Hotshots, Hotspots, and Female Preference

In some species females find a mate by visiting groups of males who are awaiting their inspection; ideas about how such a system might have evolved are being questioned, with males being given a bigger role

SOME BIOLOGISTS BELIEVE "lek" to be derived from a Swedish word meaning play, while others insist its origins are in old English. In any case, the word is now used to label a rare but fascinating mating system that can be described as follows. Males gather in groups—called leks—to advertise their qualities; females visit the groups, assess what is on offer, and select a partner for copulation; the female then moves off, eventually to raise the offspring on her own; the only thing the female gets from visiting the group is a set of genes.

Although lekking is rare in terms of absolute numbers of species that engage in this mating system, it is nevertheless widespread throughout the animal and insect worlds. Lekking therefore presents a challenge: what *general* explanation might account for its establishment and operation?

For almost two decades theoretical explanations have been dominated by a single theme, that of female choice. Jack Bradbury of the University of California at San Diego has been the most influential figure in the field, offering first the "female-preference model" in a classic 1981 paper, and then later the "hotspot model." In both models the activity of males—in forming clusters and in mating success—is shaped entirely by female behavior.

Two researchers at the Smithsonian Institution, Washington, now offer an alternative, namely the hotshot model. "We agree that there is an important element of female choice involved in the system," says Mercedes Foster, "but our concern is the relative importance of female choice versus some kind of male constraint." Bruce Beehler, Foster's coauthor, says that "in our model the males are doing something among themselves, and the females are forced to react to what the males are doing."

Bradbury welcomes the hotshot model as a "reasonable alternative," but considers it incomplete, specifically concerning the factors that influence the number and dispersion of leks within a population.

In all lekking species the female must be able to raise her offspring by her own efforts: the male contributes nothing but his genes. Beyond this basic ecological constraint, however, lekking species display great variation in the form and function of the system.

"Despite this great variation in lekking systems, I still believe it is reasonable to seek a unitary explanation," says Bradbury. He acknowledges, however, that investigators tend to produce theories that are influenced by the particular systems they study. Beehler and Foster agree, and argue that Bradbury's emphasis on the importance of female preference derives in part from his early work on certain West Africa bats, in which the males do indeed appear to be rather passive players in the lekking game. By contrast, their own study animals—manakins for Foster, birds of paradise for Beehler—display in some cases a good deal of male influence.

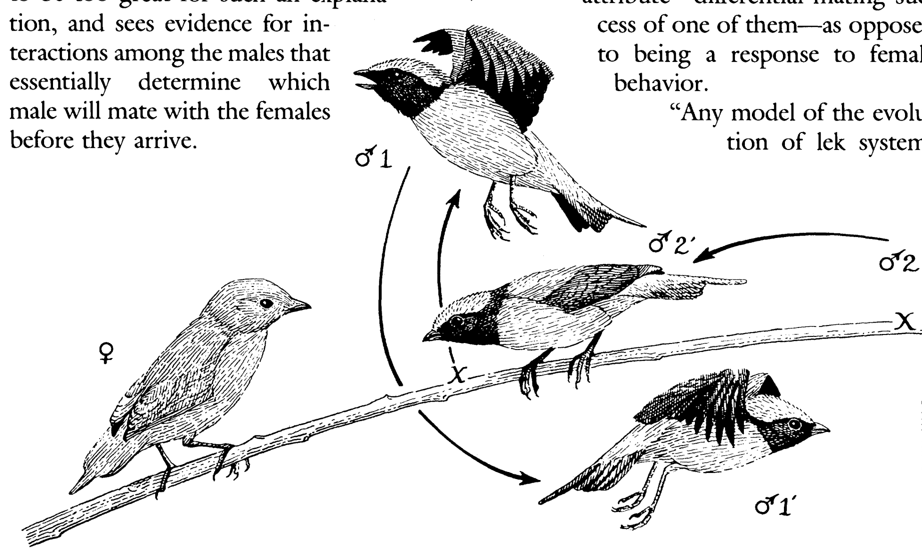
For instance, in one study on the lesser bird of paradise Beehler observed that a single male of eight in the lek performed 24 of 25 successful copulations. Now, a skew in mating success among males is typical of lekking, and traditionally Beehler's observation would be interpreted solely in terms of female preference. Beehler believes the skew to be too great for such an explanation, and sees evidence for interactions among the males that essentially determine which male will mate with the females before they arrive.

