Sexual stereotypes

Males are promiscuous and females are choosy, according to evolutionary dogma embodied in a theory called Bateman's principle. Only recently have researchers begun to test the theory's limits, says Jonathan Knight.

The mating game: the image of coy females and ardent males is an old one. Bateman's principle argues that these roles stem from the economics of sperm and egg production (main picture).

MEHAU KULYK/SPL; INSET: CORBIS

"The female, with the rarest exceptions, is less eager than the male ... she is coy, and may often be seen endeavouring for a long time to escape."[1]

With these words, Charles Darwin cast the die for evolutionary studies of male and female sexual roles. Darwin realized that the peacock's tail and the lion's mane owe their existence to aeons of fierce competition between their male ancestors for mates. Competitive males, Darwin assumed, will attempt to mate at every opportunity; females, he reasoned, are inherently choosy, reserving their favours for the strongest or gaudiest suitor.

Fly guy: Angus John Bateman (inset) used *Drosophila* to study the benefits of promiscuity.

These ideas were later crystallized in a theory known as Bateman's principle. In 1948, the British biologist Angus John Bateman concluded from experiments with fruitflies that promiscuity is more valuable to the reproductive success of males than to that of females. Males, he concluded, have therefore evolved an "undiscriminating eagerness" to mate, whereas females display "discriminating passivity"[2] — a fundamental dichotomy that Bateman suggested even applies, to an extent, to our own species.

The explanation, Bateman argued, is that sperm are small and cost next to nothing to produce — so the wider a male can spread them, the better off he will be. A female, on the other hand, produces many fewer eggs, and invests a relatively large amount of energy in each one. All she really needs is one good male to fertilize them to reach her maximum reproductive output. It all seemed to make sense, and Bateman's principle soon became one of the grounding truisms of behavioural biology.

But several researchers have since taken exception to this characterization of male and female sexual roles. Objections were first heard, but largely ignored, in the 1970s. Today, behavioural biologists are finding evidence that the world of sex is more complicated than Bateman thought. It's not that his principle is invalid, they say, but rather that it has been used to extend dated preconceptions about human sexual behaviour to the entire animal kingdom, sometimes to the detriment of scientific knowledge.

Despite the Victorians' reputation for prudishness, nineteenth-century natural philosophers spent lots of time watching animals mate. At the height of the British Empire, there were few places in the world where courting animals could escape the note-taking naturalist, and Darwin relied heavily on these descriptions in developing his theory of sexual selection[1], with its underlying assumptions of eager males and reluctant females.

Counting on success

Bateman, who worked at the John Innes Horticultural Institution near London, was one of the first biologists to furnish the theory with experimental evidence. In a series of genetic experiments[2], Bateman combined groups of male and female fruitflies (*Drosophila melanogaster*) in vials. Each fruitfly carried a different dominant genetic marker, so Bateman could score the breeding success of each individual by counting the number of times the marker showed up in the next generation.

His conclusion was that, for males, promiscuity pays off. Males that mated with several females produced three to four times as many offspring as their monogamous peers. But females gained little by playing the field — on average, their reproductive output less than doubled when their progeny were sired by more than one male.

Bateman couched his explanation in terms of the relative energetic costs of produc-

CLAUDE NURIDSANY & MARIE PERENNOU/SPL; INSET COURTESY OF THE JOHN INNES FOUNDATION TRUSTEES

ing sperm and eggs, but today the principle that bears his name includes an important modification made in 1972 by Robert Trivers of Harvard University, one of the founders of the discipline of sociobiology[3]. He expanded Bateman's concept beyond gametes to include a parent's entire investment in its offspring — including gestation, feeding and protection. The sex that invests more, Trivers argued, should be more passive and discriminating, whereas that with the smaller investment should court more mates and be ready to fight over them. This competition in turn drives Darwin's sexual selection by favouring traits such as showy colours and aggressiveness.

As evidence, Trivers cited well-known examples of sexual role reversal, such as seahorses and pipefish, and birds such as the greater painted snipe (*Rostratula benghalensis*). In this species, males incubate the eggs and rear the young. As the Bateman principle predicts, female painted snipes have brighter coloration and aggressively court males.

