organisms ranging from water fleas to worms and typically allow only one individual per generation to breed, so that if that individual has picked up a mutation, it won't be eliminated by natural selection. After every 10 generations or so, researchers test the lineages' fitness and translate any fitness decline into the deleterious mutation rate.

But the experiments are tricky, and problems can crop up if selection isn't adequately limited. Additionally, mutations of very small effect may be undetectable in the lab but important in nature, where the numbers are larger and the time is longer. Counting mutations "isn't counting beans," says geneticist James Crow of the University of Wisconsin, Madison.

So far, the results are disconcertingly mixed (see table). "The state of the whole field is very much in doubt right now," says evolutionary geneticist David Houle at the University of Toronto. Benchmark studies by Terumi Mukai and Crow in the 1970s established a deleterious mutation rate of close to one per generation in the fruit fly *Drosophila*, just enough to explain sex in Kondrashov's theory. But later reanalyses of that work put the rate considerably lower. Recent worm experiments have yielded rates as low as 0.005, and recent rates in flies have ranged from just about nil to one.

Now a few scientists are bypassing the difficulties of population genetics experiments and instead simply counting mutations in sequenced stretches of DNA. They compare DNA sequences in noncoding regions in closely related species to derive a genomewide mutation rate. Then they estimate how much of the genome is functional, or subject to selection, and apply the mutation rate to the functional DNA. Beneficial mutations are thought to be so rare that they aren't considered.

One such experiment, by Michael Nachman at the University of Arizona, Tucson, assumes that 5% of the human genome is subject to selection and concludes that each human infant is born with about six mildly deleterious mutations. If a higher proportion of the genome is functional—as some scientists suspect—then the rate would be even higher. Either way, it supports the mutational hypothesis for the maintenance of sex. But researchers agree that more work, in more organisms, is needed. Only the molecular method will vindicate or doom the theory, says geneticist Peter Keightley at the University of Edinburgh, who is now counting mutations in the worm *Caenorhabditis elegans*.

While scientists scrounge for data to support one or the other of the warring theories of sex, other researchers are considering merging the two schools of thought—that sex both collects beneficial mutations and purges bad ones. "My view is they're both going on," says McGill's Bell. "Something as complex, onerous, and laborious as sexuality is probably only going to be maintained if it's doing something very important."

DELETERIOUS MUTATION RATE

Source	Experiment type	Organism	Harmful mutations per genome per generation
T. Mukai, 1972	lab experiment	*Drosophila*, sexual fly	0.6 to 1
P. Keightley, 1996	reanalysis of Mukai	*Drosophila*, sexual fly	$<<1$
A. Kondrashov, 1997	lab experiment	*Drosophila*, sexual fly	1
M. Lynch, 1998	lab experiment	*Daphnia*, asexual crustacean	0.05 to 1
P. Keightley & A. Caballero, 1997	lab experiment	*C. elegans*, self-fertilizing worm	0.005
M. Nachman, 1998	genomic sequencing	Humans	6

For example, in the "ruby in the rubbish" model, the ruby—a good mutation in an asexual organism—is buried in rubbish—a glut of bad mutations that are constantly being eliminated by selection. Thus the harmful mutations drag the good ones down with them, slowing the rate of evolution relative to sexual populations that can unhitch good genes from bad ones during recombination.

But the evidence for such theories is also very indirect, and testing them is even more of a headache than testing the old theories. "We're in a world where it's easy to say such synergism is likely and harder to say how to go about falsifying it," says Bath's Hurst. For now, biologists can offer plenty of reasons why sex is good for you, but they have a ways to go before they can prove their point.

—BERNICE WUETHRICH

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A New Look at Monogamy

NEWS

Social monogamy, in which parents cooperate to raise their brood, is relatively common among animals—but true sexual fidelity is hard to find

Researchers studying the evolution of monogamy once had a straightforward task: Find those members of the animal kingdom that form lasting pair bonds—and then figure out why fidelity is in each mate's interest. But in recent years that task has grown complex. Genetic studies of organisms from birds to gibbons to rodents have revealed that some of the offspring raised by those seemingly attached parents are in fact fathered by different males. Even among those paragons of pair loyalty, the bluebirds, it turns out that the female slips away for brief liaisons with other males. Yet the two parents continue to work together to raise the young. "The first thing you have to understand is that social monogamy, where you've got a pair bond, is not the same as genetic monogamy," says Stephen Emlen, an evolutionary behavioral ecologist at Cornell University in Ithaca, New York. Indeed, genetic, or sexual, monogamy appears to be the exception rather then the rule among pairs in the animal kingdom.

Why would organisms live and work in exclusive pairs—but sometimes have sex with outsiders? Biologists have a number of theories to explain this complex behavior, as well as its extremely rare counterpart, true sexual monogamy. To test their ideas, they are examining everything from environmental factors to neural chemistry in various species that are socially—if not always genetically—monogamous. Even as they uncover the biochemical underpinnings of fidelity, they suspect that in certain circumstances, some hanky-panky has evolutionary advantages for both males and females.

For most animals, mate partnerships are thought to be somehow related to parental care. Birds, for example, were long assumed to be monogamous because two parents are needed for the prodigious labor of incubating eggs and feeding nestlings—and it was thought that males would only do this if they were certain the young were their own. But that's not the whole story. For example, although a pair of eastern bluebirds may mate, build a nest, and rear a brood together, an average of 15% to 20% of the chicks are not sired by the male in this partnership, according to ongoing research by Patricia Adair Gowaty, a behavioral ecologist at the University of Georgia, Athens. Indeed, studies in the last 10 years of the DNA of the chicks of some 180 socially monogamous species of songbirds indicate that only about 10% are sexually monogamous, says Gowaty.

