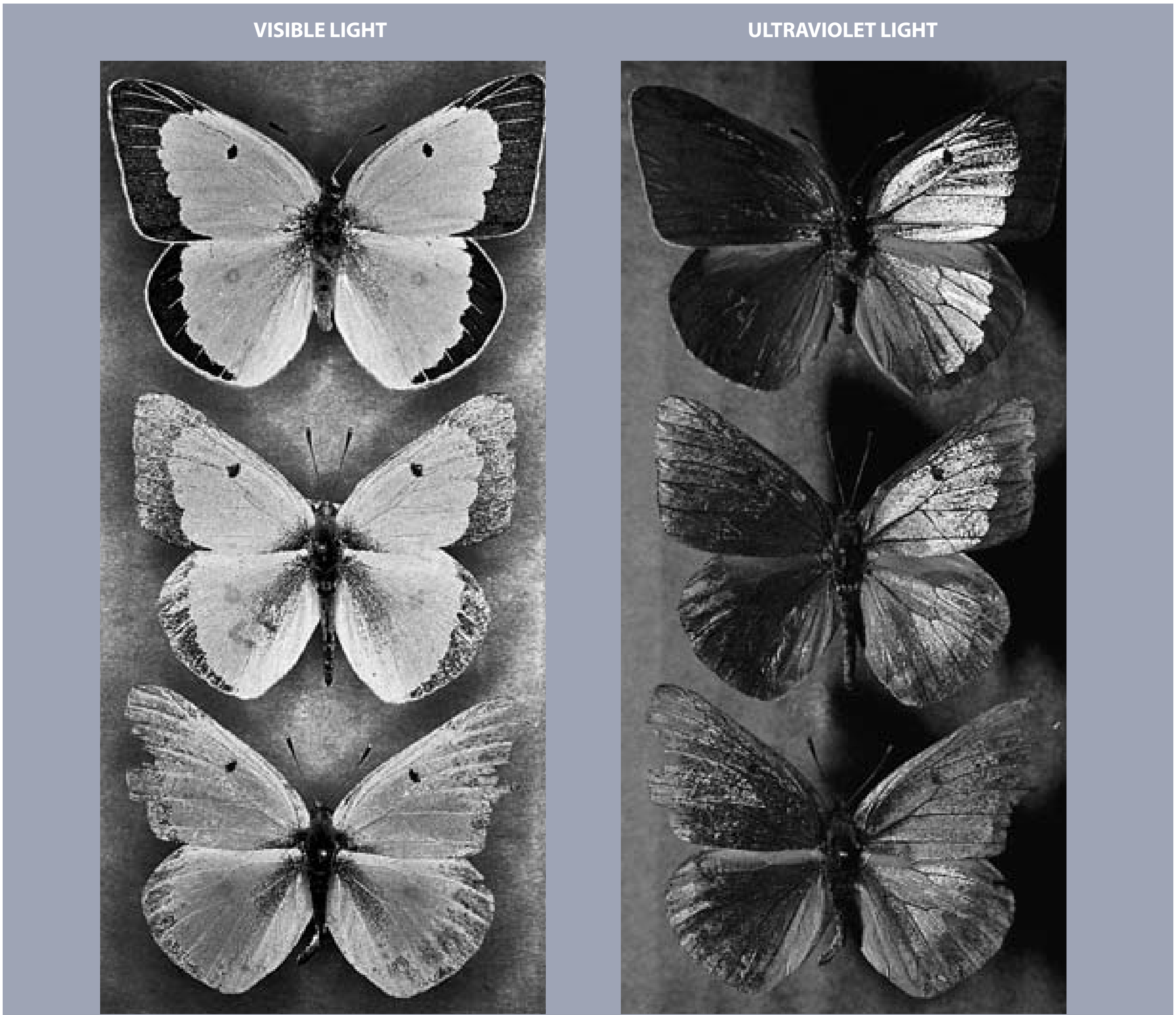
We captured Checkered Whites of both sexes and tethered them by tying one end of a thread around the waist between the thorax and abdomen and the other end to a length of stiff wire. We then used this wire like a fishing pole to display the captive butterflies in sight of females in the field. These free females often took off after the tethered butterflies. Their chases after tethered females halted quickly, whereas they showed far greater perseverance toward the males.

As with Little Yellows, male and female members of this species appear quite different in the ultraviolet wavelength, but in the opposite direction. Females reflect ultraviolet light, but the wings of male Checkered Whites contain an ultraviolet-absorbing pigment. This pigment is easily extracted, however, by dipping the wings in a dilute ammonia solution. Such treatment made male wings reflective of ultraviolet, like female wings, without altering any other markings.

I built lifelike models from ammonia-treated wings and then, using stiff angling wire, presented the specimens to butterflies in the field. Females ignored the ultraviolet-reflective male wings—but males became greatly intrigued. Clearly, both female and male Checkered Whites make use of sexual differences in color in order to discriminate potential mates from individuals of their own sex.

Some female butterflies are also picky about color when choosing a mate from among many suitors. Diane C. Wiernasz of the University of Houston investigated this behavior in the Western White, *P. occidentalis,* a butterfly closely related to the Checkered White. She released virgin females into a field and captured males that successfully courted them. These males had darker markings at the tips of their forewings than did rejected suitors. And Wiernasz was able to make males unattractive to virgin females by using white paint to reduce the size of the crucial dark markings. This is the only study of its kind that we have, but it demonstrates that some females discriminate among males on the basis of subtle differences in color.

Females that prefer colorful males may be rewarded with the youngest and healthiest mates. To test this idea, my group and I spent a hot, humid summer with Orange Sulphur butterflies in Arizona alfalfa fields. Studies from the 1970s had shown that female Orange Sulphurs find the ultraviolet reflectance of male wings attractive—but as a male's wings lose scales with age, his ultraviolet color diminishes. We wondered if aging reduces a male's seductive charms.



RONALD L. RUTOWSKI

LOSS OF SCALES WITH AGE (*top to bottom*) diminishes the ultraviolet reflectance of the male Orange Sulphur and renders him less attractive to females.

Our suspicions were confirmed when we found that virgin females indeed preferred males with intact wings to males with worn wings—a choice apparently driven by color, ensuring a younger mate.

Good Chemistry

Once a male and a female butterfly have noticed one another, courtship begins in earnest. The male's goal is to induce the female to alight and remain still for mating, which sometimes lasts an hour or more. In some species the female must also move her abdomen out from between her hindwings to grant the male access. Butterfly biologists have studied the ritual that precedes actual copulation in only a few dozen of the roughly 12,000 species of butterfly, but it seems clear that, for butterflies, what humans might think of as scent can be a language of love. The vocabulary of this language is chemical.

The best-understood case of nonvisual butterfly communication involves the Queen butterfly, *Danaus gilippus*. Males of this species produce pheromones, compounds designed to elicit specific reactions—of sexual interest in this case—from other butterflies. These pheromones disseminate from brushlike structures, called hair pencils, found at the end of the abdomen in males only. Hair pencils have a particularly large surface area for their small volume and are thus highly efficient at distributing chemicals. As a male flies up and down in front of a female, he touches her antennae with his protruding hair pencils, thereby depositing pheromones. The female responds to this chemical signal by alighting and remaining still while the male copulates with her.

Many species of butterfly probably use pheromones in courtship. Males often possess features reminiscent of the Queen's hair pencils, such as patches of unusual scales on the wings and brushlike structures on the thorax. Like hair pencils, these scales and hairs have large relative surface areas that would presumably enhance pheromone distribution. And for the family of butterflies classified as Sulphurs, special scales on the male's generally bright yellow or orange wings do indeed emit compounds that may affect female behavior.

Some species of butterfly have evolved ritualistic courtship displays that could

BOWING DISPLAY of the Grayling (*Hipparchia semele*) brings a female's antennae into contact with brushlike scales on the male's wings. These scales may produce chemicals that induce the female to accept his advances.

PATRICIA J. WYNNE

expose females to male pheromones just as the up-and-down flight of the Queen allows hair pencils to touch antennae. A male Grayling, *Hipparchia semele,* for example, will alight directly in front of a female and catch her antennae between his wings. He bows slowly forward, rubbing the female's antennae against a patch of scales suspected of carrying pheromones. The male Barred Sulphur, *Eurema daira,* perches next to a female and waves his forewing up and down, dragging the edge of his wing along her antennae with each sweep. The male Gulf Fritillary, *Agraulis vanillae,* sits next to a female and claps his wings open and closed; the female's nearest antenna is often caught between the male's wings, where it touches brushlike scales.

Elaborate interactions such as these are not the norm in the butterfly world, however. In fact, courtship in most species is fleeting—lasting less than 30 seconds and consisting mostly of the male fluttering about the female. A more representative courtship may be that of the Little Yellow, in which the male buffets the female for a few seconds before alighting and attempting to copulate. This simple activity may be sufficient to waft pheromones onto the female's antennae, making her agreeable to mating.

Despite the charming nature and eager efforts of the male, some females remain indifferent to any of these attentions. Females that have recently mated successfully can be most obstinate. These females will take defensive measures to discourage an unwanted suitor. If perched, they will flap their wings rapidly; if flying, they will flee, sometimes shooting dozens of feet upward in a maneuver called ascending flight. If the spurned male is persistent, the resulting aerial courtship can last several minutes. Just as a tale of dramatic conflict may be more compelling than one of tiresome harmony, these conspicuous rejections often attract more butterfly watchers than do the more fleeting courtships that lead to mating.

Location, Location, Location

Gaudy wings, smooth moves and pheromones do a male butterfly no good if he cannot find a female butterfly on whom to practice his seduction. Males of many butterfly species adopt a

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ATTRACTIVE CHEMICALS are disseminated by brushlike structures called hair pencils on the male Queen butterfly (*Danaus gilippus*) (*top butterfly at far left*). These pheromones are produced from chemical precursors that males obtain by sucking at plants such as Crotalaria (*below*).

RONALD L. RUTOWSKI

search-on-the-fly strategy, wandering the landscape looking for mates. Often they investigate likely areas, such as plants where females tend to lay their eggs or sites where virgin butterflies emerge from their cocoons.

Males of the Empress Leilia species, *Asterocampa leilia,* however, use a highly systematic approach. Because that species' larvae feed and pupate on desert hackberry trees and because the females mate but once in their short lives, the males actually stake out that vegetation in search of young virgins. A few hours after dawn, just when the females emerge from their cocoons and become ready to fly for the first time, the males begin their watch.

Early in the day the males perch on the ground in open, sunny spaces near the trees. This early-morning sunbathing probably allows them to keep an eye out for other butterflies while keeping their bodies warm enough to give chase. (Because they cannot regulate body temperature internally, butterflies grow sluggish if the ambient temperature is too cold.) Later in the morning the males move up into the trees to exactly the average plane of flight of Empress Leilia females, about one meter above the ground. My students and I have observed that even when the male butterflies are perched at a tilt, they hold their heads so that their eyes are looking horizontally out of the tree. This orientation seems to ensure that their area of greatest visual acuity—which lies in a band at the equator of the visual field—coincides with the plane of likeliest female flight.

Male Empress Leilias guard their territory jealously for an hour or two. They will take off after any approaching object, whether butterfly, bird or tossed rock. These vigilant males pursue females or chase away encroaching males before returning to the same perch. Many species of butterfly show even greater territoriality, laying claim to mating grounds characterized more by geography than by resources such as hackberry trees: bare spaces, sunny spots, ravines and gullies, and especially hilltops.

We can only guess why male butterflies (and, indeed, other insects) seek these territories. Sunny patches may attract females to stop and warm themselves; a bare spot might make a good vantage point for visual contact. Among the most intriguing of territories is the hilltop. The virgin females (but not mated females) in some species do tend to fly uphill, but the riddle of cause and effect in the evolution of hill-topping behavior remains unsolved.

The elements of male butterfly courtship, from attractive wing color to enticing pheromones to auspicious environs, seem geared toward ensuring as many successful matings as possible. Even a male's preference for young females has a logical basis, as the youngest females have a better statistical chance to survive long enough to produce many of his offspring.

For males, a strong imperative, related to the impulse to send their genetic material into the next generation, is to prevent their mate from mating again. Male butterflies actually make a substantial contribution to females during copulation, passing along a large quantity of nutrients. This nutrient store, called the spermatophore, can be as much as 6 to 10 percent of the male's body weight; a male cannot afford such an investment in a female who will use his competitor's sperm to fertilize her eggs [see "Glandular Gifts," by Darryl T. Gwynne; Scientific American, August 1997]. In fact, evolution has come up with a mechanism that favors the male that has succeeded in mating first. The presence of the spermatophore in the female's reproductive tract causes her to be unresponsive to further sexual advances. Experimental evidence supports this conclusion: artificially filling a virgin's reproductive tract renders her uninterested in mating, while cutting the nerves to this area in a mated female restores her sexual interest. Another male technique for barring other suitors from his mate is less elegant—he leaves a plug that obstructs the reproductive tract.

Females face different evolutionary pressures. They often get but one chance to mate and must therefore be highly selective. By accepting only the fittest male, a female can assure her own offspring a quality genetic endowment, and she might also secure for herself a more generous spermatophore—which most likely helps her live longer and, in turn, lay more of her eggs. Male colors, pheromones and displays may allow females to judge a suitor's overall fitness and success in life. We suspect that chemical signals indicate the quality of a male's diet: the crucial mating pheromone of male Queen butterflies, for instance, is produced only when the males have fed at certain plants. And vibrant colors can signal younger, healthier individuals.

As with human beings, some of the attributes and behaviors of butterfly courtship are quite elaborate, whereas others are fairly pedestrian. Intricate or simple, courtship and mating remain the mechanism by which survival and evolution take place. Whether a butterfly watcher takes in a swarming colony of Monarchs mating in the mountains of central Mexico or a dalliance between two alfalfa butterflies in a backyard, the observer is fortunate enough to be watching the results of, and the continuing course of, evolution.

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The Author

RONALD L. RUTOWSKI has studied butterfly mating behavior for almost 25 years. After receiving his Ph.D. at Cornell University in 1976, he joined the faculty of Arizona State University, where he is a professor and co-director of the Biology and Society Program in the department of biology. When not chasing butterflies, he enjoys playing the violin, making beer, and bicycling.

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How Females Choose Their Mates

Females often prefer to mate with the most flamboyant males. Their choice may be based on a complex interaction between instinct and imitation

by Lee Alan Dugatkin and Jean-Guy J. Godin

Picture a man who has a way with the ladies, and a character not unlike James Bond may spring to mind. He's clever, classy, fearless and flashy—characteristics that are almost universally appealing to the opposite sex. Throw in the powerful sports car, and you have a nearly irresistible combination.

That females often flock to the most ostentatious males is not a phenomenon unique to humans. In many different species, successful males—those that sire the most offspring—are often larger or more brightly colored or "show off" with more vigorous courtship displays.

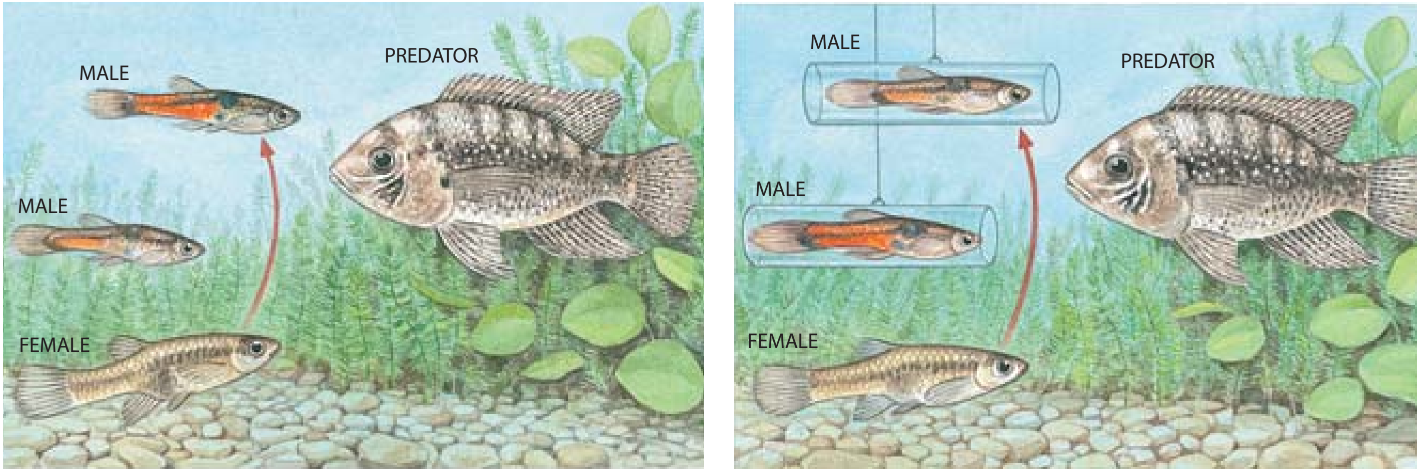
Females tend to be the choosier sex when it comes to selecting a mate, partly because males can produce millions of sperm, whereas females' eggs are few and far between. Thus, females may be more selective because they have more invested in each gamete and in the resulting offspring. And because the availability of eggs is a limiting factor in reproductive success, males tend to compete for female attention and not vice versa.

Charles Darwin was the first to propose that competition for mates plays an important role in reproductive success—a process he dubbed sexual selection. In *The Descent of Man, and Selection in Relation to Sex,* published in 1871, Darwin hypothesized that any trait that gives a male mating and fertilization advantages will evolve in a population because males with such traits will produce more offspring than their competitors. Assuming the trait is heritable, offspring expressing the beneficial trait will, in turn, achieve greater reproductive success than their competitors, and so on, through future generations. Further, Darwin proposed that some of these traits may have evolved because they attract the attention of females.

The idea that females are discriminating and can actively choose with whom to mate was controversial from its inception—perhaps because male-male battles can be quite spectacular. Males may fight amongst themselves, occasionally in dramatic battles to the death, to gain mating privileges with females. In comparison, female choice is generally much more subtle.

FEMALE TRINIDADIAN GUPPIES do the choosing when it comes to selecting a mate. Generally speaking, female guppies prefer males that are brighter or more orange in color (*upper right*). But even guppies are prone to social pressure. If, for example, an older female appears to fancy a drabber male, a young female may ignore her instincts and choose to copy her elder's mate selection (*lower left*).

ROBERTO OSTI



ROBERTO OSTI

MALE GUPPIES inspect predators; female guppies inspect the males. When a predator—such as the cichlid pictured here—approaches a school of guppies, a pair of males often swims over to inspect the potential threat. Such bold behavior may be attractive to females, which tend to choose as a mate the suitor that swims closest to the predator (*left*). Although the bravest males are often the most colorful, females will choose a less flashy contender if he appears to be more courageous than his inspection partner (*right*). In the laboratory, custom-made containers allow the authors to position the males.

Finding Mr. Right

Over the past 25 years, a considerable body of scientific evidence in support of female choice has accumulated. Females actively choose their mates in a large variety of species—particularly ones in which males are less aggressive and display individual differences in secondary sexual characteristics, such as ornamental plumage or courtship displays. Nevertheless, how and why females select their partners and how mating preferences have evolved remain hotly debated issues among evolutionary biologists.