Similarly with the swallow-tailed manakin, says Foster. Here, in the absence of females, the males engage in vigorous interactions, which eventually establish a clearly accepted hierarchy. When a female arrives, the top two males display cooperatively for a while, whereupon the second male departs leaving the top male to mate with the female. So, although the female may have exercised some choice in determining which lek she will eventually bestow her favors upon, her choice within that lek is zero.

In addition to observations of this kind, Beehler and Foster cite reports of mating interference among males as evidence of a more complex explanation of lekking than is encompassed by the established models. The original female preference model essentially argued that males formed groups as a result of the benefit it bestowed on females, who thereby had a wider choice of mate available to them. The hotspot model explained the formation of male groups as a response to locations where females might be encountered in highest numbers, perhaps being favored sites for foraging or nesting. "As an alternative, we propose the *hotshot model*," say Beehler and Foster, "which emphasizes the importance of male-male interactions in the development and maintenance of leks."

The model is based on the notion that "in some species with mating systems not based on resources, certain males, because of behavioral or morphological attributes, are extremely successful at attracting mates," explain Beehler and Foster. "Other, less successful males cluster around these hotshots and, as a result, ultimately obtain more matings than they would have, had they displayed alone." In other words, the motive for males to cluster in this model is a male attribute—differential mating success of one of them—as opposed to being a response to female behavior.

"Any model of the evolution of lek systems



Swallow-tailed manakins. *When a female arrives at the lek, the more dominant males engage in various displays, such as the cartwheel jump shown here. Eventually the less dominant male retires, leaving the alpha male to enjoy the mating privilege of his position.*

should attempt to explain at least three phenomena," say Beehler and Foster: "(1) production of an initial mating skew among males in nonclustered court systems, (2) males' shift from solitary dispersion to display clusters, and (3) behavioral adjustments that give the lek its social structure."

The first of these is probably the trickiest to explain, but, say Beehler and Foster, it could derive in part simply from conservative mating habits of females. "Field evidence indicates that females are more conservative than they are choosy," they note. In other words, once a preference is established, for whatever reason, it can build upon itself: "an initially successful male acquires more and more mates with each passing year."

In the question of male clustering, less successful males may increase both their chance of copulation by associating with a more successful individual and their chance of survival through protection offered by a group. The hotshot may tolerate companions, again for reasons of survival but also perhaps because females will be more attracted to a group than to a single individual. How large a lek may be and how they might be dispersed across female territories remains more difficult to resolve.

Lastly, the structure of the lek itself will be influenced greatly by the amount of competition between males, both in establishing hierarchies and in attempts to disrupt matings: in some cases males will coexist closely, and in others will be widely spread out. Once this is established, say Beehler and Foster, "females may largely abdicate their active role in selecting a mate and follow a passive *default strategy* of mate selection, in which the males sort out dominance among themselves and the visiting female simply selects an arena and mates with the dominant male."

The impact of the hotshot model seems likely to be a shift of emphasis—in terms of accommodating male influence in leks—rather than a complete replacement of established models. It is not so much that all of the field data that Beehler and Foster adduce in their hotshot model are new, but what the Smithsonian researchers have done is bring them together in a coherent construct. "I'm glad to see the idea formalized," Bradbury told *Science*, "but I should also like to see their verbal model put on a more quantitative basis." ■ ROGER LEWIN

ADDITIONAL READING

B. M. Beehler and M. S. Foster, "Hotshots, hotspots, and female preference in the organization of lek mating systems," *Am. Nat.* **131**, 203 (1988).

