Judging Paternity in the Hedge Sparrow's World

An individual animal's behavior is expected to be shaped by the Darwinian constraint of reproductive success; DNA fingerprinting helps measure how good a fit is achieved

HEDGE SPARROWS are not the most striking of birds—small, brown, busily flitting hither and thither: they are no bird of paradise. But to Nicholas Davies, a behavioral ecologist at Cambridge University, they are just about as fascinating as a bird can be. "Their social organization is much more complicated than anyone imagined," he says. "In one small area you can find monogamy, polygyny, polyandry, and even odd combinations, where two or three males will share two, three or sometimes four females."

Davies and various colleagues have been studying these birds—which are called dunnocks—for the past half dozen years, and have begun to build up a relatively clear picture of their seemingly anarchic social dynamics. "We have begun to see how the dunnocks' behavior maps onto reproductive success," Davies told *Science*. In other words, from this apparent anarchy there emerges a pattern of biological order: the birds behave as Darwinian theory predicts they should.

"We can now see that the dunnock's behavior is rather beautifully designed," says Davies. "But we can also see that it isn't perfect. A lot of behavioral ecologists in the early days assumed that animal behavior was perfect, that animals could tune everything right. That would be expecting too much."

For one thing, dunnock fathers cannot recognize their offspring, and that is potentially hazardous in Darwinian terms, especially when cuckoldry is rife. As a result, males have to have ways of regulating their behavior so as to guard their reproductive interests. It is to this problem that Davies, in combination with Terry Burke of the University of Leicester, has addressed the relatively new technique of DNA fingerprinting (see last week's issue, page 1549).

In the business of producing offspring throughout the biological world, the interests of males and females are often different: females frequently find themselves left holding the baby—literally—and are therefore often trapped into the role of sole caretaker. In birds, where the offspring may need more food than can be supplied by one provider, paternal care—often in the form of monogamy—is quite common. In any case, a clutch always does better, in terms of weight at fledging and in ultimate survival, with more providers serving their needs.

For a female dunnock, therefore, polyandry is best, because several (usually two) males will work as providers. By contrast, a male is better off if it can mate with several females, because, even though the survivorship of the offspring may be lower than in polyandry and monogamy, the total number of offspring he sires will be enough to overcome this disadvantage.

"The complex social organization we see in dunnocks is the outcome of these different interests between males and females," explains Davies. "For instance, in a monogamous pair you often see a female trying to solicit a mating from another male, which might entice him to join in provisioning the offspring. And you see the males of monogamous pairs working furiously to prevent any such extra-pair mating." Similarly, in the cases of several males mating with and guarding the territories of several females—an arrangement known as polygynandry—the males compete with each other for mating privileges and the females squabble among themselves, trying to gain the attention of all the available males.

"In each of the dunnock's mating systems we studied, the individuals appeared to behave in ways that would maximize their reproductive success," observes Davies. "But in order to obtain a clearer picture of how behavior matched reproductive success we needed a method of determining paternity and maternity of chicks. This was what DNA fingerprinting offered us."

During the 1988 breeding season Davies and his colleagues spent about 140 hours observing the social behavior at 45 dunnock nests in the Botanical Gardens of the University of Cambridge. Fights between males for access to females, scraps between females for the attention of males, sneaky maneuvers by males seeking illicit mating—all were observed and noted, as were the fruits of it all, the offspring. Then, in order to determine which offspring belonged to which adult, blood samples were obtained and DNA fingerprinted in Burke's laboratory. The results were illuminating.

For a start, resident males—whether in monogamous, polygynous, or polyandrous groups—were highly efficient at excluding sneaky matings from outsiders. There was only one such case out of 133 young. Moreover, females seemed to have escaped the danger of having other females dump eggs in their nests, a trick known as intraspecific brood parasitism: resident females were the mother in all 133 cases. Things got interesting in polyandry and polygynandry, where paternity of the offspring among resident males might be somewhat in doubt.

"When you have two males and one female, or two males and two females, it is in the individual male's interest to know if any of the offspring in the nest are his, so he can 'decide' whether to help feed them," explains Davies. "In polyandry, the two males are always unrelated, so there is no genetic interest in one male helping feed the offspring if all are sired by the other male."

In fact, when two males share a female, one is usually older than the other, the two being known as the alpha male and the beta male, respectively. In skirmishes over access to the female, the alpha male usually wins, but his attempts are sometimes thwarted, not least because the female often escapes

Dunnocks: *Mating systems in these birds are highly variable, the outcome of a Darwinian struggle over the different reproductive interests of males and females.*

C. H. Greenewalt/VIREO

the alpha male's attention and encourages mating from the beta male.

It turns out that the degree of success a beta male has in mating with the female determines his willingness to help provision the offspring: in 80% of cases where the beta male mated with the female, it also helped provision, compared with only 9% of cases where no mating occurred. The beta males also adjust the amount of provisioning work they are prepared to give, increasing it in direct proportion to the amount of mating access they had achieved.

"The DNA fingerprinting data show that the beta males' measure of potential reproductive success is pretty accurate," says Davies. "But it is still a crude measure." It is accurate only inasmuch as most of the time a male has an offspring of his own in the nest—which Davis and his colleagues can determine with DNA fingerprinting—the male will help feed the offspring. However, the male does not discriminate between the offspring in the nest, usually feeding each of them at some point during rearing. "It is clear from this and other behavior that the males cannot recognize their offspring," concludes Davies. "They are therefore forced to use an indirect measure of paternity, one that works rather well, even though it is imperfect."