A choosy female faces two general tasks in selecting a mate. First, she must search for and locate a male. This task can be difficult if the population is sparse or if the danger of predators prevents her from spending a good deal of time searching for a suitable mate. Once she has encountered a male, the female must then decide whether to accept or reject him as a mate. The decision often involves some shopping around. In certain mating systems, females may encounter a group of available males and can compare them on the spot. For example, in early spring, male sage grouse (*Centrocercus urophasianus*) aggregate "cheek-to-jowl" in temporary communal mating arenas called leks, where they strut their stuff for the females. A female typically observes the displays of a number of males, apparently comparing them before mating with one lucky suitor. She then leaves the lek to nest and raise her brood elsewhere. Of all the potential mates on a lek, a few preferred males receive the bulk of the female attention.

But males are not always conveniently displayed like chocolates in a sampler box. More commonly, females encounter males one at a time. Comparing males in this case is presumably a more challenging cognitive task, as it involves remembering the characteristics of an individual that is no longer in sight. Studies have shown that females can rank the characteristics of sequentially presented males. Theo C. M. Bakker and Manfred Milinski of the University of Bern in Switzerland found that female three-spined sticklebacks (*Gasterosteus aculeatus*) will tailor their mate choice to the relative attractiveness of the present and previously encountered males. Females were more likely to show interest in a male if his red nuptial coloring was brighter than the previous male's and more likely to reject a suitor whose coloring was less bright than his predecessor's.

Whether a female chooses her mate from among a dozen dancing grouse or between a pair of crimson fish, she generally selects the most conspicuous contender. Empirical evidence indicates that females commonly prefer male traits that most strongly stimulate their senses. (This evidence has recently been reviewed by Malte Andersson of the University of Göteborg in Sweden and by Michael J. Ryan of the University of Texas at Austin and Anne C. Keddy-Hector of Austin Community College.) For example, when given a choice, female green tree frogs (*Hyla cinerea*) are preferentially attracted to males that call the loudest and most frequently; female guppies (*Poecilia reticulata*) to the most brightly colored males; and female mallards (*Anas platyrhynchos*) to males that court them most frequently. Because of such preferences, males have typically evolved exaggerated secondary sexual traits to attract the opposite sex.

Why Be Choosy?

Even though evidence indicates that females can actively choose their mates, the question of why females discriminate, rather than mate at random, remains largely unresolved. How did female choice originate and evolve? What are its benefits and costs to individual females?

In some cases, females may favor mating with a male that is loud or brightly colored simply because he is easy to locate. Reducing the amount of time it takes to find a mate may reduce a female's risk of being killed by a predator. But for many species, mate choice is probably more complex. For many birds and mammals, natural selection appears to favor females who choose mates that provide them with some direct benefit that will increase their fecundity, their survival or the survival of their offspring. Such benefits might include food, a safe haven or even the prospect of fewer parasites.

In a long-term study of the barn swallow (*Hirundo rustica*), Anders P. Møller of the CNRS in Paris observed that females prefer to mate with males possessing elongated tail feathers. As it turns

females may have evolved a preference for the flashier males because color is a proxy for boldness and fitness.

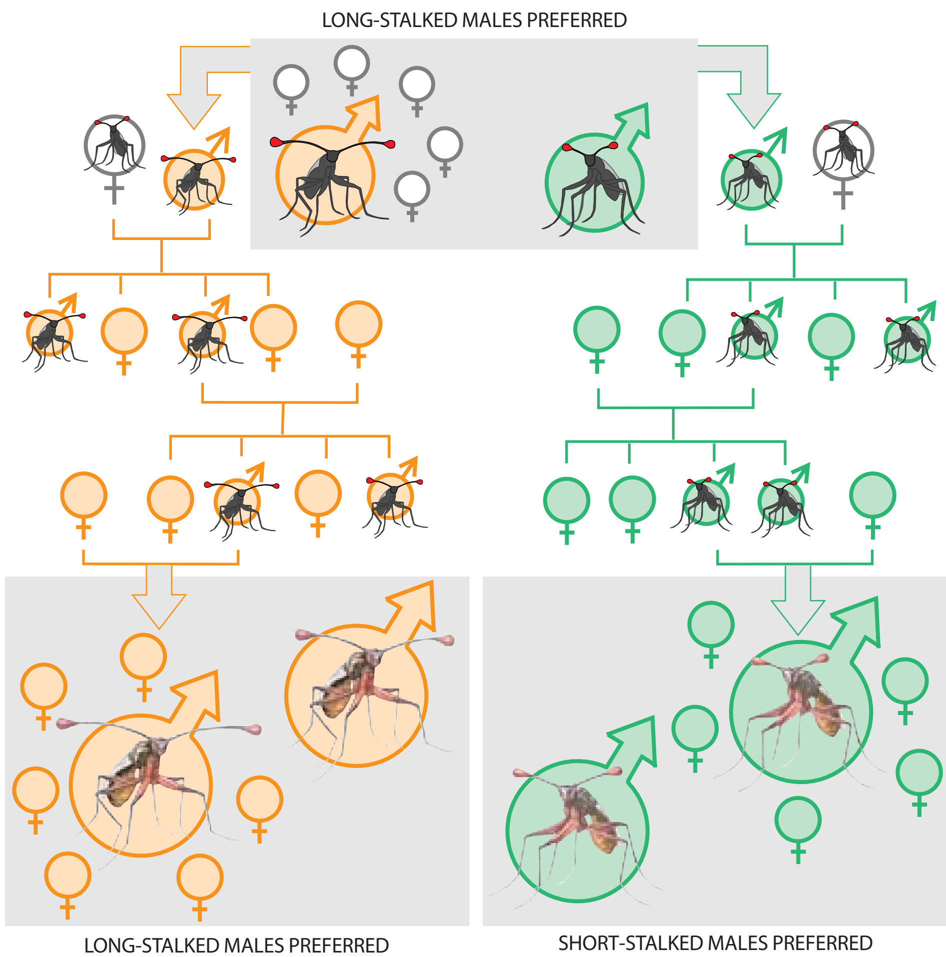
out, the long-tailed males are infected with fewer bloodsucking mites than their short-tailed counterparts. Because these parasites can jump from bird to bird, females that mate with long-tailed males benefit by avoiding infection and by producing greater numbers of healthier chicks than females that mate with shorter-tailed males. Unfortunately, because selecting a mate that offers direct benefits seems so obvious, few studies have tested this evolutionary model in a rigorous way.

When males provide no obvious resources, such as food or protection, females may choose to mate with the males that appear to have the best genes. How do they know which males have good genes? And why don't males just cheat by faking the traits associated with such genes? In 1975 Amotz Zahavi of the University of Tel Aviv in Israel suggested that females assess only those traits that are honest indicators of male fitness—a hypothesis known as the handicap principle. Honest indicators, which are "costly" to produce and maintain, should be associated with the most vigorous males.

While studying antipredator behavior in the Trinidadian guppy, we recently obtained some evidence that is consistent with the handicap principle. When a predatory fish nears a school of guppies, males, often in pairs, cautiously approach the potential threat to "inspect" it. Such risky behavior has been observed in many species, and behavioral ecologists have suggested that bold males may swim close to a predator to advertise their vigor to nearby females. In fact, laboratory studies have shown that when no females are present, no male guppy plays the hero by approaching the predator more often than his counterpart.

We hypothesized that boldness exhibited during predator inspection might be attractive to females because it should be a reliable indicator of fitness. Less vigorous guppies who tried to "fake" competence in predator inspection would likely be eaten. By using small, custom-built containers that allowed us to position males at different distances from a predator fish, we found that females indeed preferred the most intrepid males. Such courage appears to correlate with color: the males that swim closest to the predator are usually the most colorful. Thus, in the wild, females may have evolved a preference for the flashier males because color is a proxy for boldness and fitness.

Once females have expressed a preference for a certain trait, a process called runaway selection can occur. The model, first brought to the attention of evolutionary biologists by Ronald Fisher in 1958, suggests that a male trait and the



RUNAWAY SELECTION may shape mate preferences in stalk-eyed flies. Females of the species normally choose to mate with males that sport the longest stalks (*top center*). But when researchers used selective breeding techniques to generate two lines of flies—one in which males have long stalks (*left*), the other in which males' stalks are short (*right*)—they found that female preferences evolved along with male stalk length. Females from the long-stalk line were partial to males with longer stalks (*bottom left*), and females from the short-stalk line preferred shorter-stalked males (*bottom right*).

DRAWINGS BY ROBERTO OSTI; DIAGRAM BY JENNIFER C. CHRISTIANSEN female preference for that trait coevolve. For example, females that prefer to mate with large males should produce large sons as well as daughters that show a preference for large males. Under certain conditions, this process can escalate, producing increasingly exaggerated male traits and stronger female preference for those traits.

A number of behavioral ecologists have found some evidence for runaway coevolution of orange body coloration in male guppies and of female preference for this male trait. But a more convincing example of runaway selection has recently been presented by Gerald S. Wilkinson and Paul Reillo of the University of Maryland in their study of the stalk-eyed fly (*Cyrtodiopsis dalmanni*). In this species, females generally prefer to mate with males possessing widely spaced eyes. By selectively breeding the flies for 13 generations, Wilkinson and Reillo generated one line of flies in which the males had large eyestalks and another line of shorter-stalked males. They found that females in each line preferred the male trait selected for in that line—that is, females from the large-stalk line preferred males with the longest stalks, and females from the short-stalk line preferred shorter-stalked males. Female preference thus coevolved with the selected male trait.

What Females Want

MALE TRAIT	FEMALE PREFERENCE	SPECIES
Call (song)	Greater intensity	Meadow katydid
	Greater frequency	American toad
	Longer duration	Green tree frog
	Greater complexity	Tungara frog
	Larger repertoire	Song sparrow
Courtship display	Greater frequency	Sage grouse
Body size	Larger size	Convict-cichlid fish
Tail	Longer tail	Barn swallow
	Greater tail height	Crested newt
	Greater number of "eyespots"	Peacock
Comb	Larger comb	Red jungle fowl
Bower	More decorated bowers	Satin bowerbird
Breast stripe	Larger stripe size	Great titmouse
Body color	Greater brightness	House finch
	Greater area of orange	Guppy

JENNIFER C. CHRISTIANSEN

How do preferences about mate choice originate? In some cases, females may have a preexisting sensory bias for a certain trait, not because it represents anything but because it attracts attention—a hypothesis championed most prominently by Ryan and by John Endler of James Cook University in Australia. For example, female swordtails (*Xiphophorus helleri*) prefer males with long "swords" on their tail fins. And although males of a related species—the platyfish *Xiphophorus maculatus*—lack swords completely, Alexandra L. Basolo of the University of Nebraska found that when she attached artificial, plastic swords onto these naturally swordless males, female platyfish showed an immediate, strong and consistent preference for the males with the counterfeit swords. In other words, platyfish females harbored a preexisting bias for long swords, even though swords reveal nothing about the fitness of platyfish males.

These evolutionary models may be operating separately or in conjunction; it is difficult to untangle them experimentally. Female guppies, for instance, may be partial to orange males because bright coloring is a proxy for boldness or for good health (males with the brightest pigments are probably eating well). But the preference could have originated because females are more attuned to colors of a particular wavelength and then further evolved through a runaway mechanism.

All these models assume that female preference is genetically determined. Recent studies indicate, however, that social factors, such as imitation, also influence mate choice.

Copycat Birds and Fish

Some guys get all the girls. On a crowded grouse lek, for example, the top male may receive 80 percent of the mating opportunities. Is he simply irresistible? Or do females take one another's choices into account when selecting a mate? In the early 1990s a group of Scandinavian researchers, led by Jacob Höglund and Arne Lundberg of Uppsala University and Rauno Alatalo of Jyväskylä University, initiated a detailed study of mate-choice copying in the black grouse (*Tetrao tetrix*). Using stuffed dummies to represent interested females, the researchers showed that female grouse mated preferentially with the male that appeared to have other females in his territory.

Why copy? Perhaps imitation teaches females what to look for in a male. In an extensive series of experiments on mate-choice copying in guppies, we determined that young females are more likely to copy the mate choice of older, more experienced females than vice versa. Further, copying may save time. Relying on the judgment of others may allow a female to assess a potential mate quickly and efficiently, leaving her more time to forage for food or hide from predators.

For species in which females copy, a fascinating question emerges: How much of female mate choice is based on instinct and how much on imitation?

To tease apart the relative contributions of genetic and social factors involved in mate choice in guppies from the Paria River in Trinidad, one of us (Dugatkin) carried out a behavioral "titration" experiment. First, a female guppy was allowed to choose between two males that differed in the amount of orange that covered their bodies. As expected, females virtually always chose the more orange of a pair of males. Then a copying opportunity was staged, in which the test female was allowed to observe another female apparently choosing the less orange male as her putative mate.

Which male did she then choose for herself? Remember that the female's genetic predisposition is "pulling" her toward the more orange male, but social cues and the potential to copy are tugging her toward the drabber male. In the end, her choice depended on how much the males differed in coloration. When the paired males differed by small (12 percent) or moderate (25 percent) amounts of orange, the female consistently chose the less orange of the two. In this case, the female succumbed to peer pressure, her tendency to copy overriding her genetic preference for orange males. If, however, the males differed by a large amount (40 percent) of orange, the female ignored the seemingly bad advice and chose the more orange male, her genetic predisposition masking any copying effects.

It appears as if there exists in guppies a color threshold, below which social cues steer female mate choice and above which genetic factors predominate. Dugatkin is performing further experiments to assess whether copying behavior in guppies is itself heritable. Although imitation appears to be based on social cues, perhaps genes govern the likelihood that a female guppy will engage in copying behavior.

Sadie Hawkins Day

Although people are more complex than guppies and grouse, some of the same mate-choice rules may apply to human dating games. According to popular wisdom, it is human females who are the choosier sex when it comes to selecting a mate. As a species, humans meet the criteria for female choice: men, for the most part, will avoid fighting to the death for the hand of a young maiden. And females can distinguish between various males on the basis of differences in their characteristics: some men are brasher, some are brighter and some have bigger bank accounts.

Women may even engage in mate-choice copying. After all, imitation is important in many types of human learning. To determine whether copying plays a role in how women rate a man's attractiveness, Dugatkin is currently collaborating with social psychologists Michael Cunningham and Duane Lundy of the University of Louisville. Although their results are preliminary, they find that women are more likely to express an interest in going out with a man if they are told that other women also find him attractive.

Of course, evolutionary theory will never be able to explain fully singles bars, personal ads or cyber-romance. Even for animals, it appears that the benefits and costs of being choosy when selecting a mate differ for different species, in different environments and sometimes at different times of day. In any case, if animals as simple as guppies can consider the opinions of their peers when choosing a mate, imagine how complex the cues must be that guide humans in their search for the perfect mate. SA

although people are more complex than guppies and grouse, some of the same mate-choice rules may apply to human dating games.

The Authors

LEE ALAN DUGATKIN and JEAN-GUY J. GODIN first joined forces in Trinidad, where they became fascinated by the mating behavior of guppies. An evolutionary biologist, Dugatkin has been an assistant professor of biology at the University of Louisville since 1995. He received his Ph.D. in biology from the State University of New York at Binghamton in 1991. His research interests include the evolution of cooperation and altruism and the interaction of genetic and social factors in shaping behavior. Godin, a behavioral ecologist, is professor of biology at Mount Allison University in New Brunswick, Canada, where he has been on the faculty since 1981. He received his doctorate in zoology from the University of British Columbia and has been a visiting fellow at the University of Oxford. His research focuses on the behavioral ecology of antipredator, foraging and mating decisions in animals.

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GLANDULAR GIFTS

The way to a katydid's heart is through her stomach

by Darryl T. Gwynne

originally published in August 1997

In 1859, the year evolutionary theory burst onto the scene with the publication of Charles Darwin's *On the Origin of Species*, Captain John Feilner of the U.S. Cavalry was exploring northern California. He was eventually killed by Indians, but not before he had reported to the Smithsonian Institution his observations on the habits of grasshoppers. After the mating act, he noted, "a small bag—evidently the ovary—is attached to the body of the female close to the tail."

Almost half a century later, across the globe in France, pioneer ethologist Jean Henri Fabre filled in the details of this curious copulation. In *The Life of the Grasshopper*, a volume devoted to orthopteran insects in his *Entomological Memories (Souvenirs entomologiques)*, Fabre correctly identified the bag as originating from the male. He wrote that an opalescent structure "similar in size and color to a mistletoe berry" was attached to the spermatophore, a separate sperm-filled package, and eaten by the female in a "final banquet" culminating the mating sequence.

Such extreme investments in mating are typically viewed by biologists as a mystery. Male animals usually commit only genetic material in their cheap gametes—the sperm. Their greatest reproductive benefit is thought to come from a strategy of multiple copulations rather than from putting much of their resources into any one. Females, on the other hand, produce expensive gametes—eggs containing both genetic and nutritive material—and often use up considerable effort in ensuring that each mating is productive. As a result, they choose their mates very carefully.

The roots of male investment may lie in either natural or sexual selection, the processes proposed by Darwin as the causes of biological evolution. Natural selection arises from the struggle to survive and reproduce. Sexual selection derives solely from competition for mates—or, as I shall explain in the case of glandular gifts, for inseminations.

The donations typical of many crickets and katydids are postcoital meals: females eat them after copulation, while the externally attached spermatophore is ejaculating with a syringelike action. Thus, in these species, ejaculation can occur after the pair has parted. In 1915 the fact that eating the nuptial meal coincides with sperm transfer led the Russian biologist B. T. Boldyrev to suggest a reason for such contributions as the katydid's food bag. He speculated that this bag, which he called the spermatophylax, served to distract the female from eating the spermatophore, which would probably supply some nutrition in itself. Any such delay should result in fertilization of more eggs, because more of the ejaculate would be transferred, helping the gift-giving male's sperm to outcompete numerically the sperm of other males already stored within the female. (Sperm storage is the rule in insects, and females have a special organ, the spermathecae, which evolved for this purpose.)

The hypothesis that the nuptial meal is a result of sexual selection was elaborated on by Nina Wedell of Stockholm University, who suggested that an evolutionary arms race had occurred between the sexes. Males had evolved the tempting spermatophylaxes to prevent females from eating their sperm. Females then evolved to mate many times—perhaps to get additional meals—prompting the males to provide ever more sperm to wash out their rivals' gametes. So a larger meal bag became necessary to protect the larger sperm bag.

Robert L. Trivers of Rutgers University offered an alternative hypothesis for nuptial gifts. He noted that the male investment may be a form of indirect paternal care: natural selection could have acted on males to induce them to give nutrients that would be incorporated into eggs, thereby providing benefits to their own progeny.

All in the Family

These ideas, it should be noted, are not mutually exclusive; a male's investment may procure dual returns. It is even possible that the trait evolved originally for one purpose but is today maintained for another. I decided to probe the latter possibility by looking closely at the historical record.

Scientists examine the origins of an adaptation by tracing it among different taxa (groups of related organisms). If, for instance, all the organisms at the tips of a phylogenetic tree—a family tree showing the relationships and descent of related organisms—have a certain trait, one may deduce that the ancestral organism had it as well. I used this logic to address the origin of male nuptial offerings within the cricket-katydid group.