J. Bradbury *et al.*, Hotspots and the evolution of leks," *Anim. Behav.* **34**, 1694 (1986).

Mapping by X-Ray Zapping

Tracking down genes can be a frustrating business, as David Cox and Richard Myers well know. Even after a gene has been assigned to a chromosome, it can still take years to find the gene itself with conventional genetic linkage mapping. The gene for Huntington's disease is a case in point. It was mapped to chromosome 4 in 1983 but still remains elusive.

Now Cox and Myers, both at the University of California at San Francisco, think they have circumvented at least part of the problem with a new mapping technique, which they announced at a recent meeting at Cold Spring Harbor Laboratory. They call it a new type of genetic mapping, but others, like Charles Cantor at Columbia University, say it is more akin to physical mapping. Whatever it is called, this hybrid genetic-physical mapping strategy promises to expedite work on both fronts.

Where conventional linkage mapping falls short, says Cox, is in determining the order of closely spaced DNA markers, the landmarks in a genetic map. Genetic maps are used to intuit the actual physical order of genes and markers on chromosomes. In linkage mapping, a gene's location is calculated by how often it is inherited along with a known marker on the chromosome. The closer the gene and the marker, the less frequently they will be separated during meiosis, when genetic recombination occurs. Once the rough location of a gene has been determined this way, the usual strategy to narrow the search is to find more markers in the vicinity, determine their order along the chromosome, and then try to locate the gene between two of them. The catch is that the closer the markers are to each other, the trickier it is to determine their relative positions.

What Cox and Myers have devised is essentially a new unit of measurement: instead of looking at how often two markers are separated during meiosis, they look at how often they are broken apart if the chromosome is zapped with x-rays. The crux of this idea was laid out some 10 years ago by Henry Harris and Steve Goss, says Cox, but "no one believed it would work." It does.

They start with a somatic cell hybrid—a hamster cell that contains a single human chromosome, say chromosome 21, in just one copy. They then zap it with enough x-rays to shatter the chromosome into pieces. Before doing anything else they must "resurrect" the cell, which has been so heavily irradiated that it is essentially dead. They do so by fusing it with another hamster cell. They end up with about 100 hybrid clones, each containing different pieces of chromosome 21. Then they look at these cells to see how often various sets of markers have broken apart. For any two markers, say markers A and B, some cells will contain just A, some just B, some both, and some neither. (That a cell contains both or neither is not illuminating in itself, since the two could have been retained or lost together or separately.)

To compute the genetic distance, Cox and Myers have devised a mathematical algorithm that can reconstruct how often A and B were broken apart according to how many cells contain A only, B only, both, or neither. This process is then repeated for all pairs of markers to determine their order and thus construct a genetic map.

Cox and Myers have now tried the technique on two chromosomes: on 21, where they are looking for the putative Alzheimer's gene; and on 4, where they are looking for the Huntington's gene. Using pulsed field gel electrophoresis, they have confirmed that the order predicted by this genetic map is indeed the order in which the markers appear in the physical world.

What's more, says Cox, if a high dose of radiation is used, this approach can offer 20-fold greater resolution than conventional linkage mapping. Resolution simply depends on the number of breakpoints in the chromosome. By zapping a chromosome with 7000 rads, breaks occur roughly every 50 kilobases, as compared with the 1-million-base resolution offered by linkage mapping. With a genetic map of this resolution, say Cox and others, it should be relatively easy to construct a physical map, which in turn makes it possible to clone the DNA between flanking markers and pull out the desired gene.

Cox cautions, however, that the genetic distance in this map will not necessarily mirror physical distance. Just as there are "hotspots" of recombination on chromosomes where the genetic distance far exceeds the physical distance, there will likely be certain regions that are more susceptible than others to breakage by x-rays.

■ LESLIE ROBERTS