But over the next few years, a handful of primatologists began to notice behaviour in apes and monkeys that did not fit the Bateman mould. When doing field research in India on Hanuman langur monkeys (*Presbytis entellus*), Sarah Hrdy, then a graduate student at Harvard University, observed that, around the time of ovulation, females would aggressively seek copulations with multiple males. And when a new male rose to power in a group of langurs, even pregnant females would copulate with him.

Although female langurs are promiscuous, this is not a classic case of sexual role reversal — the females still take on most of the burden of parental care. Hrdy, who is now an emeritus professor at the University of California, Davis, proposed an alternative explanation[4]. In langurs, as in several other primate species, males sometimes kill the unweaned young of females with which they mate, presumably so that more attention will be lavished on their own offspring when they are born. As a defence against infanticide, Hrdy argued, females may confuse the issue of paternity through flagrant promiscuity.

Hrdy's idea that promiscuity might have an adaptive value for females met with a great deal of criticism at the time[5]. Hrdy and her supporters became characterized as 'feminist' behavioural ecologists, and were seen by many researchers as a marginal group. But over the years, the number of cases of female promiscuity described in the animal-behaviour literature has mushroomed, particularly since the advent a decade ago of techniques for determining paternity by DNA analysis.

A degree of female promiscuity now seems to be the rule rather than the exception[6]. It has been documented in animals as diverse as whales[7], rodents[8] and bees[9]. In some animals, such as pseudoscorpions — arthropods that are related to scorpions and spiders — females prefer to switch partners much more often than males[10].

Bateman would not have predicted that what is good for the gander is good for the goose. And behavioural biologists are now striving to understand what females gain from promiscuity. According to Hrdy's 'confused paternity' argument, a promiscuous female stands to get more help, or at least less interference, with raising her young. In certain insect species, where males often make nuptial gifts of food items, the benefits may be primarily nutritional[11].

JULIE MEECH/NHPA; INSET: ANULA JAYASURIYA

Sarah Hrdy (inset) argued that female langurs' promiscuity helps to safeguard their offspring.

But several recent studies have suggested that there may also be a benefit to the health of the offspring. John Hoogland of the University of Maryland's Center for Environmental Science in Frostburg has found that female prairie dogs (*Cynomys gunnisoni*) that mate with multiple males end up with larger litters, and that their pups are more healthy[8]. Female sand lizards (*Lacerta agilis*) and adders (*Vipera berus*) also do better with multiple mates[12].

Fishing for genes

Why should this be? Evolutionary biologists Jeanne and David Zeh of the University of Nevada in Reno argue that promiscuous females gain a genetic benefit: they improve their chance of finding a genetically compatible male. In 1999, the Zehs published an experiment[13] that confirmed this principle in the pseudoscorpion *Cordylochernes scorpioides*. They allowed females to mate either twice with one male or once each with two males. Even though all females received the same amount of sperm, females that mated with multiple males had a higher percentage of offspring mature to adulthood. The Zehs argued that promiscuity can help a female by reducing problems with low offspring viability that can result from mating with a partner whose genes don't happen to complement her own. In essence, promiscuity means that a female does not have to put all her eggs in one basket.

Earlier this month, Tom Tregenza and Nina Wedell of the University of Leeds, UK, reported that female field crickets (*Gryllus*

JONATHAN BLAIR/CORBIS

RIGHT: TONY HEALD/BBC WILD;FAR RIGHT: DARYL BALFOUR/NHPA

Role reversal: the male frigatebird (left) shows off to impress the ladies, but in the painted snipe it is a different story — males (below left) rear the young and are outshone by females (below).

bimaculatus) may use promiscuity to avoid the cost of inbreeding[14]. In their experiment, females were allowed to mate with two brothers, with a brother and an unrelated male, or with two unrelated males. The second and third groups had similar reproductive success, but eggs laid by females in the first group were less likely to hatch. By some unknown mechanism, females that mate with multiple males seem able to fertilize their eggs selectively with the sperm of unrelated males, and so avoid the problems of poor embryo viability that are a consequence of inbreeding.

Multiple orgasms

The flip side of the Bateman equation — that males are boundlessly eager to mate because of their almost inexhaustible sperm supply — has also come under scrutiny. Although it may take very little energy to make a single sperm, males never deliver just one at a time. And in certain circumstances, the energetic costs of fertilizing a single female's eggs can be high.