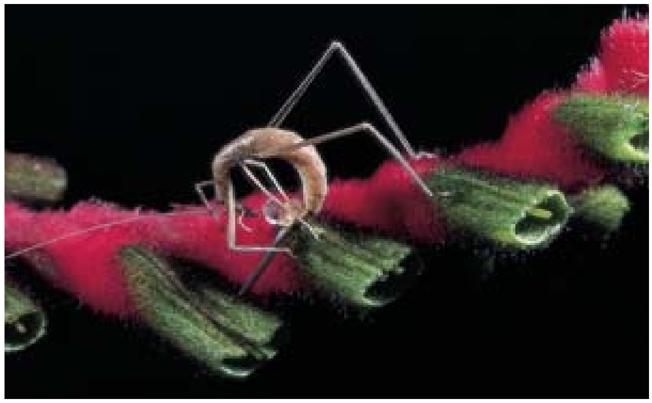
As in short-horned grasshoppers, spermatophores of most insects are placed inside the female. So if male contributions originated to prevent interference with sperm transfer, they would have evolved only after the first appearance of both an externally located spermatophore and the female's consumption of this vulnerable package. My analysis supported this sequence of evolutionary events. In virtually all taxa of the cricket-katydid tree, the female eats the spermatophore, suggesting that the ancestral cricket at the base of the tree did so as well. In addition, virtually all taxa on the left-hand branch of the tree—and a few on the right-hand branch—offer a spermatophylax gift, indicating that this refinement developed somewhat later. Indeed, the comparisons reveal about a dozen independent origins of glandular and body-part meals, including three distinct origins of a spermatophylax. (Curiously, the most common nuptial offering in the animal kingdom—prey or other food items harvested by the male, as opposed to its tissues or secretions—does not exist in the Orthoptera at all.)

Several experimental studies show that males typically supply no more food than necessary to allow time for safe transfer of sperm, suggesting that the ancestral protective role for glandular meals is also the present role in most katydid and cricket species. Moreover, effective sperm transfer, allowed by an ample meal, does seem to bring a reward in terms of increased paternity. Wedell mated two males of *Decticus verrucivorus* (literally, the "wartbiter" katydid) to the same female. She found that the proportion of offspring sired by a male directly relates to the size of the meal it donates as compared with its rival's.

Another analysis of paternity revealed a remarkably similar pattern in a quite different arthropod—one in which the meal ends the male's reproductive career. The tiny male Australian redback spider is cannibalized in about two thirds of all matings because it somersaults into the jaws of its much larger mate during insemination. One explanation offered for this morbid meal is that the male's complicity evolved as a final act of paternal nutritive investment. Experiments conducted by Maydianne C. B. Andrade, then at the University of Toronto, have shown, however, that male self-sacrifice is instead like most other mating meals: it helps to prolong coitus rather than to provide nourishment.

This suicidal snack distracts the female, thus extending the time for sperm transfer and increasing the number of eggs fertilized. Furthermore, although both the spider's somatic gift and the wartbiter's meal must contain some nutrition, it is not of any detectable reproductive or survival value to the female. Thus, these males' extreme offerings do not violate the rule that the male's mating effort is an aid for fertilizing as many eggs as possible, rather than for nurturing the offspring.

The Australian redback is one of the black widow spiders



DARRYL T. GWYNNE

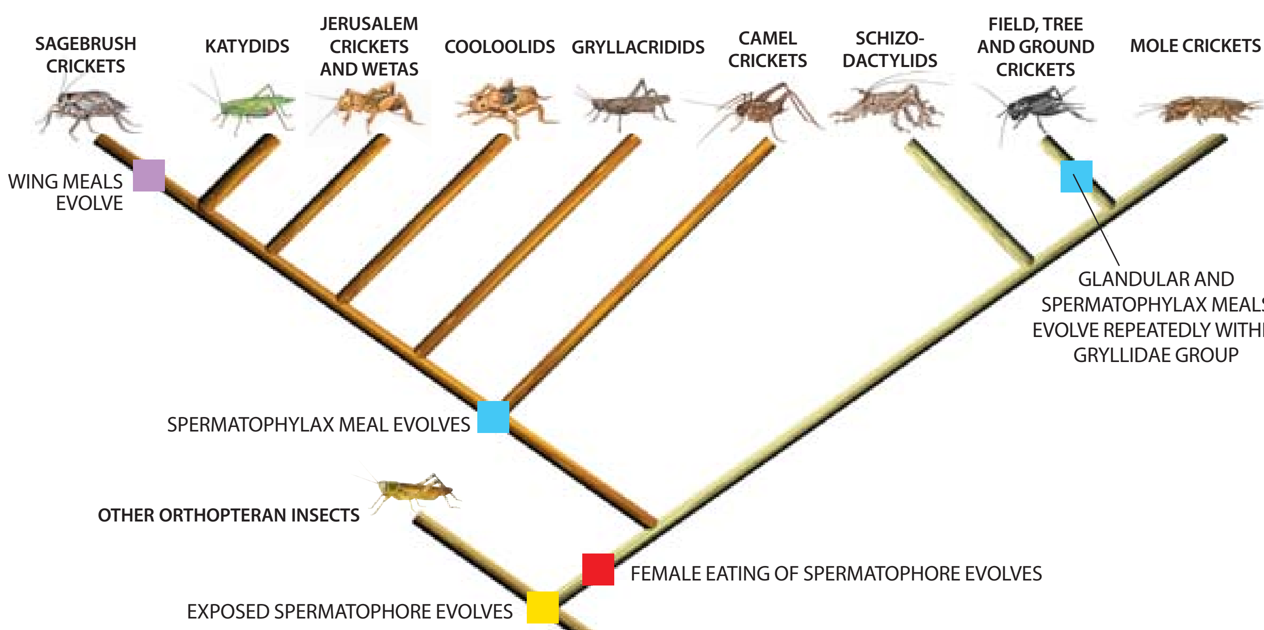
SPERMATOPHYLAX, a food bag transferred with the sperm, is the most common gift among katydids (Tettigonidae) and related crickets. Shown eating one is an Australian pollen katydid (*Kawanaphila nartee*).

(genus *Latrodectus*). Females of other black widow species sometimes consume the male after mating. But for the most part, this cannibalism does not appear to be an instance of gift giving, as males show no complicity in the act. The same is true of many other perilous copulations, such as those of some praying mantises, where the males try hard to escape their mate's clutches.

Sexual selection therefore appears to be the general rule in nuptial feedings. Some of these meals improve the genetic fitness of females, perhaps because the ancestral females preferred more nutritious gifts. The mating meals of some katydids are known to boost not only the number but also the size of the eggs; increased weight enhances the chances of an egg surviving the winter. And work by William Brown of the University of Toronto showed that secretions lapped by the female from a tiny "soup bowl" gland on the male's back contain a Methuselah substance—glandular material of unknown composition that enhances the female's longevity.

Such positive effects do not by themselves confirm the paternal hypothesis, however: a meal that serves as a sexually

EVOLUTIONARY TREE of crickets and katydids (orthopteran suborder Ensifera) indicates that exposed, vulnerable spermatophores evolved first (yellow). Nuptial meals, in the form of a spermatophylax, or meal bag, followed (blue). The sequence suggests the banquets evolved to prevent the female from eating the sperm.



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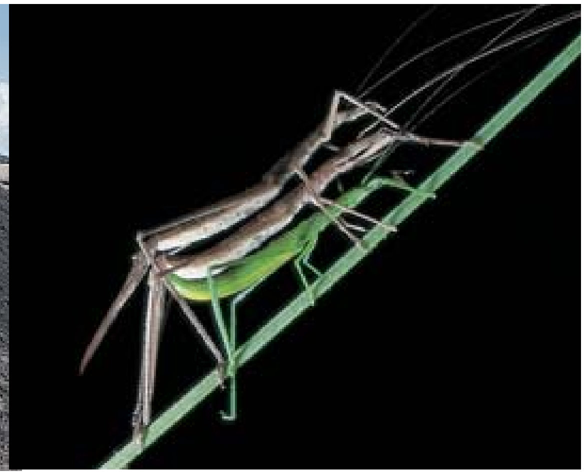

DARRYL T. GWYNNE

MIGRATING MORMON CRICKETS near St. Anthony, Idaho, can find very little food. In order to get spermatophylax meals, females aggressively seek to mate, as do female Australian pollen katydids (*right*). Two females jostle for position over an available male.

selected distraction may also be a nutritious one. To support a paternal function, there should also be a clear pattern of the male nurturing its own offspring, rather than those of a rival. In two species of Australian katydids, males appear to be confident of their paternity because the eggs are laid before the female takes a second mate; moreover, these eggs are fatter when the nuptial meal is more substantial.

Male fire-colored beetles (*Neopyrochroa flabellata*) may also have evolved to invest in offspring—not with food but with a chemical secretion that protects the progeny from predators. Thomas Eisner and his colleagues at Cornell University examined the beetles' use of cantharidin, the active chemical in the (rather dangerous) aphrodisiac "Spanish fly." After eating cantharidin, the male stores some in a gland in its head; but most goes to specialized abdominal glands. During courtship, females taste the head glands and mate with males that have eaten cantharidin, rejecting the others. The males subsequently ejaculate most of their reserve of cantharidin into the females, who incorporate it into their eggs. Thus, the males are honest advertisers—they give away their cache of cantharidin instead of saving it to attract more females. So the chemical meal might have more of a nurturing, paternal function than an exploitative sexual one.

Changing Roles

One of the two katydids in which the spermatophylax appears to have changed from its ancestral distractive role to a more nurturant function is Western Australia's garden katydid (*Requena verticalis*). A male *Requena* provides a larger meal than necessary to distract its mate and ensure full insemination. Even so, the pressures of sexual selection never quite go away. Leigh W. Simmons and his colleagues at the University of Western Australia showed that males save the best banquets for matings with healthy young females. A young female is no more than a week past molting into adulthood; an old one has spent three weeks as an adult and will most likely have stored sperm from rival males. In matings with older females—the paternity of whose offspring is questionable—males show a subtle form of discrimination by transferring smaller spermatophylax meals.

The idea of males choosing mates brings me to a final twist to the story of seminal gifts. The evolution of a large, nutritious spermatophylax in several species has, somewhat paradoxically, caused a complete turnaround in the more familiar patterns of sexual selection, in which males compete for mates and females choose. One such katydid is the Mormon cricket, a pest in parts of the American West, and almost certainly the grasshopper that Captain Feilner observed "in such numbers as actually to cover the ground." At these densities, very little food is available, and starvation has curious effects. Males mate less often because they can no longer produce many meals; females, in contrast, become more libidinous, with an increased urge to forage for mating meals. These changes dramatically reverse the more typical sexual behavior.

If Feilner had survived to spend more time observing his grasshoppers, he might well have noted this consequence. It is the females, not the males, that grapple for access to mates. Meanwhile the coy males become quite choosy about which female to provide with their costly, edible gifts. SA

The Author

DARRYL T. GWYNNE studies the evolutionary and behavioral biology of insects and spiders. He received his Ph.D. from Colorado State University in 1979. After research stints in New Mexico and Australia, Gwynne joined the faculty of the University of Toronto in the department of zoology. He is a Fellow of the Animal Behavior Society.

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Monogamy and the Prairie Vole

Studies of the prairie vole—a secretive, mouselike animal—have revealed hormones that may be responsible for monogamous behavior

by C. Sue Carter and Lowell L. Getz

originally published in June 1993

Observation of the mating and pup-rearing habits of nondescript, brown rodents that live under weeds and grasses might not seem an obvious way to improve knowledge of monogamy. After all, most humans can attest to the complexity of male-female relationships. Yet studies of the prairie vole (*Microtus ochrogaster*), a common pest throughout the midwestern U.S., have led us on a fascinating scientific journey from our starting point in ecology to the exploration of the neuroendocrinology of social bonds. Unlike most rodents, prairie voles form long-lasting pair bonds, and both parents share in raising their young. Our studies have provided a new understanding of the importance of two hormones, oxytocin and vasopressin, which are well known for their respective roles in reproduction and body water regulation. Work with voles now suggests that these hormones are involved in the development of monogamy.

The chief criterion that defines monogamy is a lifelong association between a male and a female. Within this broad definition lie several characteristics that are easily observed. Males and females of monogamous species tend to be about the same in size and appearance. Mated pairs will defend the nest and territory from intruders, and both parents care for the young. Monogamous mammals may form complex social groups that include an extended family and o›spring of various ages. Incest is avoided within these families; adult young usually do not reproduce as long as they live with related family members. Finally, we should point out that although common in birds, monogamy is rare in mammals. In an exhaustive survey, Devra G. Kleiman of the National Zoological Park in Washington, D.C., found that only about 3 percent of mammals are monogamous.

Sexual exclusivity, however, is not a feature of monogamy. Studies of the prairie vole as well as those of other mammals and birds have indicated that absolute sexual monogamy is not necessarily associated with social monogamy. In fact, DNA fingerprinting tests have shown that offspring of female prairie voles are not always fathered by the cohabiting males. In some cases, a litter may have mixed paternity.

Because prairie voles incorporate the defining features of monogamy, they make excellent subjects for the exploration of the biological foundations of monogamy, at least as it exists among nonhumans. Prairie voles are also small, weighing only a few ounces, and are easily reared in the laboratory. But of particular importance for understanding the biology of monogamy is the fact that not all voles are monogamous. The meadow vole (*M. pennsylvanicus*) and the montane vole (*M. montanus*) show no indications of monogamy. Voles of these species are rarely retrapped with the same partner and do not establish stable families, and males of these species do not usually care for their young. Therefore, comparisons of prairie voles with their nonmonogamous relatives can yield insights into the causes of monogamy.

One of the first surprises that came from studies of prairie voles was the observation that social cues regulate the reproductive physiology of this species. Even to enter estrus (sexual heat), a female prairie vole must sniff a male. Indeed, Milo E. Richmond, now at Cornell University, found that female prairie voles do not have the ovarian cycles that are typical of nonmonogamous mammals. In monogamous voles, a female must have a male partner to induce estrus.

Furthermore, not just any male can bring a female into heat. Fathers and brothers do not seem capable of eliciting sniffing. This may be an adaptive mechanism designed to prevent incest.

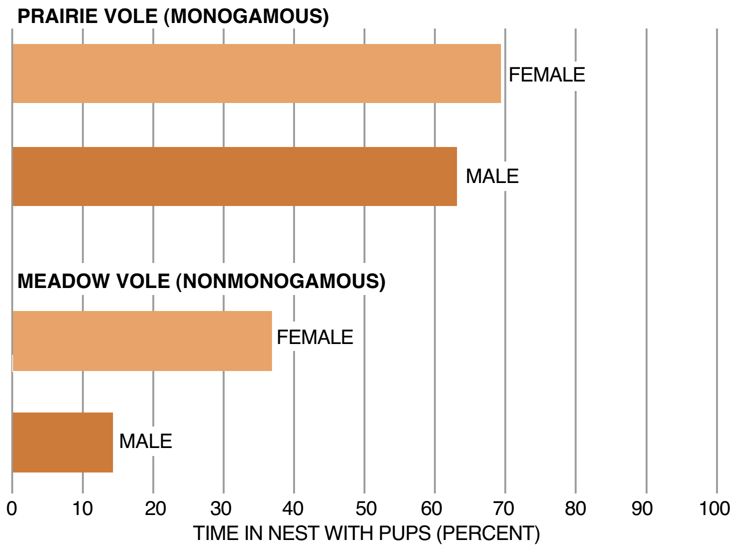
C. SUE CARTER and LOWELL L. GETZ have collaborated on their respective studies of behavioral endocrinology and fieldwork to investigate the biology of monogamy. Both are fellows of the American Association for the Advancement of Science. Carter received her Ph.D. from the University of Arkansas at Fayetteville. Before taking on her current position as professor of zoology at the University of Maryland, she was professor of psychology and ecology, ethology and evolution at the University of Illinois. Getz heads the department of ecology, ethology and evolution at the University of Illinois. He received his Ph.D. from the University of Michigan. The work described here reflects a 15-year collaboration and arose from observations made during approximately 35 years of fieldwork by Getz.

In fact, both males and females will essentially remain prepubescent as long as they stay with their families.

By sniffing an appropriate male, the female picks up a chemical signal called a pheromone. Pheromones in turn trigger the hormonal events needed to activate the ovaries and to induce heat. A small chemical sense organ, known as the vomeronasal organ, helps to mediate the effects of pheromones. John J. Lepri, now at the University of North Carolina at Greensboro, and Charles J. Wysocki of the Monell Chemical Senses Center in Philadelphia found that removal of the vomeronasal organ in the female prevented the start of heat. A similar effect occurs when the olfactory bulb is detached. By removing the bulb, Jessie R. Williams, Brian Kirkpatrick and Burton Slotnick, working in our University of Maryland laboratory, disrupted the sexual and social behaviors of the prairie voles.

In our laboratory, Dean E. Dluzen found that once a female is exposed to male odors, levels of norepinephrine, a neurotransmitter, and luteinizing hormone–releasing hormone (LHRH) change within minutes. These biochemical events occurred within the area of the olfactory bulb that receives input from the vomeronasal system. The stimulation of the olfactory system and the secretion of LHRH cause the pituitary gland to release a surge of luteinizing hormone into the bloodstream. In conjunction with other endocrine changes, the release of luteinizing hormone begins a cascade of chemical and neural events that stimulates the ovary to secrete gonadal steroids. Two of the most important steroids secreted are estradiol, a potent kind of estrogen, and progesterone.

Might estrogen and progesterone also be involved in monogamous behavior? In collaboration with Janice M. Bahr of the University of Illinois, we searched for patterns of gonadal steroid production that varied between estrus and nonestrus female prairie voles and compared the results with data from nonmonogamous species. Estradiol, a hormone known to be essential in inducing estrus in rodents, was elevated only in female prairie voles in heat. It declined after mating. This pattern is similar to that displayed by polygamous rodents. Analysis of the patterns of progesterone levels, however, presented an unexpected finding. In the nonmonogamous rats and montane voles, progesterone is released in the bloodstream shortly after mating begins. This rise in progesterone probably helps to regulate the duration of sexual activity by bringing these rodents into and out of heat. In contrast, we found that in prairie voles progesterone levels in the blood did not increase until many hours after coitus began.



PARENTAL CARE demonstrated by prairie voles far exceeds that shown by nonmonogamous meadow voles. The difference is most apparent with male prairie voles, which are with the pups four times as often as male meadow voles are.

The delayed secretion of progesterone explains an observation made in previous studies: that female prairie voles in their first estrus mate for prolonged periods. In our laboratory, Diane M. Witt observed that when the female was in natural estrus, males and females continued to engage in bouts of mating for about 30 to 40 hours. This extended mating period contrasts sharply to that seen in nonmonogamous species. Mating in meadow and montane voles persists for a few hours, and Syrian hamsters become nonreceptive after about 45 minutes of mating.

It is possible that the lengthy sexual interactions of prairie voles help the sperm enter the uterus and reach the egg. Studies of rats by Norman T. Adler of the University of Pennsylvania have shown that complex patterns of sexual behavior can influence the release of hormones and alter the ability of sperm to enter the female's reproductive tract and fertilize an egg.

Yet improving the chances of fertilization is probably not the sole reason for these extended bouts of mating. Once mating begins, females ovulate within about 12 hours, and successful pregnancy can occur shortly thereafter. Thus, prairie voles in their first heat continue to copulate for hours after they have met the requirements for pregnancy.

We suspect that, like humans and some other primates, prairie voles may copulate to facilitate the formation of monogamous social bonds. Protracted mating would be particularly crucial for prairie voles that are interacting for the first time, because they need to establish their lifelong monogamous bond. Indeed, some evidence for this idea comes from observations of females that have previously mated and become pregnant. Witt found that these experienced females engaged in brief copulations, sometimes limited to a few minutes. Having established a social bond, experienced males and females may not need to mate for long periods.

Social interaction that follows mating may be one of the mechanisms that reinforces monogamy in a species. Such interplay in nonmonogamous species often is restricted to a brief interval when the female is in heat. For example, Michael H. Ferkin, now at Cornell, observed that male and female meadow voles did not remain in physical contact after mating. In the Syrian hamster, which is an especially solitary animal, one of us (Carter) found that a female that has mated becomes extremely aggressive toward the male. In fact, the female may try to kill her sexual partner if he does not leave after coitus.

