HOTSHOTS, HOTSPOTS, AND FEMALE PREFERENCE IN THE ORGANIZATION OF LEK MATING SYSTEMS

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Edward Selous, perhaps the first field student of Darwinian sexual selection, used the term "lek" to characterize the polygynous arena mating system exhibited by two European game birds, the ruff (*Philomachus pugnax*; Selous 1906–1907) and the black grouse (*Tetrao tetrix*; Selous 1909–1910). In this mating system, promiscuous males cluster at a mating site and are visited by females for copulation. Because competition for mates is among the most intense in the animal world, biologists value the lek system for studying the components of sexual selection.

In the first of two thought-provoking theoretical papers, Bradbury (1981) developed a socioecological model of lek evolution in which male clustering is promoted by the dominant effect of female choice (the "female-preference model"). Subsequently, Bradbury and Gibson (1983) critically reexamined the female-preference model and offered an alternative, the "hotspot model," in which male clustering is produced by sequential settlement of males onto sites or pathways preferentially used by females. At present, the two above-named hypotheses dominate the theoretical perception of lek systems.

Using field data collected from a variety of natural systems (e.g., Brosset 1982; Beehler 1983a,b, 1987; Foster 1983; Rhijn 1983; Avery 1984; Merton et al. 1984; Trail 1984, 1985a,b; Pruett-Jones 1985), we critically examine currently accepted generalizations about lek mating systems. We offer the "hotshot model" as an alternative hypothesis explaining the development of lek systems. In brief, our model is driven by (1) an increasing inequality in male mating success, which is produced by a combination of male-male dominance interactions plus conservative or "default" mate choice by females, and (2) the resulting association of novice and subdominant males with successful court holders. We call the model "hotshot" to highlight the importance of male social dominance and to downplay the relative importance of female mate choice based on male phenotype (contra Bradbury et al. 1985).

In the following treatment, we consider leks to be only those court-based

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systems in which displaying males are clustered in space (Bradbury 1981). All non-clustered site-based systems are treated as non-lek "court" systems (see Beehler and Pruett-Jones 1983).

<div style="text-align:center">DEVELOPMENT OF LEK BEHAVIOR</div>

We begin our analysis with an appraisal of the two most widely accepted current hypotheses explaining lek behavior. Bradbury (1981, pp. 140–144) has provided detailed critiques of earlier hypotheses related to (1) predator avoidance (Koivisto 1965; Hjorth 1970; Wiley 1974), (2) increased stimulus to females (Alexander 1975), (3) ability of males in groups to signal to more females (D. Snow 1962; Hjorth 1970), (4) social dispersion (Hjorth 1970; Wiley 1974), and (5) population density (B. Snow 1973). (Additional critical reviews of these ancillary hypotheses can be found in Oring 1982; Bradbury and Gibson 1983.)

Models and Predictions

Female-preference model.—In this model Bradbury (1981) assumed that individual males gain no intrinsic advantage from spatial clustering, but that clustered males are favored by females for mating. The presumed advantage to females is that clustered males facilitate efficient phenotypic comparison of potential mates, thereby promoting rapid mating (see Alexander 1975). Bradbury argued that females should prefer the largest clusters within their home ranges. Unanimity of female choice of favorite leks would produce a dispersion in which the distance between the "active space" of adjacent leks should approximate the diameter of one female home range, and most females should visit only a single arena (the largest) before mating.

Bradbury hypothesized that the costs of clustering to males would be overcome only when the benefits in terms of mating success were high; this is possible when each lek has the potential of being visited by many females. He suggested that this would occur when females have large home ranges with high overlap. Bradbury (1981) further supposed that foraging demands promote the enlarged ranges of females, and thus that foraging ecology is a critical determinant of lek behavior.

The hotspot model.—In this model lek formation is the product of attempts by individual males to place their display courts at sites where females can be encountered in the highest numbers (see Lill 1976; Emlen and Oring 1977; Payne and Payne 1977; Bradbury and Gibson 1983). Males aggregate at "hotspots" independently, taking cues from female ranging habits or some characteristic of the habitat (e.g., presence of a food source or nesting site). Initial males presumably settle at the best sites, and to avoid sharing females, successive males settle at sites separated from other males by a distance greater than one female home range. Eventually, newly arriving males are forced either to share hotspots already occupied by other males or to settle solitarily at sites where access to females is reduced, but exclusive. Novel predictions of the hotspot model are that males tend to settle into leks separated by a distance less than the diameter of one

female home range and that females visit more than one lek before mating. Both models include the notion of unconstrained female choice.