Again, dissenting voices were first raised against this facet of the Bateman principle in the 1970s. Donald Dewsbury, a comparative psychologist at the University of Florida in Gainesville, noticed that male deer mice, hamsters and other rodents tended to copulate several times with the same female. It turned out that females are more likely to release the hormones needed for pregnancy if they are stimulated by multiple ejaculations, regardless of the amount of sperm they receive[15].

As a result, Dewsbury pointed out in a 1982 review[16] that a hit-and-run mating strategy might not always be the best option for males. If a male mates once and takes off, leaving the female in question open to the attentions of rival males, his sperm may not fertilize her eggs, and he also has to spend time and energy searching for another mate. Particularly when the number of receptive females is relatively low, a male may be better off sticking to one mate, and guarding her against rival suitors. This is a complexity that Bateman failed to recognize, Dewsbury argued. Under such conditions, he concluded, males might well be the choosy sex.

Bateman didn't actually report on the choosiness of his fruitflies, nor on any other aspect of their behaviour, notes Patricia Gowaty, an evolutionary biologist at the University of Georgia in Athens. "I think the reason Bateman's observation became 'Bateman's principle' is that it appealed to people's intuition about the behaviour of individuals," she says. "Very few people actually questioned the basic statement about the ubiquity of coy females and competitive males."

But if the layers of behavioural complexity are removed, how well does Bateman's basic theory about the relative benefits of promiscuity for the two sexes hold up? To find out, several groups are now putting Bateman's principle to more rigorous tests.

T. KITCHIN & V. HURST/NHPA

The Oregon newt is at the centre of a current study to evaluate Bateman's principle in the wild.

Species that exhibit sexual role reversal are particularly useful for this purpose. In the pipefish *Syngnathus typhle*, for example, the males carry the young, whereas the females compete with one another for mates. In 2000, researchers at the University of Georgia and at Uppsala University in Sweden showed that the relationship between the number of mates taken and the number of offspring produced, which they termed the Bateman gradient, was also reversed. Taking multiple mates was of greater value to the fertility of females than to that of males[17].

These experiments were done with captive fish. But the study's lead author, Adam Jones, who is now at Oregon State University in Corvallis, is attempting for the first time to measure Bateman's gradient in a natural setting — this time in a species with conventional male and female roles. He is gathering data from a local population of Oregon newts (*Taricha granulosa*), which conveniently breed in large aggregations so that every parent and offspring can be counted. The results are preliminary, but Jones says that so far they fit the Bateman model.

Cricket supporter

Leigh Simmons, of the University of Western Australia near Perth, meanwhile, has found empirical support for Bateman's principle in the bushcricket *Requena verticalis*. In this species, the male donates a droplet of nutrients to his mate. This is no problem when there is lots of food around. But under starvation conditions, males become reluctant to mate and females must compete for them. Simmons has shown in the laboratory that, when sexual roles are reversed in this way, the Bateman gradient is also reversed[18]. This, he argues, indicates that the basic Bateman principle is sound, despite the overlying layers of complexity. "Bateman was naively simplistic, but then it was 1948," Simmons says.

"The basic principle is right," agrees Tim Clutton-Brock, a behavioural ecologist at the University of Cambridge, UK. Females can gain from promiscuity, but the fact that they more often get left holding the baby means that males can usually take more mates in a given time period[19].

Although the principle remains valid, recent experiments have revealed intriguing complexities — even among Bateman's own experimental subjects. In 1999, researchers at University College London and Cornell University in Ithaca, New York, described proteins in fruitfly seminal fluid that increase the time that a female waits before allowing another male to copulate with her[20].

Gowaty likens the proteins to a chemical chastity belt. "Everybody assumes Bateman was about coy females and ardent males," she says. "Now here's a modern discovery that suggests maybe the reason females were holding back from mating is that they were being manipulated by a male protein."

This theory has yet to be tested. But if Gowaty is correct, Bateman's experimental observations may have had much less to do with inherent female coyness than he assumed — another example, perhaps, of the truth being obscured by nineteenth-century sexual stereotypes. ■

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