In contrast, mated monogamous mammals remain highly social toward their mates, even during nonreproductive periods. Leah Gavish, in our laboratory, demonstrated that prairie voles often touch and remain near their sexual partner. But this friendliness does not extend to strangers. After mating, both males and females became exceptionally aggressive toward unfamiliar members of their own sex. In nature, this behavior translates into territoriality or mate defense. In the laboratory we have used this model to examine the physiological processes responsible for pair bonding.

Specifically, we hypothesized that hormonal events induced by copulation might account for the dramatic behavioral changes that occurred after mating. Working in our laboratory, Kerry O'Banion took a first step toward examining this idea. O'Banion studied how females choose male partners before and after mating. In his experiments, familiar and unfamiliar males were tethered at opposite ends of an arena. O'Banion gave a female 10 minutes to choose. For the most part, females chose to mate with familiar and unfamiliar males equally. But if they had lived with a male, females showed a tendency to engage in nonsexual physical contact with the familiar male, not the stranger. These results illustrate the importance of social contact as an index of partner choice. They also confirm the DNA tests revealing that in nature female voles do not show absolute sexual monogamy.

More recently Williams examined female preferences in tests that lasted for at least three hours. She placed female prairie voles in a relatively large maze that contained three chambers. The females could elect to spend time alone or with males tethered in the two other chambers. The animals were monitored on videotape for their social and sexual preferences. After exploring both the stranger and the partner for about 30 minutes, females usually chose the familiar male.

In similar studies, Williams discovered that a female in her first heat developed a preference for a male if she was allowed to live with him for at least 24 hours. If the pair copulated, however, cohabitation produced clear social preferences in as few as six hours. These studies demonstrate that some aspect of the sexual interaction hastens the onset of a partner choice. We believe that hormones or neurochemicals released during mating or cohabitation may explain the experimental results.

One clue to the identity of the hormones came from work by Peter H. Klopfer of Duke University. He recognized that social bonds between mothers and their offspring were associated with the release of oxytocin and hypothesized that the compound might be the hormone of "mother love." Niles Newton of Northwestern University extended these observations to speculate that maternal and sexual bonds could be influenced by the secretion of the hormone. Oxytocin is produced primarily as a result of breast or gen-ital stimulation, such as that which occurs during mating, birth and lactation. More recently E. Barry Keverne and Keith M. Kendrick of the University of Cambridge have shown that in sheep either vaginal stimulation or oxytocin treatments can speed the formation of mother-infant bonds. Kerstin Uvnäs-Moberg of the Karolinska Institute in Stockholm has demonstrated that even simple touch can release oxytocin.

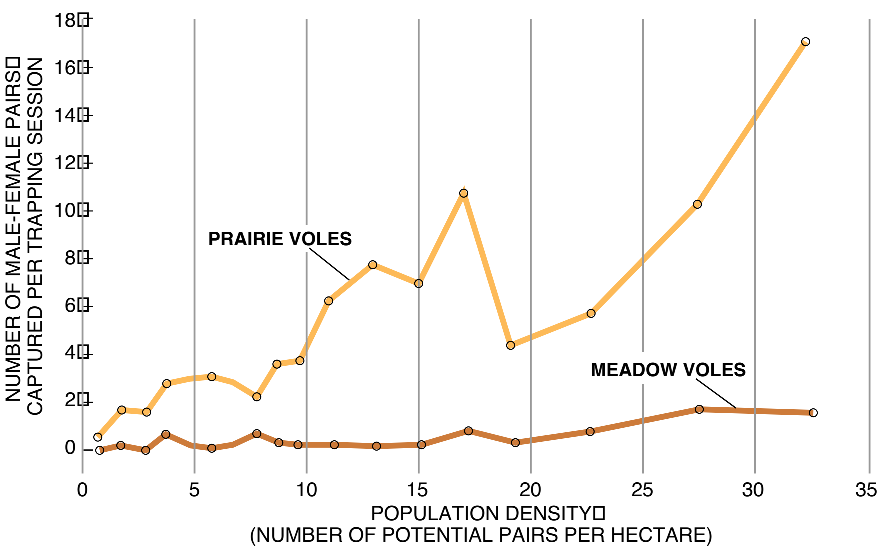
Based on these studies, we hypothesized that in prairie voles stimulation experienced during mating, or perhaps more slowly by touch and cohabitation, might release oxytocin. Oxytocin would, in turn, hasten the formation of social bonds between males and females.

Several recent findings support this supposition. Witt injected oxytocin into the central nervous system of females. As a result, the females became more sociable and less likely to fight with males, as compared with females that did not receive the oxytocin or females that received the hormone administered into the peripheral circulation. The positive social effects of oxytocin in the brain have now been documented in other species. Witt found improved social behavior in rats, and James Winslow and Thomas R. Insel of the National Institute of Mental Health (NIMH) reported similar results in squirrel monkeys.

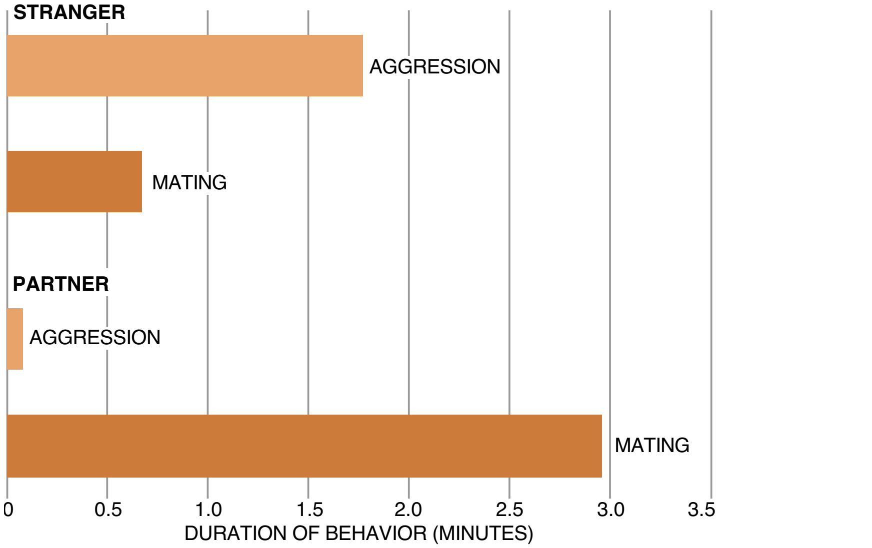
Williams examined the role of oxytocin more directly. She repeated her preference tests on prairie voles whose cerebral ventricles were infused with oxytocin. She found that females formed rapid preferences for males if they were exposed to oxytocin over a six-hour period. But when combined with a drug that blocks the oxytocin receptors, oxytocin no longer exerted the social effect. These results suggest that oxytocin's action within the brain may be one of the physiological events that lead to the formation of monogamous pairs.

Because the receptors for a hormone can regulate the behavioral effects of that hormone, we also looked at the patterns of oxytocin receptors in the prairie vole. These receptors are scattered throughout the mammalian central nervous system. Witt found that the distribution of oxytocin receptors in prairie voles differed from the pattern in rats. The differences were especially striking within the limbic system, the area of the brain involved in sexual and social behavior. Insel and his NIMH colleague Larry E. Shapiro subsequently showed that the distribution of oxytocin receptors in prairie voles and in pine voles, another monogamous species, differs from that in the polygamous montane and meadow voles. That the patterns of oxytocin receptors correlate with monogamy further substantiates the idea that oxytocin has an essential role in social organization.

The pair bonding in monogamy also leads mated pairs to guard one another or the shared territory. Reproductively naive prairie voles rarely fight, but mated prairie voles can be extremely vicious toward strangers.



MALE-FEMALE PAIRS of prairie voles are caught far more frequently than are such pairs of meadow voles. Furthermore, the same pairs are often captured repeatedly. Such studies provided the first clue of monogamy in the prairie vole.



AGGRESSION by female prairie voles is revealed in 10-minute tests comparing hostility with mating preference. Females spent more time attacking strangers rather than mating with them. In contrast, they show little aggression toward their partners.

Because studies have implicated testosterone, a major reproductive hormone manufactured by the testes, in aggression in other animals, we initially hypothesized that testosterone might also be responsible for the postmating hostility in prairie voles. But in our laboratory Nicholas Hastings found that neither castration nor testosterone injections had an effect on male aggression after mating.

If testosterone does not regulate aggression or mate guarding, then what does? Many pieces of evidence suggested that vasopressin, a hormone best known for its role in regulating the human body's water content, might play a role in mate guarding. First, Craig F. Ferris of the University of Massachusetts Medical Center in Worcester and Elliott H. Albers of Georgia State University had implicated vasopressin in territoriality and aggression in hamsters. Second, vasopressin shares a molecular structure similar to that of oxytocin; the molecules differ from one another in only two of their nine amino acids. In addition, both hormones may be released under similar circumstances, such as during sexual behavior and other social actions. The cellular and behavioral functions of vasopressin and oxytocin, however, tend to be antagonistic. Therefore, we reasoned that if oxytocin encourages social contact, perhaps vasopressin causes the antisocial or mate-guarding behavior shown by male prairie voles after they have mated.

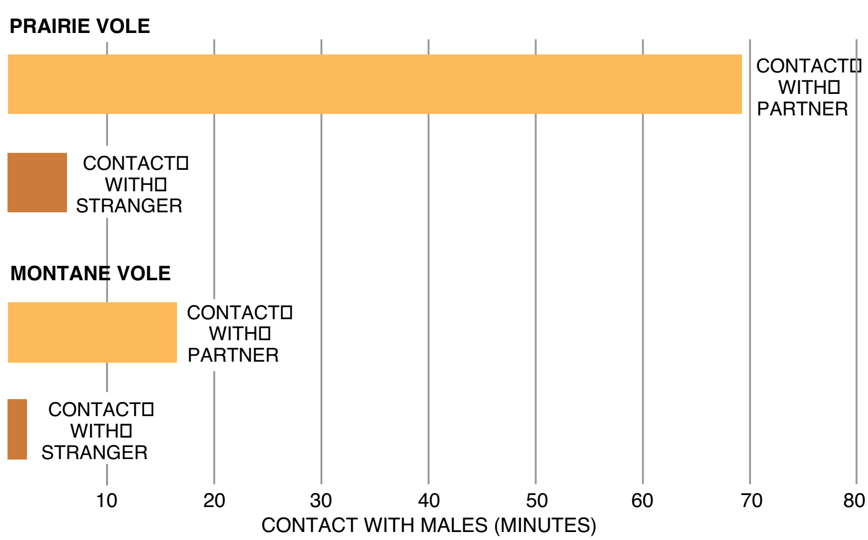
Winslow, Hastings and Insel tested this hypothesis in a collaborative study. In one experiment, males were injected before mating with a drug that blocks vasopressin receptors. The injections eliminated the increase in attacks directed toward strangers that usually follows mating. The effect was not a general inhibition of aggression. The antivasopressin drug did not stem attack behavior when given to males that had completed their mating. In a separate experiment, Winslow and Insel infused vasopressin into a male while a female was present. Such males then displayed increased hostility toward male intruders.

Vasopressin may also play a role in male parental care. Recent findings by Maryam Bamshad, Melinda A. Novak and Geert J. De Vries of the University of Massachusetts show the behavior in male prairie voles correlates with characteristic changes in vasopressin levels.

The experiments on the effects of oxytocin and vasopressin on prairie vole behavior suggest that these two compounds have a much broader behavioral significance than was previously thought. Rather than just being a homeostatic compound, vasopressin may have a more general role as a neuropeptide involved in eliciting parental care and defensive behavior with respect to self and family. Oxytocin, which has a well-established role in reproduction, might block the more primitive, antisocial actions induced by vasopressin, thus permitting social behaviors to emerge. Finally, monogamy may be a refined expression of sociality in which interactions between oxytocin and vasopressin are particularly apparent.

Although these studies have provided strong clues to some of the neuroendocrine mechanisms underlying mo-nogamous behavior, a major puzzle persists. Besides prairie voles, monogamy occurs in such diverse species as wild dogs, tamarins and marmosets. Why, in a physiological sense, should such taxonomically different mammals show the unique features of monogamy?

One solution to this mystery may be found in the adrenal system and its effects on the developing embryo. The adrenal system produces steroids called glucocorticoids. Individuals release these hormones, particularly corticosterone and cortisol, in response to stress. Yet the endocrine systems of adult prairie voles and



SOCIAL PREFERENCE for sexual partners is demonstrated by female prairie voles in three-hour tests. They prefer contact with their partners over contact with male strangers. Female montane voles actually spend more time alone.

MONOGAMOUS CHARACTERISTIC	HORMONE
FEMALE BONDING TO MALE	OXYTOCIN (RELEASED BY MATING OR CONTACT)
AGGRESSION BETWEEN MALES AFTER MATING	VASOPRESSIN (HIGH)
SIMILAR SIZE AND APPEARANCE OF MALE AND FEMALE	CORTICOSTERONE (HIGH) TESTOSTERONE (LOW)
MALE AND FEMALE PARENTAL CARE	CORTICOSTERONE (HIGH) VASOPRESSIN (HIGH)
SOCIAL REGULATION OF REPRODUCTION	CORTICOSTERONE (HIGH)

FEATURES OF MONOGAMY in the prairie vole correlate with specific hormones and their amount in the body. The high and low levels of hormone are relative to those found in nonmonogamous but closely related species.

marmosets secrete unusually copious amounts of glucocorticoids, even when the animals are not under stress. Our work with prairie voles leads us to hypothesize that the interactions between the adrenal and gonadal hormones during early life might account for some of the monogamous patterns that emerge later.

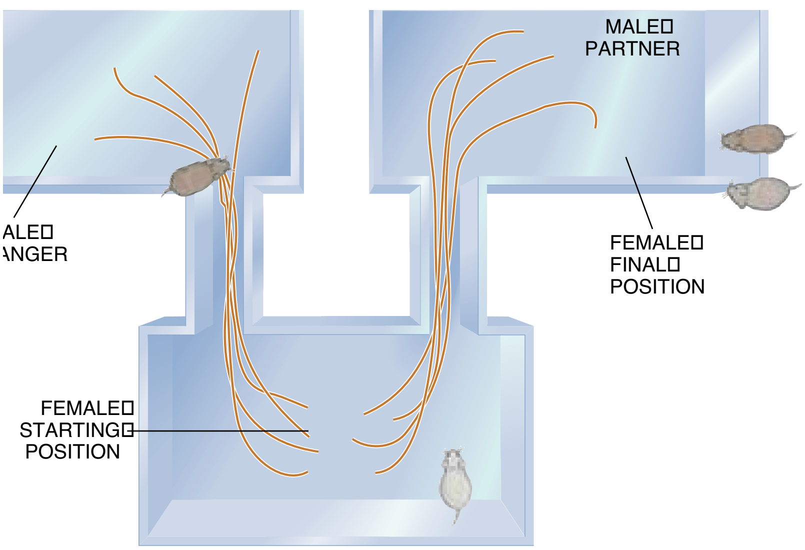
This supposition is based in part on research pioneered by Ingeborg L. Ward of Villanova University. Ward documented the developmental effects of interactions between adrenal and gonadal ste-r-oids in rats. Exposure to stress during the perinatal period—the period of sexual differentiation in mammals—influences subsequent reproductive development. For example, male rats that have been stressed early in life tend to show a more feminine pattern of development as adults. Even the genital anatomy is somewhat demasculinized. Apparently, high levels of stress during the perinatal period inhibit the normal secretion or the action of masculinizing hormones called androgens. Craig H. Kinsley, now at the University of Richmond, and Robert S. Bridges of Tufts University demonstrated that perinatal disturbance also increases the probability that male rats will show, as adults, parental care. Thus, in rats stress appears to alter reproductive functions in a direction that is considered normal in monogamous mammals.

We believe that adrenal activity in prairie voles might account in part for their monogamy. Shapiro and Insel found that shortly after birth prairie voles have an unusually reactive adrenal system. Simply removing the mother for a few minutes elevates the levels of glucocorticoids in pups. In contrast, the nonmonogamous montane voles and rats require greater disturbance before adrenal activity increases.

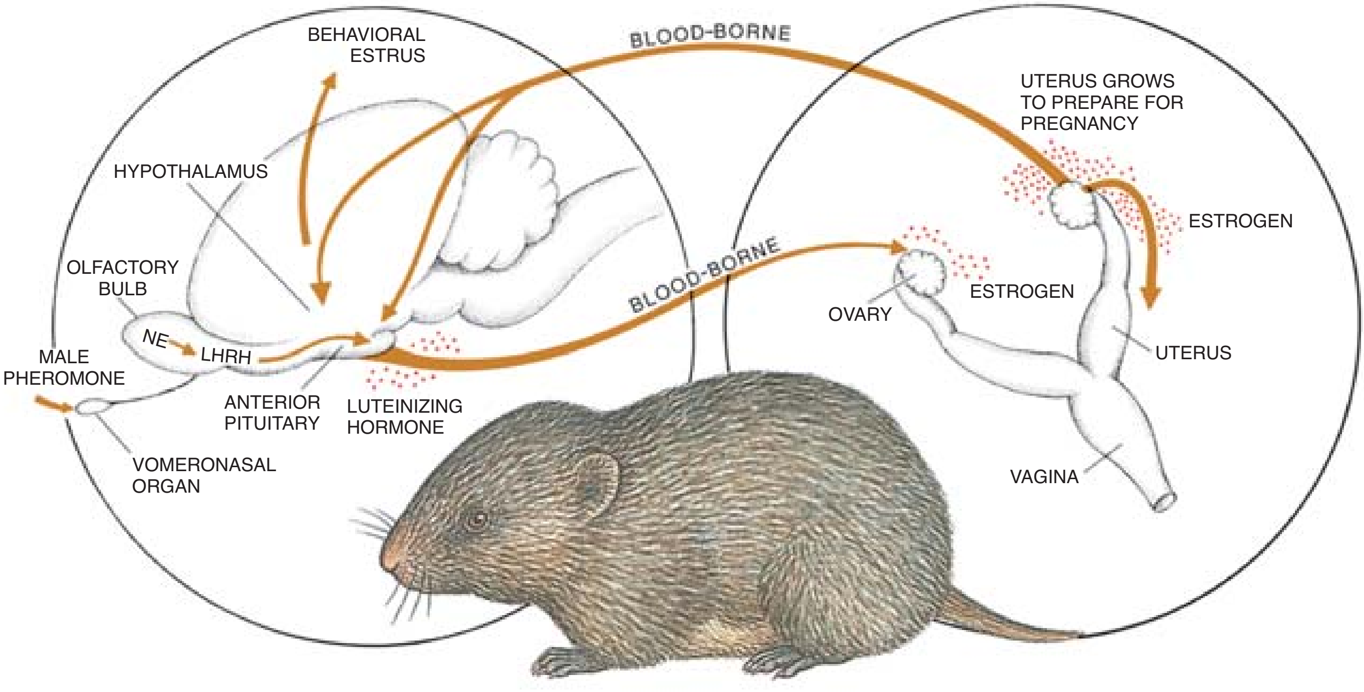
In prairie voles the reactivity of the adrenal glands, during late pregnancy or the early postnatal period, might contribute to the appearance in the adult of some of the definitive characteristics of monogamy, including reduced sexual dimorphism and increased male parental care. Preliminary experiments conducted in our laboratory by Luci Roberts offer some evidence. In those analyses, postpartum exposure to higher than normal levels of androgen reduced the tendency of adult male prairie voles to care for pups. Research in progress is examining the importance of interactions between the adrenal and gonadal systems in the development of other components of monogamy.