Males on the prowl are simple to explain in evolutionary terms—

they're just trying to get their genes into as many future offspring as possible. Inseminating—and then leaving—a female is an efficient way to do this, explains Emlen, and is by far the most common strategy in mammals. But why would females cast a wandering eye? New work on individual variation in sexual fidelity in birds has helped spur some new theories. "It used to be thought that was all due to forced copulations, that these were male-driven events," says Gowaty. "But increasingly we're finding that the females have a lot to do with it." Female songbirds must actively receive sperm and can probably dump it if they choose, so they "probably can't be forced," she says. Indeed, some females take an active part in these liaisons: Female hooded warblers have a special song soliciting extrapair matings.

Gowaty and others theorize that the females have good genetic reasons for choosing their extrapair partners, perhaps seeking to maximize the variability of their offspring in case the environment changes. Females may choose one male for a social mate (perhaps because he has a crucial resource, such as a good territory with a nesting tree) and another for a sexual—that is, genetic—mate.

For example, in recent studies of the Scandinavian great reed warbler, females seemed to prefer mating with certain types of males, particularly those with a large repertory of songs, says Emlen. A study in 1996 by Dennis Hasselquist of Lund University in Sweden showed that males with a broad range of songs father healthier, more viable offspring. In the warbler and other species, says Emlen, females mated to "lesser males" seek extrapair matings, but females mated to "high-quality" males don't wander, apparently because they already have the best genes on the block. A handful of other recent studies have shown that the traits preferred by females are tied to these so-called "good genes" (*Science*, 19 June, p. 1928). "I think that's what she's looking for—a fitness benefit for the kids," says Gowaty, who plans to test this hypothesis next summer on the bluebirds.

Presumably, the cuckolded male in such a pair stays with his mate because that's the best way to ensure that his offspring survive. And in the densely packed bluebird colonies, his position in the nest also offers him opportunities to mate with the female next door, notes Gowaty.

One way to understand social monogamy is by comparing it to those rare creatures who are truly sexually faithful, such as the California mouse. This peach-sized golden-brown rodent is the rarest of the rare, for only 3% to 10% of mammals are even socially monogamous. But the mice never stray. "They form pair bonds well before they mate," says evolutionary biologist David Gubernick from the University of California, Davis. In his lab, such bonded males shun other females even if the females are in estrus, and bonded females ignore other males. Genetic tests of paternity confirm the species' till-death-do-us-part fidelity: In a 1991 study done by Gubernick's colleague, David Ribble, now at Trinity University in Houston, Texas, all the offspring from 28 families tested in the wild over a 2-year period were the young of their social fathers.

Gubernick attributes the rock-solid partnerships in part to a critical requirement for biparental care. "In birds, that need can vary," he says, "but here it is essential." In experiments in the wild and in the lab, Gubernick discovered that a female cannot rear the litter of one to three pups by herself. The pups, born at the coldest time of the year, are "absolutely dependent on their parents' body heat for survival," he says. The father takes turns with the mother to huddle over the young in "the nursing position" to keep them warm. If he leaves or is taken away, she will abandon or kill the pups. "It's the first demonstration of the need for male care in a mammal in the wild," Gubernick says. Because it takes both to care for the young, this helps make their evolutionary interests so congruent that sexual fidelity is favored, he says.

But this neat explanation has some untidy loose ends. Harsh conditions don't always lead to faithful hearts: Other species of mice that live in the same environment are promiscuous. It's not clear why monogamy evolved in this one species but not in the others, says Gubernick.

DAVID J. GUBERNICK

Family values. Unlike most mammals, once paired, male and female California mice never stray.

Although the evolutionary forces are not fully understood, researchers are beginning to explore the hormones underlying both sexual and social monogamy. For example, Sue Carter, a behavioral endocrinologist at the University of Maryland, College Park, has come up with a hormonal explanation for the unusual sexual behavior of prairie voles. These mouse-sized herbivores copulate numerous times over a 24-hour period, generally with one mate. The extensive mating bout apparently releases powerful neuropeptide hormones in the voles' brains, which causes them to form strong pair bonds. Carter's work suggests that in the females, oxytocin—a hormone associated with maternal behavior and lactation—is triggered; while in the males, vasopressin, a hormone associated with male aggression and paternal behavior, is released. When these hormones were experimentally blocked during mating, the pairs did not bond. "They need those chemicals to form their pair bonds," says Carter.

These hormones are found in all mammals, including humans and montane voles, close cousins of the prairie voles in which both males and females are promiscuous. However, the receptors for the hormones are found in "totally different parts of the brain" of the two species of voles and so have "totally different effects," says Thomas Insel, a neuroscientist at the Yerkes Regional Primate Research Center in Atlanta. Over the last 4 years, his team has sequenced the genes for these hormone receptors in more than 10 species, ranging from mice to humans, and found that although the coding sequences are similar, the promoter regions are strongly divergent.

C. S. CARTER

It's all in the chemistry. Hormones released during long bouts of mating may help keep male and female voles monogamous.

Does this body of research on animal promiscuity offer insight into human behavior? As anyone who has listened to country music knows, humans are more like bluebirds than the faithful California mouse. Reliable data on human paternity are essentially nonexistent and are expected to vary by culture, but molecular geneticist Bradley Popovich of Oregon Health Sciences University in Portland says that U.S. labs screening for inherited diseases typically expect to find that about 10% of children tested are not sired by their social fathers.

Still, most researchers agree that, as Sarah Hrdy, an anthropologist at the University of California, Davis, puts it, human "mothers evolved needing help with rearing the kids." Thus social monogamy, at least, was evolutionarily favored. "There's no question that children are better off with two committed parents," says Hrdy. As in birds, tending the nest is easier with two on the job.

–VIRGINIA MORELL