RDA: Original, 1977; updated 12 Nov 1990

How Leks Work

Leks are aggregations (compact or "exploded") within which many, most, or all matings of a species occur, and within which females are able to compare a few, several, or a great many males. If the males' success within the lek is based on their ability to defend a resource valuable to the female, as for example nesting sites, entrances to hibernacula or roosts, or food, the lek can be described as "resource-based." More traditionally, the term has been associated with sites where nothing of value to the female is available but the sperm of males. These have been called "non-resource-based" leks (Alexander, 1975), and there are at least three major problems in modeling their probable evolutionary background: (1) why did mating come to be concentrated away from resources? (why did males abandon efforts at control of resources?); (2) what determines how non-resource-based leks work (that is, their location and their forms); and (3) why do females seem to be even more selective in leks than in species in which males give resources to the female or to the offspring (Borgia, 1979; Taylor and WIlliams, 1982). This last question has seemed especially acute to biologists because evidently the only benefit is females is better genes for their offspring, and directional selection at leks would surely reduce the relevant genetic variation to a point where female choice would seem a triviality.

On the second and third questions I propose the following hypotheses: Once males are providing nothing but sperm for females, however this comes about, it is in the female's interest to be able most completely and inexpensively to evaluate the male as a provider of sperm that will yield viable, healthy, reproductively effective offspring of both sexes, and, especially, male offspring that will be successful in mating. Reynolds and Gross (1990) have pointed out that the female may also be deriving benefits more directly: for example, the female who chooses a healthy male may not only be providing a pathogen-resistant genotype to her offspring but as well reducing the likelihood that she will become infected.

A male's potential in these regards may be assessable by his phenotype, leading males to be favored for strutting, displaying, or exhibiting themselves most effectively to allow the female to make the least expensive and most effective evaluation. This display will usually, at least, involve improving the female's ability to compare males directly with one another, and so males are likely to be forced to group. Additionally, when the kind of display and terrain fit the proposition, males will be favored for locating and using features of topography or other aspects of environment to increase the effectiveness of their display (that is, to make it more effective and less expensive to the female, thus causing her to favor the male on this account). Most often male groupng and use of terrain will go together, but either could operate alone if the other was for some reason irrelevant. When both factors operate, and aspects of the terrain (or the enivironment otherwise) are of graded quality so that only one or a few locations are best, the males will have been selected to locate and contest for these best locations for the reasons that they represent the least expense and greatest benefit to the females. As Reynolds and Gross (1990) point out, the more males females can compare, and the more inexpensively they can carry out the comparison, the greater the net value of choosing at a lek as opposed to mating with the first available male. Thus, even if males usually have only minor heritable differences of significance to the females, the female still has no better option than to take the best available male, using his phenotype for the evaluation (because every now and then she will happen to choose on the basis of a heritable difference), and she should be expected to do this choosing where she can compare the greatest number of males with the least expense.

If, say, in a lekking bird, spots of bare soil in a prairies are favored because males can show off better, the hypothesis predicts that groups will develop at the few best such sites. Larger sites or convex ones should be favored over smaller, flatter ones. Within such sites males should contest for the center of flat sites and the highest point of convex ones. If a spot has been used

before by animals active as individuals on successive years it acquires value on that account because the crucial variable is cost and benefit to the female by judging phenotypes of males.

I believe that a model of this sort is all that is needed to explain the existence and structure or leks. This is approximately what Reynolds and Gross (1990) meant by saying that the paradox of the lek is thereby resolved.

In the kind of directional selection here posited, essentially all traits of males that are being favored will improve the quality of female as well as male offspring. These traits include:

1. Ability to locate and identify inexpensively the best display sites (females must locate and identify them too).

2. Ability to recognize the best locations within sites (for females, thus to identify least expensively the males that acquire and hold them).

3. Ability to exclude other males from the best locations (thus, in the female's terms, vigor, ability to secure and store food and to grow to strength).

4. Even bright color, flashy plumage, strutting behavior, and tendencies to form ever-larger groups, because these features lower the expense to the female of mate selection and magnify benefits: females literally gain by males evolving to tell them more and more quickly and effectively what their phenotypes are like, and males are stuck with allowing themselves to be compared at the leks, and therefore doing the things that enable female to make comparisons less expensively.

This particular way of accounting for leks has not been proposed, although most of its component parts have (some have been proposed since this essay was originally written: Reynolds and Gross, 1990). It alone, I think, can account for the leks of honeybees, located in the same places year after year despite lack of continuity between years among participants (honeybees don't survive from year to year). One only has to suppose that there are relatively few best display sites for honeybees, and honeybees are exceptionally good at locating them (queens as well as drones). The scheme presented here indicates that cumulative selective effects could cause that to be the case. (The female honeybee "compares" males by requiring that they fly after her in a strenuous mating flight in which only a minute fraction of the males succeed in inseminating her.)

Similarly the leks of cicadas (e.g., *Magicicada*) might be explained as situations in which the numbers of individuals involved, and the kind of display situation, combine to yield not one or two best sites within the lek but hundreds or thousands of closely clustered sites that do not vary significantly. The suggestion is, then, that for cicadas (or synchronizing fireflies), tree represent such sets of closely clustered sites, and some trees are better than others. Of course the signals of the males (in both fireflies and cicadas) enhance the sites as appropriate locations for choosing males). It is possible for these short-lived insects that the presence of large numbers of males is so important that it may sometimes be arbitrary which actual tree or trees come to contain the largest leks. In some cicadas, fungus infections may provide an important component of female choice, both for resistant genotypes and to avoid infection (Alexander et al, ms.).

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