Although we can now identify some of the physiological underpinnings of monogamy in the prairie vole, the ultimate (or evolutionary) cause of this behavior and its adaptive significance remain unclear. It is widely assumed that, from the perspective of the offspring, having two parents is better than having one. Trapping studies in prairie voles, however, have not provided support for this assumption. Based on field data from more than 700 prairie vole families, single mothers are as successful as mother-father pairs in rearing litters to maturity.

That sexual exclusivity is not a dominant feature of monogamy in prairie voles also raises an evolutionary question. Parental care in mammals, and especially in prairie voles, represents a significant investment of time and energy.



CHOICE TEST given to female prairie voles in the laboratory reveals a social preference for the mated males. Initially, females enter the cages of both strangers and their partners (*represented by brown lines*) and will mate with both. Within about 30 minutes, however, females tend to remain near the familiar male.



HORMONAL CASCADE that triggers estrus in the female prairie vole begins when she sniffs a male. The vomeronasal organ picks up pheromones, stimulating the olfactory bulb. Norepinephrine (NE) and luteinizing hormone–releasing hormone (LHRH) are secreted and start the production of luteinizing hormone. Luteinizing hormone reaches the ovaries via the bloodstream and stimulates them to produce estrogen. Estrogen is then carried to the hypothalamus, where it induces estrus.

It is usually assumed that such commitment from the male is a benefit of monogamy because males can increase their own reproductive success by caring for their offspring. Perhaps this strategy represents a probabilistic function. Monogamous males are increasing their fitness in general while accepting the burden of rearing some pups that are not their own.

The theoretical implications of this finding is uncertain. The prairie voles we have studied in Illinois live in an environment that provides abundant supplies of food, water and other essential resources. We believe that monogamy in prairie voles evolved when food was not plentiful. Under such conditions, monogamy might offer additional benefits not evident in the habitats we have examined. We are currently comparing Illinois prairie voles with those that live in a much harsher environment in Kansas.

Our studies also frequently elicit questions concerning the applicability of our findings to human behavior. Monogamy in Old World primates and in humans probably takes on a dierent form from that described here for voles. Yet there are some parallels. Clearly, human monogamous partners do not always stay sexually exclusive. Animals, including humans, may be more particular in the selection of a social companion than in their choice of a sexual partner.

In addition, our research highlights the general significance of positive social behavior and bonds, which are at least as meaningful to humans as to prairie voles. Disruption of these bonds in humans, such as that which occurs in the loss of a child, parent or spouse, can have disastrous consequences for mental and physical health. Yet we understand little about the behavioral physiology of the formation of such relationships in humans. In fact, the notion that social bonds have a "biology" has not been generally understood.

It is tempting to speculate that oxytocin and vasopressin could also aect human behavior. But the role of these hormones, even in animals, is difficult to document, and many obvious questions remain unexplored. Most human research is limited to correlations between changes in hormonal blood levels and behavior.

The paucity of human data raises concerns about the medical eect of these hormones, which are often administered as treatments. For example, oxytocin is used to induce uterine contractions in childbirth, and vasopressin is prescribed to treat bed-wetting in children. Actions that indirectly aect hormonal levels, such as delivering a child by cesarean section or bottle-feeding, may also aect the amount of oxytocin received by either a mother or her infant. Because oxytocin and vasopressin were at first believed to act outside the brain, on tissues such as the uterus, breast and kidney, little attention has been given to the behavioral consequences of these treatments or actions. We now know that oxytocin and vasopressin are active in the central nervous system. Findings from animal research, such as those described here for prairie voles, should encourage the biomedical community to look more carefully at the potential eects of these powerful hormones on behavior.

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The Loves of the Plants

Carl Linnaeus classified plants according to their reproductive parts, endowing them as well with sex lives reflecting 18th-century values and controversies

by Londa Schiebinger

> The flowers' leaves...serve as bridal beds which the Creator has so gloriously arranged, adorned with such noble bed curtains, and perfumed with so many soft scents that the bridegroom with his bride might there celebrate their nuptials with so much the greater solemnity. When now the bed is so prepared, it is time for the bridegroom to embrace his beloved bride and offer her his gifts...
>
> Carl Linnaeus, *Praeludia Sponsaliorum Plantarum,* 1729

From Aristotle through Darwin and beyond, observers have infused nature with sexuality and gender. The great Swedish taxonomist Carl Linnaeus was thus not alone in imagining that plants have vaginas and penises and reproduce on "marriage beds." Although naturalists tended to believe that gender was a given of nature, the traits they ascribed to organisms have changed with shifting notions of masculinity and femininity in Western culture. For Aristotle, mares were sexually wanton, going "a-horsing" to satisfy their unbridled appetites. But in later centuries, females throughout nature—with the exception of Linnaeus's lusty flowers—were said to evince a patient modesty. Even among insects, females were observed to "repel the first [sexual] attacks of the males" and, in so doing, to win the respect of their paramours.

Since the Enlightenment, science has stirred hearts and minds with its promise of a neutral and privileged viewpoint, above and beyond the rough and tumble of political life. With respect to women, however, science is not a neutral culture. Gender—both the real relations between the sexes and cultural renderings of those relations—shaped European natural history and, in particular, botany. Crucial to this story is that Europeans who wrote about nature in this era were almost exclusively male.

It is ironic in this context that botany was long considered especially suited to women. Botany's reputation as "unmanly," an ornamental branch of science appropriate only for "ladies and e›eminate youths," was such that it was sometimes questioned whether able-bodied young men should pursue it at all. (Hegel once compared the minds of women to plants because, in his view, both were essentially placid.) Eighteenth-century society condoned botany as a fitting pastime for middle-class ladies because it took them out into the air and taught them a certain intellectual discipline. This attitude rested in part on botany's historical a liations with herbal healing—a realm in which women had traditionally been active in their role as midwives.

Then, too, botany among all the sciences was considered least o›ensive to the delicate spirit. As Rousseau pointed out, the student of anatomy was faced with oozing blood and stinking cadavers, entomologists with vile insects, geologists with dirt and filth. After Linnaeus, the study of plants seemed to call for more attention to sexuality than might seem suitable for ladies. Still, botany continued to be advocated for women, especially in England, as the science leading to the greatest appreciation of God and His universe.

There was, of course, a caveat. The most important directive issued to women was that their ambitions in botany should not transcend those of the amateur. The English botanist Thomas Martyn warned women away from mastering "long files of Latin words" and encouraged his "fair countrywomen" merely to amuse themselves with natural history. Serious science in any field was to be reserved for men. Women, Jean-Jacques Rousseau and others taught, lacked a certain genius—that "celestial flame" that sets fire to the soul—required for true innovation in science. Women of Rousseau's day were formally barred from universities and scientific academies. The few prominent women


COURTESY OF PENNSYLVANIA STATE UNIVERSITY

CUPID inspires the plants with love in this plate from Robert Thornton's *Temple of Flora* (London, 1805). The "romantic lives" of vegetation aroused much interest after Linnaeus's sexual system for classifying plants gained currency.

scientists in early modern Europe had maneuvered themselves into mathematics, physics, astronomy or scientific illustration through less formal routes, such as the salons of the elite and the craft guilds. Yet, even these women learned to recognize certain limits. Maria Sibylla Merian, the adventurous botanical illustrator and entomologist who traveled to Dutch Surinam in the late 17th century in search of exotic caterpillars, presented her observations in exquisitely crafted volumes but left classification to her male colleagues.

Despite their forays into botany, women were long to remain on the margins of intellectual life. As we shall see, parochial European notions of sex and sexual hierarchy became potent principles organizing 18th-century natural history—a matter of consequence in an age that looked to nature as the guiding light for social reform.

The Private Lives of Plants

Not until the 17th century did European naturalists widely recognize that plants reproduce sexually. The ancient world, it is true, had some knowledge of sexual distinctions among plants. The Greek naturalist Theophrastus knew the age-old practice of fertilizing date palms by bringing male flowers to the female tree. Peasants working the land also recognized sexual distinctions in trees such as the pistachio. Plant sexuality, however, was not a focus of interest among naturalists of the ancient world. Eighteenth-century observers commonly charged that the ancients were ignorant of the basics: they sometimes called the seed-bearing plant "the male" and the barren plant "the female."

Between 1550 and 1700, as wonders from the voyages of discovery and the new colonies flooded Europe, the number of known plants quadrupled. Botanists were led to search for new methods of organizing this multitude of new specimens. As they sought simple principles that would hold universally, emphasis shifted from the medical uses of plants to more general and theoretical issues of pure taxonomy.

When plant sexuality exploded onto the scene, interest in assigning sex to plants outran understanding of botanical fertilization, or the "coitus of vegetables," as it was sometimes called. The English naturalist Nehemiah Grew, who developed his theory of plant sexuality from his knowledge of animals, first identified the stamen as the male organ in flowers in his 1682 treatise, *The Anatomy of Plants:*

> The blade (or stamen) does not unaptly resemble a small penis, with the sheath upon it, as its praeputium [prepuce]. And the . . . several thecae, are like so many little testicles. And the globulets [pollen] and other small particles upon the blade or penis . . . are as the vegetable sperme. Which as soon as the penis is erected, falls down upon the seed-case or womb, and so touches it with a prolific virtue.

By the early 1700s, the analogy between animal and plant sexuality was fully established. In his *Praeludia Sponsaliorum Plantarum,* Linnaeus related the terms of comparison: in the male the filaments of the stamens are the vas deferens, the anthers are the testes and the pollen that falls from them is the seminal fluid; in the female the stigma is the vulva, the style becomes the vagina, the tube running the length of the pistil is the fallopian tube, the pericarp is the impregnated ovary and the seeds are the eggs. The French physician Julien O›ray de La Mettrie, along with other naturalists of the time, even claimed the honey reservoir found in a plant's nectary gland to be equivalent to mother's milk in humans.

Most flowers, however, are hermaphroditic, with both male and female reproductive organs. As one 18th-century botanist put it, there are two sexes—male and female—but three kinds of flowers: male, female and hermaphrodite, sometimes called androgyne. Although most botanists enthusiastically embraced sexual dimorphism, conceiving of plants as hermaphroditic was more difficult: they could not or would not recognize an unfamiliar sexual type. Even 40 years later, when Linnaeus's system was in wide use, William Smellie, chief compiler of the first edition of the *Encyclopaedia Britannica* (1771), rejected the whole idea of sexuality in plants and distanced himself from the term "hermaphrodite," noting when using the word that he merely spoke "the language of the system."

The Bridal Bed

Still, the majority of European botanists gave undue primacy to sexual reproduction. Linnaeus was thoroughly taken with heterosexual coupling, confessing that "the singular structure and remarkable office of the stamens and pistil enticed my mind, to inquire what Nature had concealed in them. They commended themselves by the function they perform." He thus attributed sexual reproduction even to his *cryptogamia*—"plants that marry secretly"—by which he meant ferns, mosses, algae and fungi, whose reproductive habits were then not understood. The very fact that nonsexual reproduction is called asexual reveals the normative preference given sexual reproduction.

Not only were Linnaeus's plants sexed, they actually became "husbands" and "wives." Introducing new terminology to describe flowers, Linnaeus rejected the increasingly standard terms "stamen" and "pistil," for *andria* and *gynia*—suffixes that he derived from the Greek for husband (*aner*) and wife (*gyne*). Linnaeus's "Key to the Sexual System," published in *Systema Naturae* in 1737, was built upon the *nuptiae plantarum:* the marriages of plants. If male and female flowers occurred on the same plant, they shared the same house (*monoecia*) but not the same bed; if on separate plants, they lived in two houses (*dioecia*). Hermaphroditic flowers contained husbands and wives in one bed (*monoclinia*).

Linnaeus's classes of plants, based on the number, proportion and position of the male stamens, end in *andria. Monandria* ("having only one man") signified one stamen, or husband, on a hermaphroditic flower; *diandria* signified two stamens and so on. The classes were subdivided into roughly 65 orders, based on the number, proportion and position of the female pistils: *monogynia, digynia, trigynia* and so forth. Thus, a saffron crocus, having three stamens and one pistil, would be called *triandria monogynia*. The orders were further divided into genera, based on the calyx, flower and other parts of the fruit; then again into species, based on the leaves or some other characteristic of the plant; and finally into varieties.

Linnaeus emphasized the "nuptials" of living plants as much as their sexual relations. Before their "lawful marriage," trees and shrubs donned "wedding gowns." Flower petals opened as "bridal beds" for a verdant groom and his cherished bride, while the curtain of the corolla lent privacy to the amorous newlyweds. Linnaeus divided the plant world according to the type of marriage each plant contracted—whether, for example, it had been wed "publicly" or "clandestinely." (The latter group consisted of the *cryptogamia*.) These two types of marriage, in fact, characterized custom in much of Europe at that time; only in 1753 in England did Lord Harwicke's Marriage Act do away with clandestine marriages by requiring a public proclamation (banns).

It is significant that Linnaeus, a Swedish country parson's son, focused on marriage when he thought of sexuality. European marriage customs were undergoing rapid change as the traditional anchors of the old order began to give way. Upper-class parents and even well-off peasants less often arranged marriages for their children out of property considerations alone. Increasingly love and affection became legitimate reasons to wed. Linnaeus's own marriage followed this pattern. He courted with tender expressions of love one Sara Moraea, the daughter of a wealthy physician. Linnaeus then left the running of his house entirely to his wife, while he concerned himself with the workings of nature.

Linnaeus's plants may have celebrated their nuptials, yet the majority did not engage in "lawful marriages." Only one class of plants, the *monandria*—exemplified by the tropical genus *Canna*—practiced "monogamy." Plants in other classes joined in liaisons consisting of two, three, 20 or more "husbands" who shared their marriage bed (that is, the petals of the flower) with one wife. The common iris, for example, enjoyed three husbands.

Erasmus Darwin, one of Linnaeus's many popularizers in England (and the grandfather of Charles), did not limit sexual relations to the bonds of holy matrimony. In his *Loves of the Plants* (1789), Darwin's plants freely expressed every imaginable form of heterosexual union. The fair *Collinsonia,* sighing with sweet concern, satisfied the love of two brothers by turns. The *Meadia*—an ordinary cowslip—bowed with "wanton air," rolled her dark eyes and waved her golden hair as she gratified each of her five beaux. Darwin portrayed the tragic outcome of an ordinary *Gloriosa superba* repulsing the incestuous advances of her son:

> Fierce on the fair he fix'd his ardent gaze;
> Dropped on one knee, his frantic arms outspread,
> And stole a guilty glance toward the bed;
> Then breath'd from quivering lips a whisper'd vow
> And bent on heaven his pale unrepentant brow;
> "Thus, thus!" he cried, and plung'd the furious dart,
> And life and love gush'd mingled from his heart.

Darwin may well have been using the cover of botany to propagandize for the free love he practiced after the death of his first wife. There is no evidence, however, that Linnaeus intended his sexual vision of botany to undermine social custom. Raised in an upright, thrifty, Protestant family, he was conservative in his religious views (all of nature celebrated the glory of its Creator) and in his attitudes toward women. He would not allow his four daughters to learn French for fear that along with the language they would adopt the liberties of French custom. When his wife placed their daughter Sophia in school, Linnaeus immediately took her out again, stopping what he considered "nonsensical" education. (He did, however, allow his eldest daughter to develop a mild interest in botany: Elisabeth Christina contributed a paper entitled "Remarks on a Luminous Appearance of the Indian Cresses" to the *Transactions* of the Royal Academy of Science.)

It seems unlikely, then, that Linnaeus introduced his sexual imagery as an affront to middle-class sensibilities. Befitting the social order of the day, he simply saw anything female as a wife. He called Madeleine Basseporte, the celebrated botanical illustrator who worked at the Jardin du Roi in Paris, his second wife. He considered "Dame Nature" his other wife and true helpmate. Linnaeus called his own wife "my monandrian lily," the lily signifying virginity.

Linnaeus's system of classification was but one among many proposed systems. By 1799, 20 years after Linnaeus's death, when the English naturalist Robert Thornton published his popular version of the Linnaean system, he counted 52 different systems of botany; the "system-madness," one authority complained, was truly "epidemical." A century earlier in England, John Ray had devised a means of establishing genera based on the flower, calyx, seed and seed coat. In France, Joseph Pitton de Tournefort defined genera principally on the characteristics of the corolla and fruit. And in 18th-century Switzerland, Albrecht von Haller argued that geography was crucial to an understanding of plant life and that development as well as appearance should be represented in a system of classification.

Despite the number and variety of systems, Linnaeus's, being simple and convenient, was widely adopted across Europe, and especially in Britain, after 1740. But bloody and protracted battles erupted almost immediately over the scientific and moral implications of Linnaeus's classification. "Anti-sexualists"—those opposing the system—attacked his work, beginning a controversy that spilled over into the next century. What man, fumed Johann Siegesbeck, a professor in St. Petersburg, could believe that God Almighty would introduce such "loathsome harlotry" into the plant kingdom? In 1790 Smellie blasted the "alluring seductions" of the analogies on which the sexualist hypothesis was founded, and he maintained that it did not hold up to facts of experience. Many animals (he mentioned polyps and millipedes) reproduced without sexual embraces, and if these were destitute of "all the endearments of love," what, he asked, should induce us to fancy that the oak or mushroom enjoyed these distinguished privileges?

In addition to his ontological qualms, Smellie denounced Linnaeus for taking his analogy "far beyond all decent limits," claiming that Linnaeus's metaphors were so indelicate as to exceed the most "obscene romance-writer." Smellie's sentiments were shared by others. In 1808 the Reverend Samuel Goodenough, later bishop of Carlisle, wrote to the Linnaean Society that "a literal translation of the first principles of Linnaean botany is enough to shock female modesty." In the face of such opposition, the authors who popularized Linnaeus's system in England made little use of his sexual imagery, with the audacious exception of Erasmus Darwin.

In the uproar that surrounded Linnaeus's ardent sexing of plants, no one noticed that his taxonomy, built as it was on sexual difference, imported into botany traditional beliefs about European sexual hierarchy. Linnaeus was among the first to highlight the biological importance of sexual reproduction in plants. But the success of his system did not rest on the fact that it was "natural," capturing God's order in nature—Linnaeus's desirable but still unattainable goal. Indeed, he readily acknowledged that his system was highly artificial. He focused on purely morphological features such as the number of sexual partners. But in fact, the number of stamens and pistils can vary among different flowers of the same plant. Linnaeus did not supply resolutions to such conflicts; he sometimes placed plants with different numbers of stamens in the same class, thus making nonsense of his numerical system.

Taxonomic Sexism

Furthermore, Linnaeus devised his classification system in such a way that the number of a plant's stamens determined the class to which it was assigned, whereas the number of its pistils determined its order. In the taxonomic tree, class stands above order. In other words, Linnaeus gave male parts priority in determining the status of the organism in the plant kingdom. There is no empirical justification for this outcome; rather Linnaeus brought traditional tenets of gender hierarchy into science. Although today his classification of groups above the rank of genus has been abandoned, many of his genus and species labels have survived.

Why did the study of plant sexuality become a priority for many 18th-century botanists? There are, after all, many different ways of knowing nature. One important factor drawing naturalists' attention to plant and animal sexuality was a keen interest in gender differences among humans. This era of democratic awakening brought with it the "women question"—the question of women's social rights and privileges. Sexual dierence weighed heavily on the minds of many, as the enlightened of Europe issued the challenge that "all men are by nature equal."