Evaluating the Models

Both the hotspot and female-preference models contain compelling elements, but we find them inadequate to explain much of the variation recorded in lek systems. In addition, some predictions derived from the models are insufficiently differentiated to allow one to distinguish between them, inaccessible to empirical tests, or contradicted by currently available field data.

Exclusivity of predictions.—Bradbury and Gibson (1983) suggested that by comparing inter-arena spacing with size of female home ranges and by determining the number of arenas a female visits before mating and the degree of unanimity of female choice, one should be able to distinguish between the hotspot and female-preference models. We find that the possible alternatives are not always mutually exclusive. For example, unanimous female preferences for arenas and/or specific males should result in arenas spaced at intervals of approximately the diameter of one female home range, and females should visit only one arena before mating, regardless of whether the arenas originally formed in response to female preference or to hotspots. Bradbury and Gibson (1983, p. 116) noted that unanimity of female choice could occur under either of their models. However, if females do not choose between arenas on the basis of size, if size factors may be overridden by disparities in male quality in different arenas, or if female choice is not unanimous, then arenas will be separated by a distance smaller than the diameter of one female home range no matter what factor initially promoted male clustering.

Defining a home range.—Equally troublesome for testing both models is the difficulty of defining a "female home range." A female's range may vary considerably with the season, depending on the distribution of available food resources, the stage in the breeding cycle, and the distribution of potential mates. For at least two species of birds that display on courts, data indicate that females travel some distance outside their normal ranges in order to visit males on their courts (e.g., buff-tailed sicklebill [*Epimachus albertisi*] and band-tailed manakin [*Pipra fasciicauda*]; Beehler 1987; Foster, unpubl. data). Thus, a female could occupy a circumscribed foraging range and yet travel far off this range to mate with a favored male, a foray that may represent only a few hours (or fewer) in an entire breeding season. Does one include these travels in determining a range? Does this suggest that the females of some species may not have well-defined home ranges outside of the period when they are tied to a fixed breeding site?

The implication of the last observation is that females know the locations of the arenas that they visit. This is not surprising, at least for frugivorous lekking birds. These species spend little time searching for food but fly directly to fruit trees used over successive years, whose locations apparently are known (Foster 1977b; Beehler 1983a, 1985). If arenas are traditional, as is true for many species, then one would expect a female to know the locations of all the arenas in her vicinity.

Both juvenal and non-reproductive adult females of certain lekking species do visit arenas when males are active (Beehler 1983b; Foster, unpubl. data).

Another relevant factor with regard to female home range is the length of the display period. In many lekking species, the breeding season is long, and males cluster and display for weeks or months. In other lekking forms (e.g., some amphibians and some insects) breeding periods are short or intermittent, and males may be present in an arena for only a few days or nights when conditions for mating or oviposition are particularly favorable. This limits the opportunity for a female to contact arenas when wandering through her normal foraging range and thus diminishes the importance of female home-range size. It also underscores the potential importance of traditional placement of arenas to long-lived species in which females can learn their locations.

Defining hotspots.—Recognizing a hotspot may be even more troublesome than defining a home range. We are hostage to the questions of precedence: do arenas form at hotspots, or do hotspots form in arenas? The hotspot model predicts that males cluster preferentially at sites where they may contact the highest number of females. Although this is logical to the point of truism, it is virtually untestable. Even if one could show a statistically significant correlation between sites of leks and areas where many females are active, it would be impossible to prove that female ranging influenced lek sites, and not the reverse. One tenet of the hotspot model is that females visit more than one lek before mating. How can one control for the repeated movements of females to leks, which are determined by *male* presence, in order to prove female preference for these sites in the absence of the males?

