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Report from the London Zoo

A joint meeting of the Primate Society of Great Britain and the Association for the Study of Animal Behaviour, held at the London Zoo in December, 1992, was entitled "The Ecology of Social Systems" and contained many examples of alternative strategies, both for reproduction and for predator avoidance. A number of the talks concerned species which adopt a lek system of mating, which is widespread among birds (especially grouse), fish (especially cichlids [pronounced siklids]) and mammals (especially ungulates, and also the hammer-headed bat). A lek is "a communal area in which two or more males of a species perform courtship displays" (Encyclopedia Britannica). The area is "traditional" in that the same area is used year after year, and it may or may not be divided into small territories which are defended by individual males and are used only for mating; they contain no resources such as food or shelter; the females approach the lek as they come into oestrus, inspect a variable proportion of the males and/or territories, choose usually just one for mating, and leave shortly after mating has taken place. The lek system seems to evolve when food is widely dispersed and it is not possible for males to defend a territory in which one or more females can raise their young.

Papers about leks

Tim Clutton-Brock of Cambridge (see 1) gave a talk on "The evolution of mammalian leks" and described his work with the Uganda kob. Much interest attaches to whether the females choose between the males or between the territories. The female kobs are not more attracted to males with horns than to hornless stags, or even to males at all, but seem to be attracted to particular territories, especially those that are central in the lek. They much prefer a territory which already contains oestrus females. Additional work (heavy work) by Tony Deutch from East Anglia University showed that the topsoil of the territory is attractive, as moving the topsoil from the most popular territory to another site in the lek transformed the new site into a popular territory. Since the lek uses the same place year after year it is likely that some territories become heavily impregnated with urinary pheromones, so that popular territories become more and more popular as years go by.

Andrew Rossiter from Guelph University in Canada described the reproductive behaviour of cichlid fishes in Lake Tanganyika. The males form a lek and each male who has won a territory in the lek builds and then defends a nest composed of gravel and sand. The males weigh about 100 grams, and the nest materials weigh up to 10 kg, so the nest represents a big investment in resources for the owner (the nest may, of course, be built by several successive owners). Several territory-owners maintained their territories for the full seven months of the study period; each could expect to be visited by about twenty females per day.

The females live in a shoal near the lek, and when each comes into reproductive condition she approaches the lek and enters one of the territories. After a courtship dance, the female hovers over the nest and lays her eggs, the male at this time hovering a few feet above the female. When the eggs have been laid, the female sucks them into her mouth, and the male and female then change places. The male ejects his sperm in the place where the female laid her eggs, and then the two change places again. The female then takes the sperm into her mouth, where it fertilises the eggs, and she then swims back to the shoal, continuing to brood the eggs in her mouth.

If a male is removed from his territory, he is replaced by a "floater" or non-territorial male who has been hovering about the lek. Rossiter recognises two types of floaters. Type 1 floaters are local fish who have spent a long time around the lek and know the borders of all the territories. This is evident from the fact that when they take over a territory they spend very little time in border disputes with their neighbours, unlike the type 2 floaters who swim in from other leks and spend so much time learning the boundaries of their new territory in border disputes that their mating performance is severely curtailed. This is the first demonstration that floaters are using their time constructively in learning the geography of the lek rather than just hanging about waiting for "dead men's shoes."

In addition to the territorial males and the two types of floater, there are three other types of male, performing alternative reproductive strategies, and all of whom are morphologically distinct.

There are "sneakers" who dash into the territory as the male and female are changing places after the male has ejected his sperm and before the female has taken it into her mouth. He ejects his own sperm in large quantities over the relatively small amount of territory-holder's sperm, and then dashes off again. These sneakers are recognised by their high gonad/soma index, as the enormous amounts of testicular tissue give them a round

shape: they are specialised just for dashing in and ejecting sperm, and they do not have to deploy the musculoskeletal resources needed for nest-building and territorial defence.

Then there are "pirates" who take over a nest by force for a few days, ejecting the territory owner who may either hang around the lek or swim off elsewhere. The pirates are large, outside the range of variation of the other males.

Finally there are the female mimics, who fool not only the territorial males but also the human observers. Their strategy is to impersonate the female form, and to shadow a female as she enters a territory; in this way they are tolerated by the territorial male, and, intervening during the second exchange of places by the courting couple, they consume the sperm of the territorial male and replace it with their own.