If women were not to be given equal rights in the new democratic states (and they were not), natural causes had to justify their exclusion. That Linnaeus supposedly found European sexual hierarchies reconfirmed within the plant kingdom indicated to thinkers of the time the "naturalness" of women's continued subordination to their fathers and husbands. Rousseau spoke for many when he wrote that natural philosophers were to read in the great book of nature "everything which suits the constitution of her [woman's] species and her sex in order to fulfill her place in the physical and moral order."

Had women been among 18th-century taxonomists, would the story have been different? It is difficult or even impossible to say. The sex of the scientist should not influence the results of science. But in the modern division of labor that crystallized during the Enlightenment, science was part of the terrain that fell to the male sex. Researchers read nature through the lens of social relations in such a way that the new language of botany, among other natural sciences, incorporated fundamental aspects of the social world as much as those of the natural world.

During the past few decades, the feminist critique of science combined with the process of more and more women becoming engaged as makers of knowledge has had a tremendous impact in the humanities, social sciences and many of the sciences. We are just beginning to unravel how deeply gender has been worked into nature's body. Historical exposé, of course, is not enough, for what we unravel by night is often rewoven by day in the institutions of science. Scientists need to become aware of not only how culture shapes science but also how what is studied (or neglected) grows out of who is doing the studying and toward what ends.

The Author

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Bonobo Sex and Society

The behavior of a close relative challenges assumptions about male supremacy in human evolution

by Frans B. M. de Waal

At a juncture in history during which women are seeking equality with men, science arrives with a belated gift to the feminist movement. Male-biased evolutionary scenarios—Man the Hunter, Man the Toolmaker and so on—are being challenged by the discovery that females play a central, perhaps even dominant, role in the social life of one of our nearest relatives. In the past few years many strands of knowledge have come together concerning a relatively unknown ape with an unorthodox repertoire of behavior: the bonobo.

The bonobo is one of the last large mammals to be found by science. The creature was discovered in 1929 in a Belgian colonial museum, far from its lush African habitat. A German anatomist, Ernst Schwarz, was scrutinizing a skull that had been ascribed to a juvenile chimpanzee because of its small size, when he realized that it belonged to an adult. Schwarz declared that he had stumbled on a new subspecies of chimpanzee. But soon the animal was assigned the status of an entirely distinct species within the same genus as the chimpanzee, Pan.

The bonobo was officially classified as Pan paniscus, or the diminutive Pan. But I believe a different label might have been selected had the discoverers known then what we know now. The old taxonomic name of the chimpanzee, P. satyrus—which refers to the myth of apes as lustful satyrs—would have been perfect for the bonobo.

The species is best characterized as female-centered and egalitarian and as one that substitutes sex for aggression. Whereas in most other species sexual behavior is a fairly distinct category, in the bonobo it is part and parcel of social relations—and not just between males and females. Bonobos engage in sex in virtually every partner combination (although such contact among close family members may be suppressed). And sexual interactions occur more often among bonobos than among other primates. Despite the frequency of sex, the bonobo's rate of reproduction in the wild is about the same as that of the chimpanzee. A female gives birth to a single infant at intervals of between five and six years. So bonobos share at least one very important characteristic with our own species, namely, a partial separation between sex and reproduction.

A Near Relative

This finding commands attention because the bonobo shares more than 98 percent of our genetic profile, making it as close to a human as, say, a fox is to a dog. The split between the human line of ancestry and the line of the chimpanzee and the bonobo is believed to have occurred a mere eight million years ago. The subsequent divergence of the chimpanzee and the bonobo lines came much later, perhaps prompted by the chimpanzee's need to adapt to relatively open, dry habitats [see "East Side Story: The Origin of Humankind," by Yves Coppens; SCIENTIFIC AMERICAN, May 1994].

In contrast, bonobos probably never left the protection of the trees. Their present range lies in humid forests south of the Zaire River, where perhaps fewer than 10,000 bonobos survive. (Given the species' slow rate of reproduction,

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the rapid destruction of its tropical habitat and the political instability of central Africa, there is reason for much concern about its future.)

If this evolutionary scenario of ecological continuity is true, the bonobo may have undergone less transformation than either humans or chimpanzees. It could most closely resemble the common ancestor of all three modern species. Indeed, in the 1930s Harold J. Coolidge—the American anatomist who gave the bonobo its eventual taxonomic status—suggested that the animal might be most similar to the primogenitor, since its anatomy is less specialized than is the chimpanzee's. Bonobo body proportions have been compared with those of the australopithecines, a form of prehuman. When the apes stand or walk upright, they look as if they stepped straight out of an artist's impression of early hominids.

Not too long ago the savanna baboon was regarded as the best living model of the human ancestor. That primate is adapted to the kinds of ecological conditions that prehumans may have faced after descending from the trees. But in the late 1970s, chimpanzees, which are much more closely related to humans, became the model of choice. Traits that are observed in chimpanzees—including cooperative hunting, food sharing, tool use, power politics and primitive warfare—were absent or not as developed in baboons. In the laboratory the apes have been able to learn sign language and to recognize themselves in a mirror, a sign of self-awareness not yet demonstrated in monkeys.

Although selecting the chimpanzee as the touchstone of hominid evolution represented a great improvement, at least one aspect of the former model did not need to be revised: male superiority remained the natural state of affairs. In both baboons and chimpanzees, males are conspicuously dominant over females; they reign supremely and often brutally. It is highly unusual for a fully grown male chimpanzee to be dominated by any female.

Enter the bonobo. Despite their common name—the pygmy chimpanzee—bonobos cannot be distinguished from the chimpanzee by size. Adult males of the smallest subspecies of chimpanzee weigh some 43 kilograms (95 pounds) and females 33 kilograms (73 pounds), about the same as bonobos. Although female bonobos are much smaller than the males, they seem to rule.

> Thinking how much faster marriages would break up if people had no way of compensating for hurting each other, I set out to investigate such mechanisms in several primates, including bonobos. Although I expected to see peacemaking in these apes, too, I was little prepared for the form it would take.

Graceful Apes

In physique, a bonobo is as different from a chimpanzee as a Concorde is from a Boeing 747. I do not wish to offend any chimpanzees, but bonobos have more style. The bonobo, with its long legs and small head atop narrow shoulders, has a more gracile build than does a chimpanzee. Bonobo lips are reddish in a black face, the ears small and the nostrils almost as wide as a gorilla's. These primates also have a flatter, more open face with a higher forehead than the chimpanzee's and—to top it all off—an attractive coiffure with long, fine, black hair neatly parted in the middle.

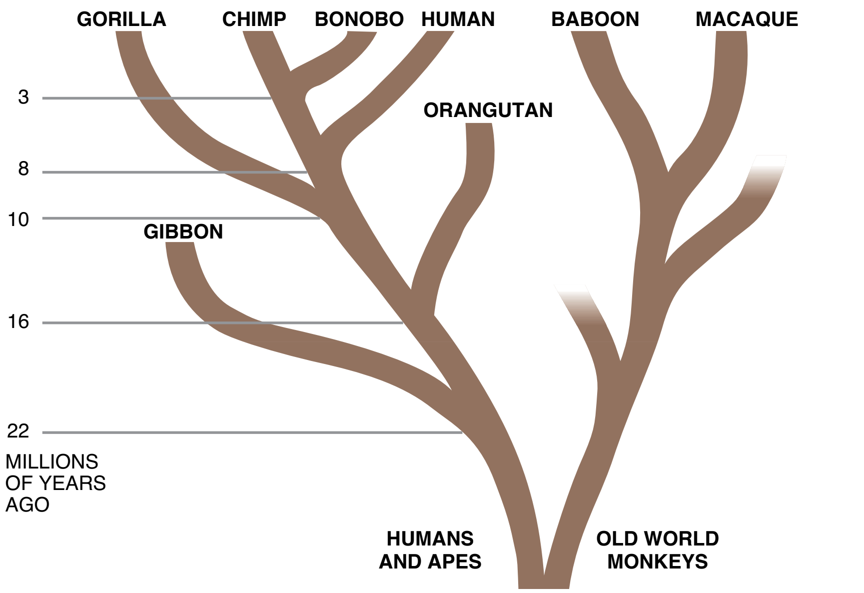
Like chimpanzees, female bonobos nurse and carry around their young for up to five years. By the age of seven the offspring reach adolescence. Wild females give birth for the first time at 13 or 14 years of age, becoming full grown by about 15. A bonobo's longevity is unknown, but judging by the chimpanzee it may be older than 40 in the wild and close to 60 in captivity.

Fruit is central to the diets of both wild bonobos and chimpanzees. The former supplement with more pith from herbaceous plants, and the latter add meat. Although bonobos do eat invertebrates and occasionally capture and eat small vertebrates, including mammals, their diet seems to contain relatively little animal protein. Unlike chimpanzees, they have not been observed to hunt monkeys.

Whereas chimpanzees use a rich array of strategies to obtain foods—from cracking nuts with stone tools to fishing for ants and termites with sticks—tool use in wild bonobos seems undeveloped. (Captive bonobos use tools skillfully.) Apparently as intelligent as chimpanzees, bonobos have, however, a far more sensitive temperament. During World War II bombing of Hellabrun, Germany, the bonobos in a nearby zoo all died of fright from the noise; the chimpanzees were unaffected.

Bonobos are also imaginative in play. I have watched captive bonobos engage in "blindman's buff." A bonobo covers her eyes with a banana leaf or an arm or by sticking two fingers in her eyes. Thus handicapped, she stumbles around on a climbing frame, bumping into others or almost falling. She seems to be imposing a rule on herself: "I cannot look until I lose my balance." Other apes and monkeys also indulge in this game, but I have never seen it performed with such dedication and concentration as by bonobos.

Juvenile bonobos are incurably playful and like to make funny faces, sometimes in long solitary pantomimes and at other times while tickling one another. Bonobos are, however, more controlled in expressing their emotions—whether it be joy, sorrow, excitement or anger—than are the extroverted chimpanzees. Male chimpanzees often engage in spectacular charging displays in which they show off their strength: throwing rocks, breaking branches and uprooting small trees in the process. They keep up these noisy performances



LAURIE GRACE

EVOLUTIONARY TREE of primates, based on DNA analysis, shows that humans diverged from bonobos and chimpanzees a mere eight million years ago. The three species share more than 98 percent of their genetic makeup.

for many minutes, during which most other members of the group wisely stay out of their way. Male bonobos, on the other hand, usually limit displays to a brief run while dragging a few branches behind them.

Both primates signal emotions and intentions through facial expressions and hand gestures, many of which are also present in the nonverbal communication of humans. For example, bonobos will beg by stretching out an open hand (or, sometimes, a foot) to a possessor of food and will pout their lips and make whimpering sounds if the effort is unsuccessful. But bonobos make different sounds than chimpanzees do. The renowned low-pitched, extended "huuu-huuu" pant-hooting of the latter contrasts with the rather sharp, high-pitched barking sounds of the bonobo.

Love, Not War

My own interest in bonobos came not from an inherent fascination with their charms but from research on aggressive behavior in primates. I was particularly intrigued with the aftermath of conflict. After two chimpanzees have fought, for instance, they may come together for a hug and mouth-to-mouth kiss. Assuming that such reunions serve to restore peace and harmony, I labeled them reconciliations.

Any species that combines close bonds with a potential for conflict needs such conciliatory mechanisms. Thinking how much faster marriages would break up if people had no way of compensating for hurting each other, I set out to investigate such mechanisms in several primates, including bonobos. Although I expected to see peacemaking in these apes, too, I was little prepared for the form it would take.

For my study, which began in 1983, I chose the San Diego Zoo. At the time, it housed the world's largest captive bonobo colony—10 members divided into three groups. I spent entire days in front of the enclosure with a video camera, which was switched on at feeding time. As soon as a caretaker approached the enclosure with food, the males would develop erections. Even before the food was thrown into the area, the bonobos would be inviting each other for sex: males would invite females, and females would invite males and other females.

Sex, it turned out, is the key to the social life of the bonobo. The first suggestion that the sexual behavior of bono-bos is different had come from observations at European zoos. Wrapping their findings in Latin, primatologists Eduard Tratz and Heinz Heck reported in 1954 that the chimpanzees at Hellabrun mated more canum (like dogs) and bonobos more hominum (like people). In those days, face-to-face copulation was considered uniquely human, a cultural innovation that needed to be taught to preliterate people (hence the term "missionary position"). These early studies, written in German, were ignored by the international scientific establishment. The bonobo's humanlike sexuality needed to be rediscovered in the 1970s before it became accepted as characteristic of the species.

Bonobos become sexually aroused remarkably easily, and they express this excitement in a variety of mounting positions and genital contacts. Although chimpanzees virtually never adopt face-to-face positions, bonobos do so in one out of three copulations in the wild. Furthermore, the frontal orientation of the bonobo vulva and clitoris strongly suggest that the female genitalia are adapted for this position.

Another similarity with humans is increased female sexual receptivity. The tumescent phase of the female's genitals, resulting in a pink swelling that signals willingness to mate, covers a much longer part of estrus in bonobos than in chimpanzees. Instead of a few days out of her cycle, the female bonobo is almost continuously sexually attractive and active [*see illustration on page 36*].

Perhaps the bonobo's most typical sexual pattern, undocumented in any other primate, is genito-genital rubbing (or GG rubbing) between adult females. One female facing another clings with arms and legs to a partner that, standing on both hands and feet, lifts her off the ground. The two females then rub their genital swellings laterally together, emitting grins and squeals that probably reflect orgasmic experiences. (Laboratory experiments on stump-tailed macaques have demonstrated that women are not the only female primates capable of physiological orgasm.)

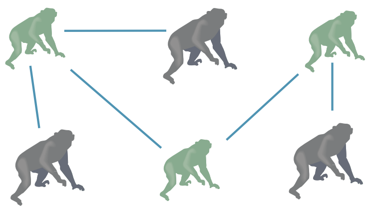
Male bonobos, too, may engage in pseudocopulation but generally perform a variation. Standing back to back, one male briefly rubs his scrotum against the buttocks of another. They also practice so-called penis-fencing, in which two males hang face to face from a branch while rubbing their erect penises together.

The diversity of erotic contacts in bonobos includes sporadic oral sex, massage of another individual's genitals and intense tongue-kissing. Lest this leave the impression of a pathologically oversexed species, I must add, based on hundreds of hours of watching bonobos, that their sexual activity is rather casual and relaxed. It appears to be a completely natural part of their group life. Like people, bonobos engage in sex only occasionally, not continuously. Furthermore, with the average copulation lasting 13 seconds, sexual contact in bonobos is rather quick by human standards.

That sex is connected to feeding, and even appears to make food sharing possible, has been observed not only in zoos but also in the wild. Nancy Thompson-Handler, then at the State Universi-

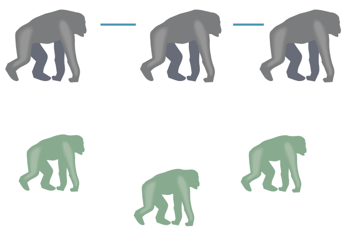
Social Organization among Various Primates

BONOBO



Bonobo communities are peace-loving and generally egalitarian. The strongest social bonds (*blue*) are those among females (*green*), although females also bond with males. The status of a male (*purple*) depends on the position of his mother, to whom he remains closely bonded for her entire life.

CHIMPANZEE

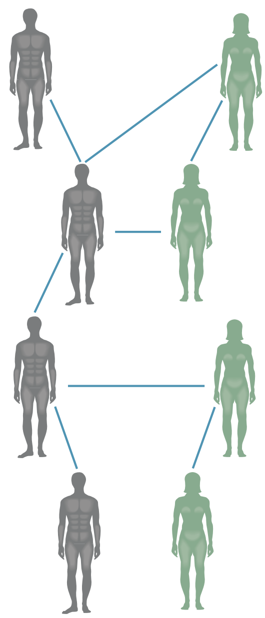


In chimpanzee groups the strongest bonds are established between the males in order to hunt and to protect their shared territory. The females live in overlapping home ranges within this territory but are not strongly bonded to other females or to any one male.

GIBBON

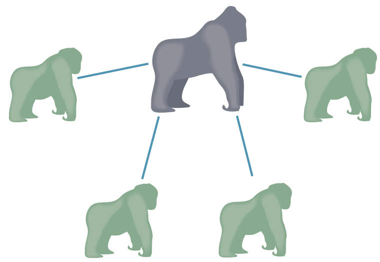
Gibbons establish monogamous, egalitarian relations, and one couple will maintain a territory to the exclusion of other pairs.

HUMAN



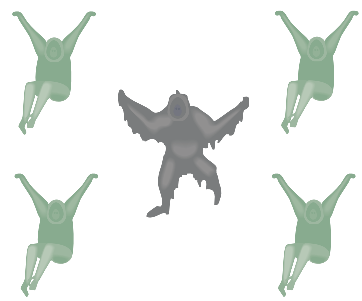
Human society is the most diverse among the primates. Males unite for cooperative ventures, whereas females also bond with those of their own sex. Monogamy, polygamy and polyandry are all in evidence.

GORILLA



The social organization of gorillas provides a clear example of polygamy. Usually a single male maintains a range for his family unit, which contains several females. The strongest bonds are those between the male and his females.

ORANGUTAN



Orangutans live solitary lives with little bonding in evidence. Male orangutans are intolerant of one another. In his prime, a single male establishes a large territory, within which live several females. Each female has her own, separate home range.

LAURIE GRACE

ty of New York at Stony Brook, saw bonobos in Zaire's Lomako Forest engage in sex after they had entered trees loaded with ripe figs or when one among them had captured a prey animal, such as a small forest duiker. The flurry of sexual contacts would last for five to 10 minutes, after which the apes would settle down to consume the food.

One explanation for the sexual activity at feeding time could be that excitement over food translates into sexual arousal. This idea may be partly true. Yet another motivation is probably the real cause: competition. There are two reasons to believe sexual activity is the bonobo's answer to avoiding conflict.

First, anything, not just food, that arouses the interest of more than one bonobo at a time tends to result in sexual contact. If two bonobos approach a cardboard box thrown into their enclosure, they will briefly mount each other before playing with the box. Such situations lead to squabbles in most other species. But bonobos are quite tolerant, perhaps because they use sex to divert attention and to diffuse tension.

Second, bonobo sex often occurs in aggressive contexts totally unrelated to food. A jealous male might chase another away from a female, after which the two males reunite and engage in scrotal rubbing. Or after a female hits a juvenile, the latter's mother may lunge at the aggressor, an action that is immediately followed by genital rubbing between the two adults.

I once observed a young male, Kako, inadvertently blocking an older, female juvenile, Leslie, from moving along a branch. First, Leslie pushed him; Kako, who was not very confident in trees, tightened his grip, grinning nervously. Next Leslie gnawed on one of his hands, presumably to loosen his grasp. Kako uttered a sharp peep and stayed put. Then Leslie rubbed her vulva against his shoulder. This gesture calmed Kako, and he moved along the branch. It seemed that Leslie had been very close to using force but instead had reassured both herself and Kako with sexual contact.

During reconciliations, bonobos use the same sexual repertoire as they do during feeding time. Based on an analysis of many such incidents, my study yielded the first solid evidence for sexual behavior as a mechanism to overcome aggression. Not that this function is absent in other animals—or in humans, for that matter—but the art of sexual reconciliation may well have reached its evolutionary peak in the bonobo. For these animals, sexual behavior is indistinguishable from social behavior. Given its peacemaking and appeasement functions, it is not surprising that sex among bonobos occurs in so many different partner combinations, including between juveniles and adults. The need for peaceful coexistence is obviously not restricted to adult heterosexual pairs.