Except in rare instances, the occurrence of traditional lek sites, used year after year, contradicts the concept of female-defined hotspots. Given the dynamic nature of most habitats and their resources, if males were actively cuing on female hotspots, one would expect lekking groups to move periodically. The examples cited above of a female leaving her normal home range to visit a male on a distant court weighs heavily against the importance of hotspots at least for the cited species.

Female preference.—Bradbury (1981) argued that males cluster because of female preference for such groups. Although it is a logically appealing notion, to date, no field data support the idea (see Lill 1976; Oring 1982; Pruett-Jones 1985). Another of the benefits postulated to accrue to females that mate in leks is the opportunity for rapid and efficient comparison of potential mates. This seems unimportant, at least for tropical birds, in which females visit leks repeatedly, often when they are not breeding (Beehler 1983b; Pruett-Jones 1985; Foster, unpubl. data). At least some females mate with the same male both within and between years, in effect remaining monogamous (Lill 1976; Pruett-Jones 1985; Trail 1985a). This suggests that females recognize individual males. Note that recognition of individual males is not equivalent to female acuity in gauging male phenotype, an important distinction discussed below.

The female-preference model suggests that male clustering imposes no cost on females. In contrast, we anticipate that females may suffer substantially more

disruptions of mating and that freedom of choice may be reduced considerably because of both disruption and male dominance relationships (see Foster 1981, 1983; Trail 1985a). This may compromise the female-preference model's main explanation for male clustering (i.e., female preference for clusters). Males in clusters may experience similar costs from disruption (Foster 1983), but costs assigned to clustered males from foraging conflicts seem trivial. Arena members of at least some species forage together without conflict (Beehler 1983a, 1985).

Freedom of female choice.—Perhaps the most troublesome aspect of the models of Bradbury (1981) and Bradbury and Gibson (1983) is the emphasis placed on female choice. Both models assume that males are unable to control or influence mating by females. In the female-preference model, the pressure of female choice supposedly creates male clusters. In computer simulations used to test the hotspot model, strict female choice made in the absence of male influence is assumed (see Bradbury et al. 1985). We doubt the generality of either assumption. In some systems, such as that of the cooperatively displaying swallow-tailed manakin (*Chiroxiphia caudata*; see Foster 1981), the control of subordinate males by dominants is nearly complete, and at least within the lek, the female has no freedom of choice. In fact, in all well-studied lek systems, male disruption of courtship or copulation is common (for summary, see Trail 1985a). Even in leks with apparent free choice for females (e.g., Beehler 1983b), a component of male dominance and control exists, as evidenced by seasonal dominance battles (see Trost 1983) and the refusal of a subordinate male within the lek to copulate with a soliciting female (Beehler 1983b).

In the lesser bird of paradise (*Paradisaea minor*), a single male (of eight) performed 24 of 25 copulations (Beehler 1983b). Similar examples of extreme domination of copulations exist for some arthropod leks (e.g., Bateman 1948). Such a skew has been attributed to unanimity of female choice. This, however, creates the paradox that Bradbury et al. (1985) highlighted in a recent paper. They asked how female preference could be so unanimous in lek systems in which the adult males, to the human eye, show remarkably little individual variation in plumage and display behavior. The authors emphasized acuity of female discrimination, but with their computer simulations were unable to duplicate many of the known degrees of extreme mating bias observed in the field. We believe that two of the basic assumptions of Bradbury et al. (1985) are probably false: (1) that "the major determinant of the distribution of matings among males is female choice" (p. 301), and (2) that "male interference did not bias mate choice" (p. 302). In fact, if male-male interactions influence female mating patterns, then the "paradox" of unanimity of female choice is an illusion.

In the sage grouse (*Centrocercus urophasianus*), Gibson and Bradbury (1985) found statistically significant correlations between male mating success and regularity of lek attendance, display rate, and an acoustic component of display vocalization. Note that these three traits are behavioral, not morphological. Because the histories of the males studied were unknown, Gibson and Bradbury could not dismiss the possibility that these behaviors, in fact, intercorrelate with male age, history of dominance in the lek, and/or past mating success. The

behavioral attributes could be a product of past (and present) success in male-male interactions rather than evidence of female discrimination. Likewise, time spent in a lek is unrelated to female acuity.