Comment about leks

Although fish are a long way from man in phylogenetic terms, Andrew Rossiter's analysis of male reproductive strategies in this cichlid illustrates the whole concept of alternative strategies in a way that might be impossible from mammalian behaviour. The cause of the variation into four separate morphological forms is not known, but must be either genetic or dependent on environmental factors during development. They are true alternative strategies, in that only one is possible for any individual at any one time, and an intermediate strategy would almost certainly result in lower payoff than any of the four strategies described. The choice between territory owner and floater is made during negotiation with other males (ritual agonistic behaviour), while that between floater 1 and floater 2 is not known. The two floaters are alternative strategies in that it seems unlikely that one male fish could keep the geography of two separate leks in mind, so the advantage of knowing one lek well balances the advantage of keeping many leks under surveillance. The two floater strategies are examples of alternative losing strategies (see ASCAP Vol 3, No 2, February 1990, pp. 7-10). In terms of the psychopathology of the lek, we could say that the type 1 floater is manifesting an in-group omega psalic, whereas the type 2 floater is manifesting an out-group omega psalic.

Although leks do not occur in man, it is instructive to consider what is our nearest equivalent. The village hop is an aggregation of nubile creatures in which mate choice is made, but there are many differences from a lek: the sex roles are less differentiated, mating does not usually occur, and there is an expectation of continued association of couples after the event. Perhaps the nearest equivalent, if we reverse the roles of the sexes, is the brothel or red light district. Here a group of potential sexual partners aggregate and display to visiting members of the opposite sex, who then choose a partner, mate, and leave without any expectation that the mating has implications for parental care; we could even say that the red light districts in which the women display themselves in the windows of their properties are equivalent to those leks in which territories are defended, whereas the brothel is equivalent to a lek in which the whole arena is common to all participants. Clearly any similarity between the lek and the brothel is due to convergent evolution. Nevertheless, squeezing the last juice of our across species comparison, can we learn anything about leks by using the brothel as a referential model in the sense of Tooby and DeVore (2); or anything about brothels by using the lek as a model? I think the answer must be no, even if we increase the similarity by considering the pimp/prostitute subsystem rather than the females on their own, and thus allow fighting for territory into the brothel scene. I think the reason the model is so lacking in heuristic value is the fact that, in spite of a formal similarity in organisation, the engine driving the two systems is different. The fuel of the engines is the thing of value transferred during the lek/brothel transaction. In the lek this is sperm, and it is of value because its reception by the female gives Darwinian fitness to the male. In the brothel, although sperm is transferred (or used to be before the introduction of safe sex) the sperm is of no value, and its transfer is incidental to the transaction, whereas the real driving force is the transfer of money. I suggest that the conceptual difference between money and sperm is the factor which renders an apparently promising referential model useless.

Papers not about leks

Alan Dixson (see 3) from Franceville reported on social asymmetry in a group of mandrills, living in a closed off area of forest in West Africa. (The mandrill is the largest monkey, and the males at 50 kg are three times the weight of the females). Of the six males, three consorted closely with the females, and these were fat, with large testes, bright red noses, and high serum testosterone; they had a clear rank order and most of the matings were performed by the highest ranking animal; DNA fingerprinting showed that the third ranking male sired no offspring at all. The other three adult males adopted a peripheral position in the group, were markedly thin and "out of condition", had small testes, dull red noses and low serum testosterone. During the study period the role of the alpha male was usurped by the former no 2, whereupon the former alpha became peripheral, lost

"condition" and finally became solitary. These observations are yet more evidence for the profound effect of ranking stress on both physiology and behaviour.

There is no space to describe the paper by John H. Crook on fraternal polyandry in Tibetan Buddhist villages (see 4), but his book "Tibetan Buddhist Villages" is shortly to be published in Delhi.

1. Clutton-Brock, T.H. (1989) Mammalian mating systems. Proceedings of the Royal Society of London B, 236, 339-372.

2. Tooby, J. & DeVore, I. (1987) The reconstruction of hominid behavioral evolution through strategic modelling. In The Evolution of Primate Behavior: Primate Models. Albany: State University of New York Press.

3. Dixson, A.F. (1987) Observations on the evolution of the genitalia and copulatory behaviour in male primates. Journal of Zoology, 213, 423-443.