Female Alliance

Apart from maintaining harmony, sex is also involved in creating the singular social structure of the bonobo. This use of sex becomes clear when studying bonobos in the wild. Field research on bonobos started only in the mid-1970s, more than a decade after the most important studies on wild chimpanzees had been initiated. In terms of continuity and invested (wo)manpower, the chimpanzee projects of Jane Goodall and Toshisada Nishida, both in Tanzania, are unparalleled. But bonobo research by Takayoshi Kano and others of Kyoto University is now two decades under way at Wamba in Zaire and is beginning to show the same payoffs.

Both bonobos and chimpanzees live in so-called fission-fusion societies. The apes move alone or in small parties of a few individuals at a time, the composition of which changes constantly. Several bonobos traveling together in the morning might meet another group in the forest, whereupon one individual from the first group wanders off with others from the second group, while those left behind forage together. All associations, except the one between mother and dependent offspring, are of a temporary character.

Initially this flexibility baffled investigators, making them wonder if these apes formed any social groups with stable membership. After years of documenting the travels of chimpanzees in the Mahale Mountains, Nishida first reported that they form large communities: all members of one community mix freely in ever changing parties, but members of different communities never gather. Later, Goodall added territoriality to this picture. That is, not only do communities not mix, but males of different chimpanzee communities engage in lethal battles.

In both bonobos and chimpanzees, males stay in their natal group, whereas females tend to migrate during adolescence. As a result, the senior males of a chimpanzee or bonobo group have known all junior males since birth, and all junior males have grown up together. Females, on the other hand, transfer to an unfamiliar and often hostile group where they may know no one. A chief difference between chimpanzee and bonobo societies is the way in which young females integrate into their new community.

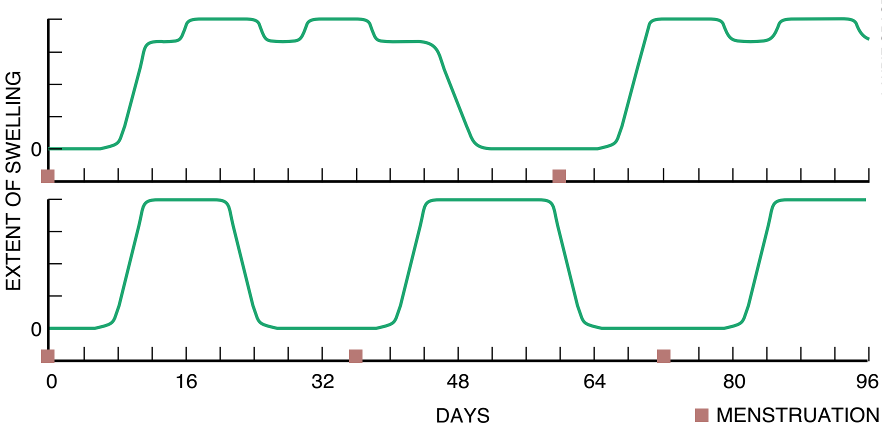
On arrival in another community, young bonobo females at Wamba single out one or two senior resident females for special attention, using frequent GG rubbing and grooming to establish a relation. If the residents reciprocate, close associations are set up, and the younger female gradually becomes accepted into the group. After producing her first offspring, the young female's position becomes more stable and central. Eventually the cycle repeats with younger immigrants, in turn, seeking a good relation with the now established female. Sex thus smooths the migrant's entrance into the community of females, which is much more close-knit in the bonobo than in the chimpanzee.

Bonobo males remain attached to their mothers all their lives, following them through the forest and being dependent on them for protection in aggressive encounters with other males. As a result, the highest-ranking males of a bonobo community tend to be sons of important females.

What a contrast with chimpanzees! Male chimpanzees fight their own battles, often relying on the support of other males. Furthermore, adult male chimpanzees travel together in same-sex parties, grooming each other frequently. Males form a distinct social hierarchy with high levels of both competition and association. Given the need to stick together against males of neighboring communities, their bonding is not surprising: failure to form a united front might result in the loss of lives and territory. The danger of being male is reflected in the adult sex ratio of chimpanzee populations, with considerably fewer males than females.

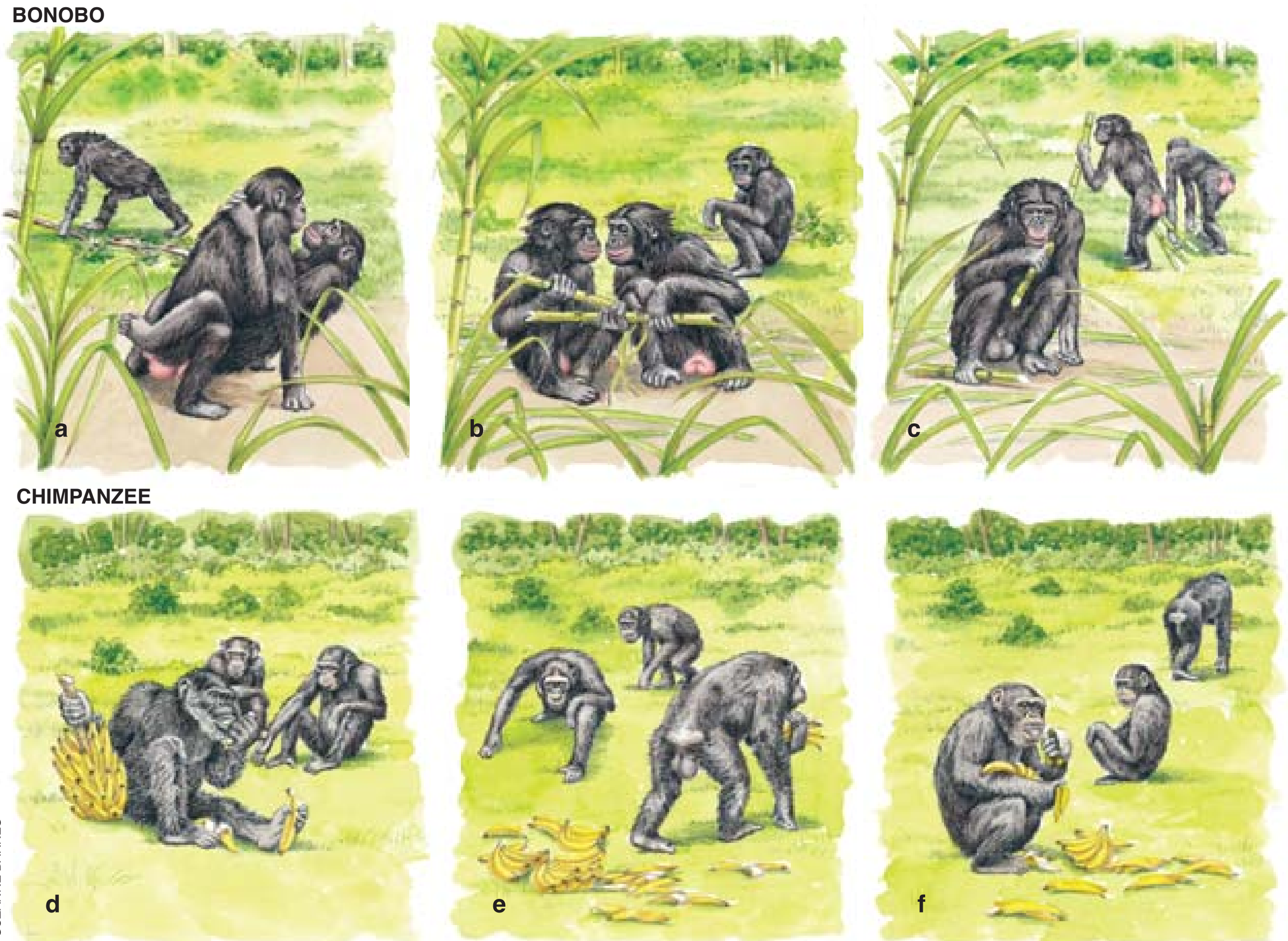
Serious conflict between bonobo groups has been witnessed in the field, but it seems quite rare. On the contrary, reports exist of peaceable mingling, including mutual sex and grooming, between what appear to be different communities. If intergroup combat is indeed unusual, it may explain the lower rate of all-male associations. Rather than being male-bonded, bonobo society gives the impression of being female-bonded, with even adult males relying on their mothers instead of on other males. No wonder Kano calls mothers the "core" of bonobo society.

The bonding among female bonobos violates a fairly general rule, outlined by Harvard University anthropologist Richard W. Wrangham, that the sex that stays in the natal group develops the strongest mutual bonds. Bonding among male chimpanzees follows naturally because they remain in the community of their birth. The same is true for female



LAURIE GRACE

FEMALE RECEPTIVITY for sex, manifested by swollen genitals, occupies a much larger proportion of the estrus cycle of bonobos (top) than of chimpanzees (bottom). The receptivity of bonobos continues through lactation. (In chimpanzees, it disappears.) This circumstance allows sex to play a large part in the social relations of bonobos. The graph was provided by Jeremy Dahl of the Yerkes Primate Center.



SUZANNE BARNES

DOMINANCE BY BONDING is evinced by female bonobos, who engage in genito-genital (GG) rubbing before eating sugarcane (a), while a bigger male displays to no avail. The females then share the food without competition (b). Only when they leave can the male get to the sugarcane (c). In male-dominated chimpanzee society the male eats first (d), while the females wait at a safe distance. After he leaves (e), carrying as many bananas as he can, the dominant female gets what is left (f). (Small amounts of sugarcane and bananas are provided at some research sites in Zaire.)

kinship bonding in Old World monkeys, such as macaques and baboons, where males are the migratory sex.

Bonobos are unique in that the migratory sex, females, strongly bond with same-sex strangers later in life. In setting up an artificial sisterhood, bonobos can be said to be secondarily bonded. (Kinship bonds are said to be primary.) Although we now know how this happens—through the use of sexual contact and grooming—we do not yet know why bonobos and chimpanzees differ in this respect. The answer may lie in the different ecological environments of bonobos and chimpanzees—such as the abundance and quality of food in the forest. But it is uncertain if such explanations will suffice.

Bonobo society is, however, not only female-centered but also appears to be female-dominated. Bonobo specialists, while long suspecting such a reality, have been reluctant to make the controversial claim. But in 1992, at the 14th Congress of the International Primatological Society in Strasbourg, investigators of both captive and wild bonobos presented data that left little doubt about the issue.

Amy R. Parish of the University of California at Davis reported on food competition in identical groups (one adult male and two adult females) of chimpanzees and bonobos at the Stuttgart Zoo. Honey was provided in a "termite hill" from which it could be extracted by dipping sticks into a small hole. As soon as honey was made available, the male chimpanzee would make a charging display through the enclosure and claim everything for himself. Only when his appetite was satisfied would he let the females fish for honey.

In the bonobo group, it was the females that approached the honey first. After having engaged in some GG rubbing, they would feed together, taking turns with virtually no competition between them. The male might make as many charging displays as he wanted; the females were not intimidated and ignored the commotion.

Observers at the Belgian animal park of Planckendael, which currently has the most naturalistic bonobo colony, reported similar findings. If a male bonobo tried to harass a female, all females would band together to chase him off. Because females appeared more successful in dominating males when they were together than on their own, their close association and frequent genital rubbing may represent an alliance. Females may bond so as to outcompete members of the individually stronger sex.

The fact that they manage to do so not only in captivity is evident from zoologist Takeshi Furuichi's summary of the relation between the sexes at Wamba, where bonobos are enticed out of the forest with sugarcane. "Males usually appeared at the feeding site first, but they surrendered preferred positions

FRANS DE WAAL

BEHAVIOR among bonobos is often reminiscent of that among humans. A female and an infant play; two juveniles practice sex without penetration; a bonobo walks upright, using his hands to carry food; and a male and female have sex *(left)*, after which the female leaves with one of the male's two oranges.

when the females appeared. It seemed that males appeared first not because they were dominant, but because they had to feed before the arrival of females," Furuichi reported at Strasbourg.

Sex for Food

Occasionally, the role of sex in relation to food is taken one step further, bringing bonobos very close to humans in their behavior. It has been speculated by anthropologists—including C. Owen Lovejoy of Kent State University and Helen Fisher of Rutgers University—that sex is partially separated from reproduction in our species because it serves to cement mutually profitable relationships between men and women. The human female's capacity to mate throughout her cycle and her strong sex drive allow her to exchange sex for male commitment and paternal care, thus giving rise to the nuclear family.

This arrangement is thought to be favored by natural selection because it allows women to raise more offspring than they could if they were on their own. Although bonobos clearly do not establish the exclusive heterosexual bonds characteristic of our species, their behavior does fit important elements of this model. A female bonobo shows extended receptivity and uses sex to obtain a male's favors when—usually because of youth—she is too low in social status to dominate him.

At the San Diego Zoo, I observed that if Loretta was in a sexually attractive state, she would not hesitate to approach the adult male, Vernon, if he had food. Presenting herself to Vernon, she would mate with him and make high-pitched food calls while taking over his entire bundle of branches and leaves. When Loretta had no genital swelling, she would wait until Vernon was ready to share. Primatologist Suehisa Kuroda reports similar exchanges at Wamba: "A young female approached a male, who was eating sugarcane. They copulated in short order, whereupon she took one of the two canes held by him and left."

Despite such quid pro quo between the sexes, there are no indications that bonobos form humanlike nuclear families. The burden of raising offspring appears to rest entirely on the female's shoulders. In fact, nuclear families are probably incompatible with the diverse use of sex found in bonobos. If our ancestors started out with a sex life similar to that of bonobos, the evolution of the family would have required dramatic change.

Human family life implies paternal investment, which is unlikely to develop unless males can be reasonably certain that they are caring for their own, not someone else's, offspring. Bonobo society lacks any such guarantee, but humans protect the integrity of their family units through all kinds of moral restrictions and taboos. Thus, although our species is characterized by an extraordinary interest in sex, there are no societies in which people engage in it at the drop of a hat (or a cardboard box, as the case may be). A sense of shame and a desire for domestic privacy are typical human concepts related to the evolution and cultural bolstering of the family.

Yet no degree of moralizing can make sex disappear from every realm of human life that does not relate to the nuclear family. The bonobo's behavioral peculiarities may help us understand the role of sex and may have serious implications for models of human society.

Just imagine that we had never heard of chimpanzees or baboons and had known bonobos first. We would at present most likely believe that early hominids lived in female-centered societies, in which sex served important social functions and in which warfare was rare or absent. In the end, perhaps the most successful reconstruction of our past will be based not on chimpanzees or even on bonobos but on a three-way comparison of chimpanzees, bonobos and humans.

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originally published in the special edition *The Hidden Mind*

sex differences in the brain

BY DOREEN KIMURA

MEN AND WOMEN DISPLAY PATTERNS OF BEHAVIORAL AND COGNITIVE DIFFERENCES THAT REFLECT VARYING HORMONAL INFLUENCES ON BRAIN DEVELOPMENT

MEN AND WOMEN DIFFER not only in their physical attributes and reproductive function but also in many other characteristics, including the way they solve intellectual problems. For the past few decades, it has been ideologically fashionable to insist that these behavioral differences are minimal and are the consequence of variations in experience during development before and after adolescence. Evidence accumulated more recently, however, suggests that the effects of sex hormones on brain organization occur so early in life that from the start the environment is acting on differently wired brains in boys and girls. Such effects make evaluating the role of experience, independent of physiological predisposition, a difficult if not dubious task. The biological bases of sex differences in brain and behavior have become much better known through increasing numbers of behavioral, neurological and endocrinological studies.

We know, for instance, from observations of both humans and nonhumans that males are more aggressive than females, that young males engage in more rough-and-tumble play than females and that females are more nurturing. We also know that in general males are better at a variety of spatial or navigational tasks. How do these and other sex differences come about? Much of our information and many of our ideas about how sexual differentiation takes place derive from research on animals. From such investigations, it appears that perhaps the most important factor in the differentiation of males and females and indeed in differentiating individuals within a sex is the level of exposure to various sex hormones early in life.

In most mammals, including humans, the developing organism has the potential to be male or female. Producing a male, however, is a complex process. When a Y chromosome is present, testes, or male gonads, form. This development is the critical first step toward becoming a male. When no Y chromosome is present, ovaries form.

Testes produce male hormones, or androgens (testosterone chief among them), which are responsible not only for transformation of the genitals into male organs but also for organization of corresponding male behaviors early in life. As with genital formation, the intrinsic tendency that occurs in the absence of masculinizing hormonal influence, according to seminal studies by Robert W. Goy of the University of Wisconsin, is to develop female genital structures and behavior. Female anatomy and probably most behavior associated with females are thus the default modes in the absence of androgens.

If a rodent with functional male genitals is deprived of androgens immediately after birth (either by castration or by the administration of a compound that blocks androgens), male sexual behavior, such as mounting, will be reduced, and more female sexual behavior, such as lordosis (arching of the back when receptive to coitus), will be expressed. Likewise, if androgens are administered to a female directly after birth, she will display more male sexual behavior and less female behavior in adulthood. These lifelong effects of early exposure to sex hormones are characterized as "organizational" because they appear to alter brain function permanently during a critical period in prenatal or early postnatal development. Administering the same sex hormones at later stages or in the adult has no similar effect.

Hormones and Intellect

WHAT OF DIFFERENCES in intellectual function between men and women? Major sex differences in function seem to lie in patterns of ability rather than in overall level of intelligence (measured as IQ), although some researchers, such as Richard Lynn of the University of Ulster in Northern Ireland, have argued that there exists a small IQ difference favoring human males. Differences in intellectual pattern refer to the fact that people have different intellectual strengths. For example, some people are especially good at using words, whereas others are better at dealing with external stimuli, such as identifying an object in a different orientation. Two individuals may have differing cognitive abilities within the same level of general intelligence.

On the whole, variation between men and women tends to be smaller than deviations within each sex, but very large differences between the groups do exist—in men's high level of visual-spatial targeting ability, for one.

Not all the behaviors that distinguish males are categorized at the same time, however. Organization by androgens of the male-typical behaviors of mounting and of rough-and-tumble play, for example, occur at different times prenatally in rhesus monkeys.

The area in the brain that regulates female and male reproductive behavior is the hypothalamus. This tiny structure at the base of the brain connects to the pituitary, the master endocrine gland. It has been shown that a region of the hypothalamus is visibly larger in male rats than in females and that this size difference is under hormonal control. Scientists have also found parallel sex differences in a clump of nerve cells in the human brain—parts of the interstitial nucleus of the anterior hypothalamus—that is larger in men than in women. Even sexual orientation and gender identity have been related to anatomical variation in the hypothalamus. Other researchers, Jiang-Ning Zhou of the Netherlands Institute of Brain Research and his colleagues there and at Free University in Amsterdam, observed another part of the hypothalamus to be smaller in male-to-female transsexuals than in a male control group. These findings are consistent with suggestions that sexual orientation and gender identity have a significant biological component.

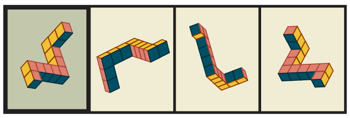
Sex differences in problem solving have been systematically studied in adults in laboratory situations. On average, men perform better than women at certain spatial tasks. In particular, men seem to have an advantage in tests that require the subject to imagine rotating an object or manipulating it in some other way. They also outperform women in mathematical reasoning tests and in navigating their way through a route. Further, men exhibit more accuracy in tests of target-directed motor skills—that is, in guiding or intercepting projectiles.