THE HOTSHOT MODEL

The preceding two models explain the clustering of males in a lek through preferential female choice of clustered males (female preference) or male settlement patterns dependent on female movements or use of space (hotspot). The models presume that mating skew and intra- and inter-lek organization reflect female preferences and female mate choice. Although we agree that female choice is exerted at some level in all species, we believe that its significance has been overstated. As an alternative, we propose the *hotshot model* (fig. 1), which emphasizes the importance of male-male interactions in the development and maintenance of leks. The model suggests 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. Other, less successful males cluster around these hotshots and, as a result, ultimately obtain more matings than they would have had they displayed alone.

We believe that a combination of four factors, (1) male competition for dominance, (2) an initial inequality of mating success among males, (3) simple and conservative female mating patterns, and (4) secondary male reproductive strategies, can produce the spatial, demographic, and behavioral shifts necessary for the development of a lek system. In this case, a *hotshot* is one of the behaviorally dominant, court-holding males that receives a disproportionate percentage of the available copulations.

Starting with a dispersed, court-based system, we outline the details of the selective forces we believe promote the male clustering observed in some species.

1. *Mating inequality.*—Ultimately, males cluster into leks because of the "magnetic" effect of mating skew. Less successful males associate with a hotshot because the association leads to successful mating. The practice of most females tending to mate with but a few hotshot males develops in five stages. The initial skew is produced in a dispersed-male setting, in which only a percentage of the available males in a given segment of habitat, through intrasexual physical and psychological aggression, obtain and hold display courts. This is comparable to territory holders and floaters in monogamous systems. A secondary heightening of intermale mating inequality results when some court-holding males are chosen by several females, whereas others receive no copulations as a result of chance, male location in the habitat, or female choice based on male age, behavior, and/or phenotype. A third increase in skew occurs when numbers of the "unsuccessful" males on courts abandon their courts and defer active attempts to acquire mates (immediate costs exceed benefits). A fourth factor is the adoption of simple and conservative mating tactics by females (e.g., "copying"). The fifth cause for heightened skew occurs when a hotshot begins attracting attendant males. At this point, physical aggression, disruption of mating, and direct dominance further reduce attempts by subordinate males to mate and reduce female selection of

|—— FEMALES ——| |———————————— MALES ————————|

(Immediate Breeding)   (Breeding)   (Non-breeding)
(Access to Many ♂♂)

MATE
COMPETITION

♂♂ Compete
for Dominance   Competition
Intense

Winning ♂♂   Young ♂♂ Delay
Establish Courts   Participation

Initial ♀♀ Choose
Mates at Random   Delayed Breeding
                                                        (+ or - Delayed
♂♂ that Mate   Plumage Maturation)
Maintain their Courts

Successful ♀♀ Mate
with Previous Partners
                                       Losing ♂♂
Reduced Number of
Court-holding ♂♂

Novice & Inexperienced   FLOATERS
♀♀ Imitate Mothers   (Cycle Repeated)
or Successful ♀♀   N   times

                                       Some ♂♂ Join
HOTSHOT   a Hotshot
MALES

♀ Choice   LEK   FORMATION
Restricted

(Within-Lek Behavioral)
Adjustments
                                                        Some ♂♂
                                                        Desert Lek
SUBORDINATES   HOTSHOTS