With the accurate measure of paternity provided by DNA fingerprinting, Davies and his colleagues were able to rationalize one intriguing behavioral vignette. This concerns polyandry, in which an alpha and a beta male share a female. From earlier work Davis knew that, *per nest*, polyandry had the highest reproductive success of any of the mating systems available to dunnocks, because of the greater provisioning that is available to the chicks. And yet alpha males object vigorously to the presence of the beta male, so what does this imply about the costs and benefits to all concerned?

"An alpha male would need at least 60 to 70% of the paternity in trio-fed broods for cooperative polyandry to bring greater reproductive success than monogamy," explain Davies and his colleagues. The DNA fingerprinting data show that the alpha male fails to achieve this, the mean split of paternity being 55% alpha and 45% beta. "This suggests that alpha males do not achieve the critical proportion above which it would pay them to share the female, and explains why, although females encourage the presence of males, alpha males attempt to drive them away." ■ ROGER LEWIN

ADDITIONAL READING

T. Burke *et al.*, "Parental care and mating behaviour of polyandrous dunnocks," *Nature* **338**, 249 (1989).

N. B. Davies, "Reproductive success of dunnocks in a variable mating system," *J. Anim. Ecol.* **55**, 123 (1986).

Brain Protein Yields Clues to Alzheimer's Disease

β-Amyloid, the principal protein component of Alzheimer's plaques, may be a key that will help unlock the mysteries of the degenerative brain disease

RESEARCHERS LOOKING FOR THE CAUSE of the devastating brain deterioration of Alzheimer's disease once had high hopes that they had found it in the gene encoding the protein β-amyloid, a prominent component of the abnormal plaques that stud the brains of Alzheimer's patients. By the end of 1987, however, it was clear that an amyloid gene defect was not the primary cause of Alzheimer's disease.

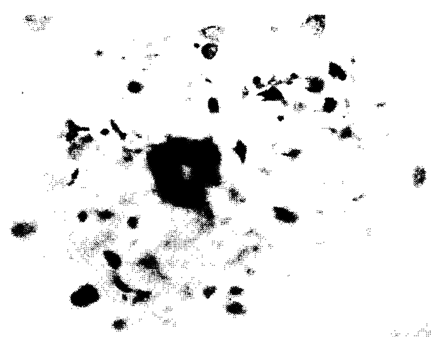
Nevertheless, the intervening year has not seen any diminution of interest in β-amyloid. Research during that time has, if anything, increased the likelihood that the protein contributes in a major way to the pathology of Alzheimer's disease, even though the abnormal deposition of β-amyloid in the brains of the patients may be secondary to some other, as yet unidentified, event. "It's getting more and more interesting all the time," says Dennis Selkoe of Harvard Medical School. "I'm getting even more convinced that it plays a role in the disease."

New evidence suggests, for example, that the protein that gives rise to the β-amyloid of Alzheimer's plaques has a normal function in the brain. This protein, called the β-amyloid precursor protein, may help to maintain nerve cell connections or survival. Anything that disrupts the precursor's ability to perform normally might therefore lead to the degeneration of brain neurons seen in Alzheimer's disease.

The current surge of research on β-amyloid began about 2 years ago with the cloning and sequencing of the gene encoding it. Although this opened the door to a molecular analysis of what goes wrong in Alzheimer's brains, the first outcome was a disappointment.

The β-amyloid gene had been mapped to chromosome 21, in or near a region that genetic studies had shown to contain a gene causing a hereditary form of Alzheimer's disease. Moreover, individuals with Down syndrome have an extra copy of chromosome 21 and therefore of the β-amyloid gene. They also begin developing plaques at an early age and often show dementia symptoms, similar to those of Alzheimer's disease, in their thirties or forties.

This suggested that Down's patients might develop the plaques because they make too much β-amyloid. Perhaps, the reasoning went, the β-amyloid gene was the "Alzheimer's gene." It might in some people have a defect that causes them to overproduce the protein, thereby leading to the plaque formation and brain degeneration of Alzheimer's disease. Researchers soon learned, however, that the β-amyloid gene could not be the Alzheimer's gene (*Science*, 4 December 1987, p. 1352).



C. Abraham, D. Selkoe, and H. Potter

Alzheimer's plaques *consist of a core of β-amyloid fibrils (dark circle) surrounded by a halo of degenerating nerve terminals and glial cells. [Reprinted with permission from* Cell *52, 487 (1987) © Cell Press]*

Nevertheless, the sequencing of the β-amyloid gene had revealed that the material found in Alzheimer's plaques is synthesized as part of a larger precursor protein, the structure of which has changed little during the course of evolution. This implies that the precursor protein has a critical function in the normal brain. "This must be a very important gene and protein in that it has been so closely conserved in evolution," notes Donald Price of Johns Hopkins University School of Medicine.

Researchers do not know exactly what the β-amyloid precursor protein does, although there are two leading possibilities. One is that it helps to establish or maintain connections between nerve cells, possibly acting as an intercellular adhesion molecule that makes direct connections between neurons. Its structure and cellular location are consis-