Women, on average, excel on tests that measure recall of words and on tests that challenge the person to find words that begin with a specific letter or fulfill some other constraint. They also tend to be better than men at rapidly identifying matching items and performing certain precision manual tasks, such as placing pegs in designated holes on a board.

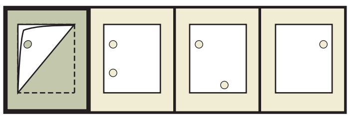
In examining the nature of sex differences in navigating routes, one study found that men completed a computer simulation of a maze or labyrinth task more quickly and with fewer errors than women did. Another study by different researchers used a path on a tabletop map to measure route learning. Their results showed that although men learned the route in fewer trials and with fewer errors, women remembered more

Problem-Solving Tasks Favoring Men

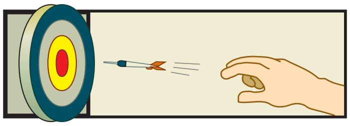
Men tend to perform better than women on certain spatial tasks. They do well on tests that involve mentally rotating an object or manipulating it in some fashion, such as imagining turning this three-dimensional object



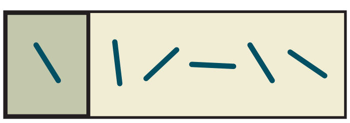
or determining where the holes punched in a folded piece of paper will fall when the paper is unfolded:



Men also are more accurate than women at target-directed motor skills, such as guiding or intercepting projectiles:



They do better at matching lines with identical slopes:

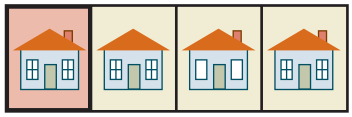


And men tend to do better than women on tests of mathematical reasoning:

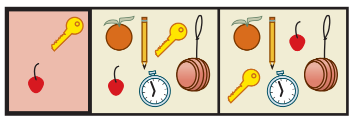
1,100	If only 60 percent of seedlings will survive, how many must be planted to obtain 660 trees?

Problem-Solving Tasks Favoring Women

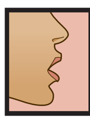
Women tend to perform better than men on tests of perceptual speed in which subjects must rapidly identify matching items—for example, pairing the house on the far left with its twin:



In addition, women remember whether an object, or a series of objects, has been displaced:

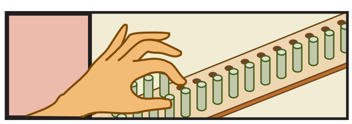


When they are read a story, paragraph or a list of unrelated words, women demonstrate better recall:



Dog, shadow, hamburger, cloud, flower, eyelash, pencil, paper, water, light, fork, road, building ...

Women do better on precision manual tasks—that is, those involving fine-motor coordination—such as placing the pegs in holes on a board:



And women do better than men on mathematical calculation tests:

77	$14 \times 3 - 17 + 52$
43	$2\,(15 + 3) + 12 - \frac{15}{3}$

of the landmarks, such as pictures of different types of buildings, than men did. These results and others suggest that women tend to use landmarks as a strategy to orient themselves in everyday life more than men do.

Other findings seemed also to point to female superiority in landmark memory. Researchers tested the ability of individuals to recall objects and their locations within a confined space—such as in a room or on a tabletop. In these studies, women were better able to remember whether items had changed places or not. Other investigators found that women were superior at a memory task in which they had to remember the locations of pictures on cards that were turned over in pairs. At this kind of object location, in contrast to other spatial tasks, women appear to have the advantage.

It is important to keep in mind that some of the average sex differences in cognition vary from slight to quite large and that men and women overlap enormously on many cognitive tests that show average differences. For example, whereas women perform better than men in both verbal memory (recalling words from lists or paragraphs) and verbal fluency (finding words that begin with a specific letter), we find a large difference in memory ability but only a small disparity for the fluency tasks. On the whole, variation between men and women tends to be smaller than deviations within each sex, but very large differences between the groups do exist—in men's high level of visual-spatial targeting ability, for one.

Although it used to be thought that sex differences in problem solving did not appear until puberty, the accumulated evidence now suggests that some cognitive and skill differences are present much earlier. For example, researchers have found that three- and four-year-old boys were better at targeting and at mentally rotating figures within a clock face than girls of the same age were. Prepubescent girls, however, excelled at recalling lists of words.

Male and female rodents have also been found to solve problems differently. Christina L. Williams of Duke University has shown that female rats have a

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greater tendency to use landmarks in spatial learning tasks, as it appears women do. In Williams's experiment, female rats used landmark cues, such as pictures on the wall, in preference to geometric cues: angles and the shape of the room, for instance. If no landmarks were available, however, females used the geometric cues. In contrast, males did not use landmarks at all, preferring geometric cues almost exclusively.

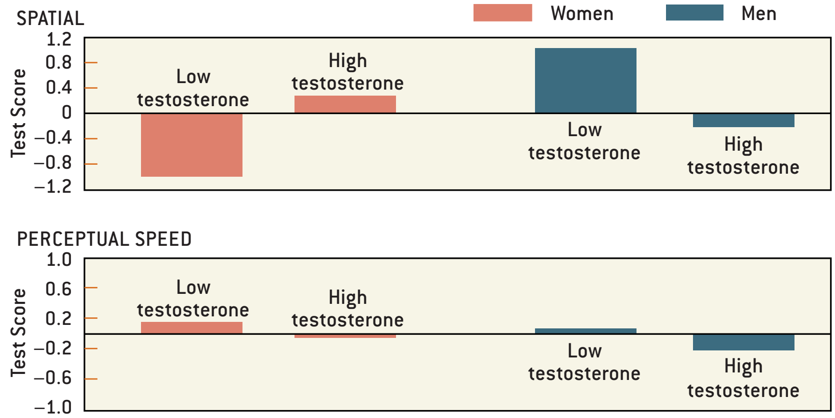
Hormones and Behavior

WILLIAMS ALSO FOUND that hormonal manipulation during the critical period could alter these behaviors. Depriving newborn males of sex hormones by castrating them or administering hormones to newborn females resulted in a complete reversal of sex-typed behaviors in the adult animals. Treated males behaved like females and treated females, like males.

Structural differences may parallel behavioral ones. Lucia F. Jacobs, while at the University of Pittsburgh, discovered that the hippocampus—a region thought to be involved in spatial learning—is larger in several male species of rodents than in females. At present, there are insufficient data on possible sex differences in hippocampal size in human subjects.

One of the most compelling areas of evidence for hormonally influenced sex differences in humans comes from studies of girls exposed to excess androgens in the prenatal or neonatal stage. The production of abnormally large quantities of adrenal androgens can occur because of a genetic defect in a condition called congenital adrenal hyperplasia (CAH). Before the 1970s a similar condition also unexpectedly appeared in the offspring of pregnant women who took various synthetic steroids. Although the consequent masculinization of the genitals can be corrected by surgery and drug therapy can stop the overproduction of androgens, the effects of prenatal exposure on the brain are not reversed.

Sheri A. Berenbaum, while at Southern Illinois University at Carbondale, and Melissa Hines, then at the University of California at Los Angeles, observed the play behavior of CAH girls and compared it with that of their male and female siblings. Given a choice of transportation and construction toys, dolls and kitchen supplies, or books and board games, the CAH girls preferred the more typically masculine toys—for example, they played with cars for the same amount of time that boys did. Both the CAH girls and the boys differed from unaffected girls in their patterns of choice. Berenbaum also found that CAH girls had greater interest in male-typical activities and careers. Because there is every reason to think parents would be at least as likely to encourage feminine preferences in their CAH daughters as in their unaffected daughters, these findings suggest that these preferences were altered by the early hormonal environment.



TESTOSTERONE LEVELS can affect performance on some tests [*see boxes on previous page for examples of tests*]. Women with high levels of testosterone perform better on spatial tasks (*top*) than women with low levels do, but men with low levels outperform men with high levels. On a test of perceptual speed in which women usually excel (*bottom*), no relation was found between testosterone and performance.

Other researchers also found that spatial abilities that are typically better in males are enhanced in CAH girls. But in CAH boys the reverse was reported.

Such studies suggest that although levels of androgen relate to spatial ability, it is not simply the case that the higher the levels, the better the spatial scores. Rather studies point to some optimal level of androgen (in the low male range) for maximal spatial ability. This finding may also hold for men and math reasoning; in one study, low-androgen men tested higher.

The Biology of Math

SUCH FINDINGS are relevant to the suggestion by Camilla P. Benbow, now at Vanderbilt University, that high mathematical ability has a significant biological determinant. Benbow and her colleagues have reported consistent sex differences in mathematical reasoning ability that favor males. In mathematically talented youth, the differences were especially sharp at the upper end of the distribution, where males vastly outnumbered females. The same has been found for the Putnam competition, a very demanding mathematics examination. Benbow argues that these differences are not readily explained by socialization.

It is important to keep in mind that the relation between natural hormone levels and problem solving is based on correlational data. Although some form of connection between the two measures exists, we do not necessarily know how the association is determined, nor do we know what its causal basis is. We also know little at present about the relation between adult levels of hormones and those in early life, when abilities appear to become organized in the nervous system.

One of the most intriguing findings in adults is that cognitive patterns may remain sensitive to hormonal fluctuations throughout life. Elizabeth Hampson of the University of Western Ontario showed

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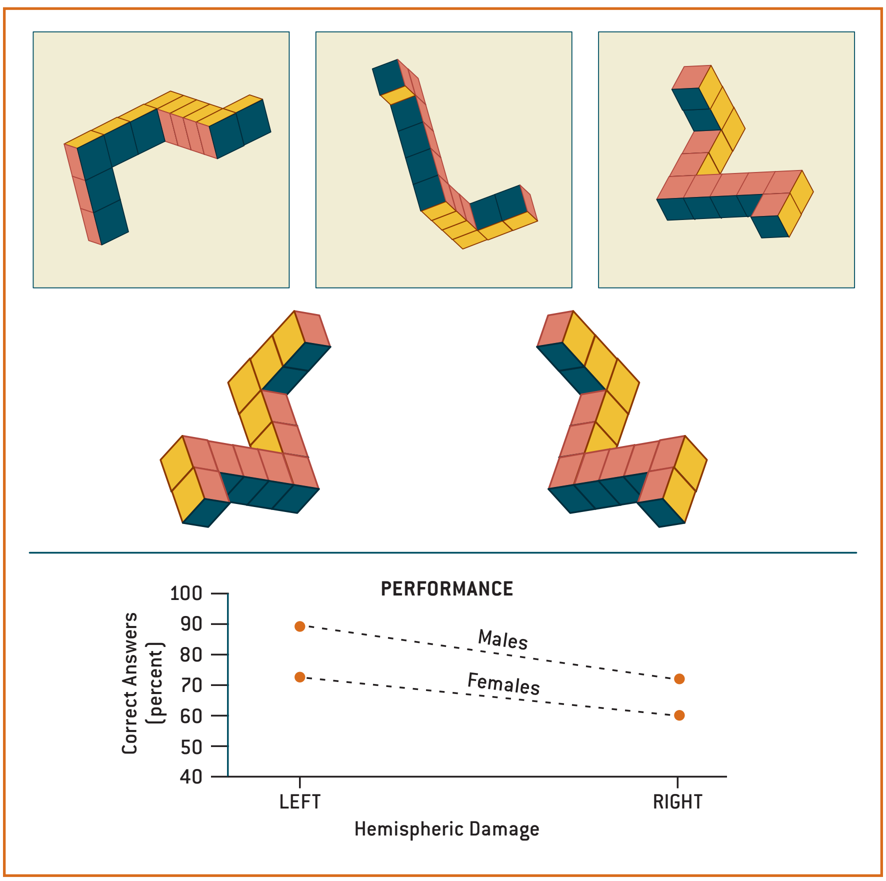
that women's performances at certain tasks changed throughout the menstrual cycle as levels of estrogen varied. High levels of the hormone were associated not only with relatively depressed spatial ability but also with enhanced speech and manual skill tasks. In addition, I have observed seasonal fluctuations in spatial ability in men: their performance is better in the spring, when testosterone levels are lower. Whether these hormonally linked fluctuations in intellectual ability represent useful evolutionary adaptations or merely the highs and lows of an average test level remains to be seen through further research.

A long history of studying people with damage to one half of their brain indicates that in most people the left hemisphere of the brain is critical for speech and the right for certain perceptual and spatial functions. Researchers studying sex differences have widely assumed that the right and left hemispheres of the brain are more asymmetrically organized for speech and spatial functions in men than in women.

This belief rests on several lines of research. Parts of the corpus callosum, a major neural system connecting the two hemispheres, as well as another connector, the anterior commissure, appear to be larger in women, which may permit better communication between hemispheres. Perceptual techniques that measure brain asymmetry in normal-functioning people sometimes show smaller asymmetries in women than in men, and damage to one brain hemisphere sometimes has less of an effect in women than the comparable injury in men does. My own data on patients with damage to one hemisphere of the brain suggest that for functions such as basic speech and spatial ability, there are no major sex differences in hemispheric asymmetry, although there may be such disparities in certain more abstract abilities, such as defining words.

If the known overall differences between men and women in spatial ability were related to differing dependence on the right brain hemisphere for such functions, then damage to that hemisphere might be expected to have a more devastating effect on spatial performance in men. My laboratory has studied the ability of patients with damage to one hemisphere of the brain to visualize the rotation of certain objects. As expected, for both sexes, those with damage to the right hemisphere got lower scores on these tests than those with damage to the left hemisphere did. Also, as anticipated, women did not do as well as men on this test. Damage to the right hemisphere, however, had no greater effect on men than on women.

The results of this study and others suggest that the normal differences between men and women on rotational and line orientation tasks need not be the result of different degrees of dependence on the right hemisphere. Some other brain systems may be mediating the higher performance by men.



RIGHT HEMISPHERE DAMAGE affects spatial ability to the same degree in both sexes (*graph*), suggesting that women and men rely equally on that hemisphere for certain spatial tasks. In one test of spatial-rotation performance, photographs of a three-dimensional object must be matched to one of two mirror images of the same object.

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Patterns of Function

ANOTHER BRAIN difference between the sexes has been shown for speech and certain manual functions. Women incur aphasia (impairment of the power to produce and understand speech) more often after anterior damage than after posterior damage to the brain. In men, posterior damage more often affects speech. A similar pattern is seen in apraxia, difficulty in selecting appropriate hand movements, such as showing how to manipulate a particular object or copying the movements of the experimenter. Women seldom experience apraxia after left posterior damage, whereas men often do.

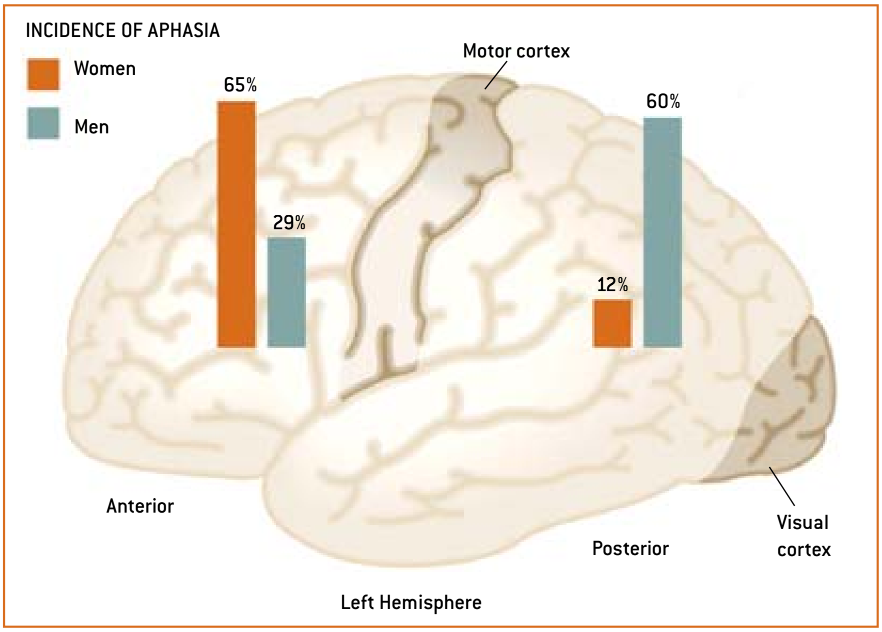
Men also incur aphasia from left hemisphere damage more often than women do. One explanation suggests that restricted damage within a hemisphere after a stroke more often affects the posterior region of the left hemisphere. Because men rely more on this region for speech than women do, they are more likely to be affected. We do not yet understand the effects on cognitive patterns of such divergent representation of speech and manual functions.

Although my laboratory has not found evidence of sex differences in functional brain asymmetry with regard to basic speech, movement or spatial-rotation abilities, we have found slight differences in some verbal skills. Scores on a vocabulary test and on a verbal fluency test, for instance, were slightly affected by damage to either hemisphere in women, but such scores were affected only by left hemisphere damage in men. These findings suggest that when using some more abstract verbal skills, women do use their hemispheres more equally than men do. But we have not found this to be true for all word-related tasks; for example, verbal memory appears to depend just as much on the left hemisphere in women as in men.

In recent years, new techniques for assessing the brain's activity—including functional magnetic resonance imaging (fMRI) and positron emission tomography (PET), when used during various problem-solving activities—have shown promise for providing more information about how brain function may vary among normal, healthy individuals. The research using these two techniques has so far yielded interesting, yet at times seemingly conflicting, results.

Some research has shown greater differences in activity between the hemispheres of men than of women during certain language tasks, such as judging if two words rhyme and creating past tenses of verbs. Other research has failed to find sex differences in functional asymmetry. The different results may be attributed in part to different language tasks being used in the various studies, perhaps showing that the sexes may differ in brain organization for some language tasks but not for others.

The varying results may also reflect the complexity of these techniques. The brain is always active to some degree. So for any activity, such as reading aloud, the comparison activity—say, reading silently—is intended to be very similar. We then "subtract" the brain pattern that occurs during silent reading to find the brain pattern present while reading aloud. Yet such methods require dubious assumptions about what the subject is doing during either activity. In addition, the more complex the activity, the more difficult it is to know what is actually being measured after subtracting the comparison activity.



APHASIAS, or speech disorders, occur most often in women when damage is sustained in the anterior of the brain. In men, they occur more frequently when damage is in the posterior region. The data presented above derive from one set of patients.

JARED SCHNEIDMAN DESIGN

Looking Back

TO UNDERSTAND human behavior—how men and women differ from one another, for instance—we must look beyond the demands of modern life. Our brains are essentially like those of our ancestors of 50,000 and more years ago, and we can gain some insight into sex differences by studying the differing roles men and women have played in evolutionary history. Men were responsible for hunting and scavenging, defending the group against predators and enemies, and shaping and using weapons. Women gathered food near the home base, tended the home, prepared food and clothing, and cared for small children. Such specialization would put different selection pressures on men and women.

Any behavioral differences between individuals or groups must somehow be mediated by the brain. Sex differences have been reported in brain structure and organization, and studies have been done on the role of sex hormones in influencing human behavior. But questions remain regarding how hormones act on human brain systems to produce the sex differences we described, such as in play behavior or in cognitive patterns.

The information we have from laboratory animals helps to guide our explanations, but ultimately these hypotheses must be tested on people. Refinements in brain-imaging techniques, when used in conjunction with our knowledge of hormonal influences and with continuing studies on the behavioral deficits after damage to various brain regions, should provide insight into some of these questions. SA

MORE TO EXPLORE

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