Disruption   Social Dominance
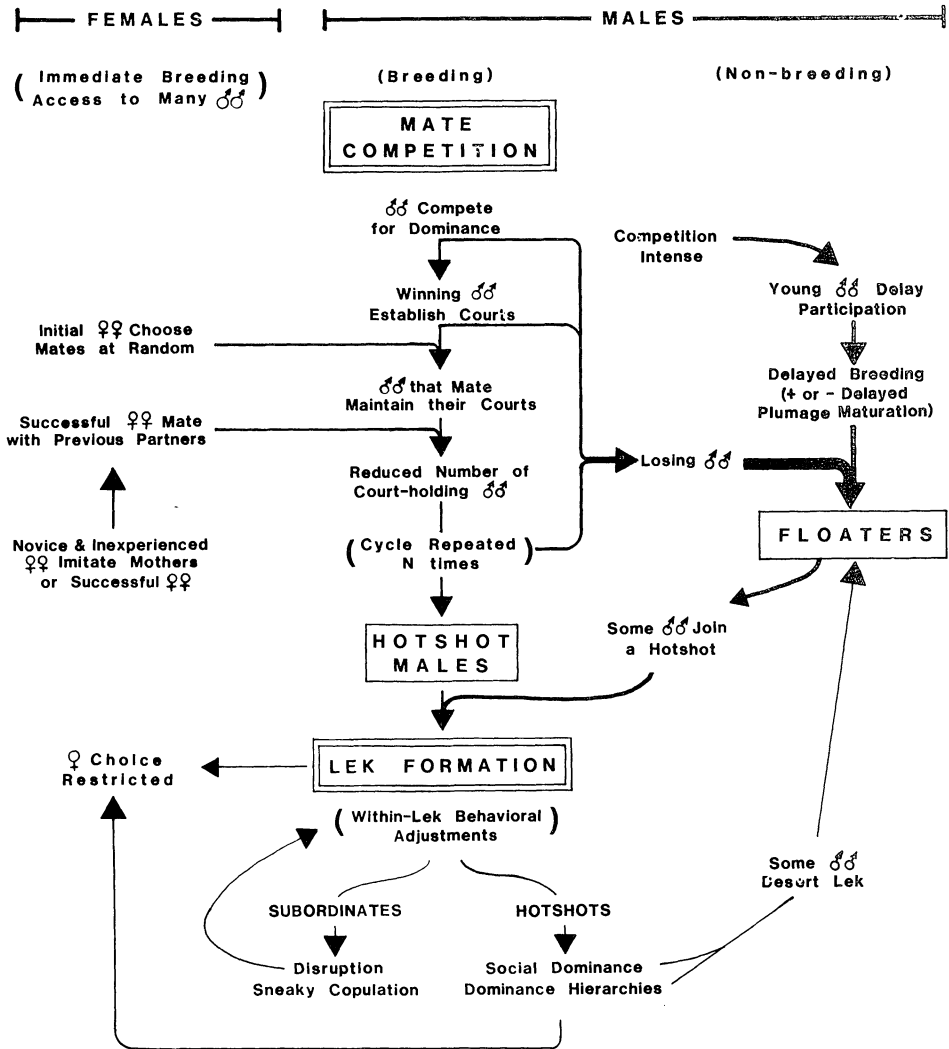Sneaky Copulation   Dominance Hierarchies

FIG. 1.—A graphical representation of the hotshot model of lek organization. The thickness of the flow lines denotes the relative importance of the interaction.

males other than hotshots. All of these combine to produce a population with a small proportion of successful males.

2. *Social dominance*.—Hotshots gain and maintain their positions by an often very subtle dominance: intermittent physical and continuous psychological control over subordinate males within the population.

3. *A large pool of available females*.—The mating inequality that characterizes hotshots can occur only when females are wide-ranging and/or show high overlap of home ranges (see Bradbury 1981). Only when a large pool of females is available at a mating site is the potential for high mating inequality achievable.

4. *Simple female mating rules*.—Depending on the system in question, a varying combination of strongly conservative mating habits of females and/or a default strategy of mate selection by females will contribute to the mating skew. We explain these fully below.

5. *Delayed reproduction in males*.—The presence of a strong mating skew forces males recruited to a population to develop a long-term mating strategy. Some or many individuals may temporarily forgo participating in mate competition (becoming floaters instead) and only subsequently (or intermittently) assume a competitive role in association with a hotshot. These strategies reinforce the mating skew and reduce the number of males available as mating partners for females.

THE MODEL'S EXPLANATION OF LEK PHENOMENA

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

Mating Inequality: Hotshots among Dispersed Males

Females of monogamous, territorial species use criteria associated with quality of a male's territory in choosing a mate (e.g., Wittenberger 1980; Proctor-Gray and Holmes 1981). These criteria, coupled with the steadily decreasing pool of unmated males from which successive females may choose a mate, form a basis for the polygyny-threshold model (Orians 1969). If a mating attempt is successful, females generally remain with a mate through the season and often in subsequent years (Oring 1982). In most species with solitary-court and lek mating systems, the criteria that females use to choose a mating partner remain enigmatic (but see Borgia 1985*a*; Borgia and Gore 1986). Nonetheless, data indicate that mating skew among males in both systems is extremely high (Payne 1984).

We suggest that female mate selection in dispersed court systems may be influenced by two factors: cues to male dominance (see Payne and Payne 1977; Borgia 1985*b*) and conservative mating. Although males do not defend territories in the usual sense, they do occupy areas over which they exert dominance. We do not mean that males exclude rivals from the area or prevent them from foraging there, but they do prevent rivals from establishing courtship sites. Neighboring male bowerbirds systematically attempt to destroy their rivals' bowers (Pruett-Jones and Pruett-Jones 1982; Borgia 1985*b*). In the magnificent bird of paradise (*Cicinnurus magnificus*), a nonterritorial species in which each male displays on a solitary terrestrial court (Beehler and Pruett-Jones 1983), three males occupied display courts on a 20-ha study plot. Mist-netting data showed that at least 9 adult and 14 female-plumaged males, as well as 23 females, used this plot (sex ratio 23:23 = 1). Even if each of the three court-holding males received an equal number of matings in a single year, the "hidden" mating skew would be considerable, under the reasonable assumption that the 20 males not holding courts either failed to mate or only rarely did so. Presumably, the court-holding males suppress breeding in the other males by some sort of intermittent dominance interaction.

Another example of such behavioral control is the failure of a subordinate swallow-tailed manakin to assume immediately the role of a dominant when the dominant was removed from an arena; rather, for several days subordinates maintained their places, behaving as if the dominant male were still present (Foster 1981). Adult floaters in all species are also indicative of the inability of many males in a population to establish suitable court sites.

Although a female does not receive any direct benefit, in terms of resources, as a result of male dominance in an arena, she still may be able to use the quality of the area that a male occupies as an indication of his quality. Because males are tied to a court and must feed in its vicinity, they may compete for the best foraging areas as well as for the best sites for contacting females. Females could preferentially mate with the males most successful in these respects, although we have no indication from empirical studies that this is so (see Payne and Payne 1977). It is plausible that females nest near the male with whom they mate and benefit from the relative richness of the habitat near the display site.

We prefer this alternative to the model in which females supposedly exhibit high levels of discrimination of phenotypic traits of males (see Borgia et al. 1985; Bradbury et al. 1985). In the habitat-based model, the characters among which the females must discriminate are those that females presumably used before the shift from monogamy to polygyny and those that have some direct bearing on survival. Likewise, the degree of female discrimination of male phenotypes required to produce mating skews observed in nature (see Bradbury et al. 1985) far exceeds that demonstrated by the best manipulative experiments conducted to date (see Andersson 1982).

We believe that male mating skew in wide-ranging, polygynous species can be produced more simply by conservative mating habits among females. For birds, at least, we suggest that initially this is nothing more than the tendency of the adult female to mate with the same male within and between years, regardless of the number of arenas she visits in a season, coupled with the tendencies of inexperienced or unsuccessful females to imitate the mating habits of other successful females, or of daughters to imitate their mothers. A "quality" component is provided in the suggested rule that a female changes mates if a copulation fails to produce viable offspring. Once established, a mating preference becomes a selective force in its own right.

Although data are few, field evidence indicates that females are more conservative than they are choosy. In at least four lekking species, some females appear to be monogamous both within and between years (Lill 1976; Foster 1981; Trail 1984; Pruett-Jones 1985). Likewise, in many species, males are visited by groups of females (Watts 1968; Watts and Stokes 1971; Foster 1977a, 1981; Trail 1985b; Beehler, unpubl. data). A female may be choosing a mate on the basis of her flock-mates' choices.

As a result of these two factors, an initially successful male acquires more and more mates with each passing year, eventually achieving hotshot status. This will be especially true if female preference has a genetic component, as demonstrated for some organisms (Majerus et al. 1982). With time, and with the added influence of male social dominance, the mating skew in long-lived species will increase to the levels observed in nature.

Clustering of Males

Our model predicts that, initially, clusters of males will form as the product of a subordinate mating strategy in which novice males or older, unsuccessful males settle in the vicinity of a hotshot. We would expect this phenomenon to occur with increasing frequency as mating skew and the value of certain courts, in terms of the number of female visits, increases. For a subordinate, we presume that the long-term potential for mating exceeds that on a solitary court. Likewise, a subordinate male in a cluster might enhance survival by living in a group (Stallcup and Woolfenden 1978; Brown 1986), improve his display tactics by observing and imitating the dominant male hotshot, or increase his chances of taking over the dominant display position with the death of the owner (Foster 1977a, 1981, 1985). The latter might be particularly important if a female tends to return to her "usual" mating site when seeking a new partner following the disappearance of a regular mate. The prediction that devolves from these arguments is that, all other things being equal, for systems in which females are more variable (less conservative) in choice of mates, males should tend to establish solitary courts; if female choice is more conservative, the less successful males should cluster. To prove this, one would have to show conclusively that female mating pattern influences male dispersion, and not the reverse.

Why would a hotshot tolerate the presence of potential rivals around his display court? Benefits might accrue from decreased chances of predation and increased effectiveness of attraction of females to the arena (see Hogan-Warburg 1966). As long as the hotshot maintains control over mating (see below), any increase in the absolute number of females visiting the lek is to his benefit (Foster 1985).

Male Relationships: Structuring the Lek

The ingredients of conflict are clearly present in any system in which closely associated males compete for mates. We would expect a hotshot male to tolerate the initial clustering by other males only if he could control attempts of these potential rivals to solicit females or to disrupt his courtship activities. But, as is clear from some systems (e.g., cock-of-the-rock; Trail 1985a), once a clustering system develops, the dominant birds may eventually lose control, the result being disruption and actual fighting between rivals in the lek.

In some species, such as the swallow-tailed manakin, satellite males maintain a passive and stealthy presence around the arena. In the manakin, subordinate males are generally quiet and inconspicuous but attempt to court visiting females in the absence of the alpha male (Foster 1981, 1987). This behavior may also explain the occurrence of delayed plumage maturation in males of many species of lek-breeding birds (Foster 1987, unpubl. data). Juvenal and subadult plumages can minimize the severity of the aggression directed by a dominant male toward a subordinate (but reproductively capable) male, thereby increasing the subordinates' opportunities to breed opportunistically and decreasing their costs (Foster 1987). It has been demonstrated for several frog species that smaller males, which do not participate in the breeding chorus, intercept and engage in amplexus with females on their way toward more-dominant individuals (Howard 1978; Perrill et al. 1978).

Without the dominating behavior of the hotshot, subordinates of most species probably would not behave in so passive a fashion, since the most effective way to gain in the mating hierarchy is to displace rival males. Likewise, successful males or those at particularly high-quality sites might resist being joined by other males, because of the potential for dilution of the benefits they might otherwise enjoy. Thus, it is not surprising that varying levels of disruption are documented for most species of lek-breeding birds (Trail 1985a), as well as for many species of lek-breeding insects (e.g., Spieth 1968; Campanella and Wolf 1974; Ringo 1976; Hodosh et al. 1979; Boake and Capranica 1982).

The most likely means by which hotshots might control subordinates would be through the development of dominance relationships (Foster 1983). For example, in swallow-tailed manakins, rank in a linear hierarchy, structured by means of male-male interactions in the absence of females, determines the right of males to court females and to copulate (Foster 1981). Similarly, in the lek-breeding dragonfly *Plathemis lydia*, males establish a dominance hierarchy by means of aggressive interactions, and the highest-ranking males achieve the greatest reproductive success through their ability to control interference during mating (Campanella and Wolf 1974).

For the greater prairie chicken (*Tympanuchus cupido pinnatus*), Robel and Ballard (1974) demonstrated the importance of the presence of hotshots and their within-lek dominance control in maintaining the lek. After they removed dominant males from the lek, levels of intermale aggression rose. During the first season after removal, females continued to visit the lek in good numbers, but the number of successful copulations decreased by 90%. During the second season after removal, the numbers of visits by females, of males in attendance in the lek, and of successful copulations all decreased.

In some species, the formation and maintenance of the dominance relationships may be overt (Trail 1985b). In others, but particularly among those that are long-lived and faithful to their sites, the attendant rituals associated with male-male dominance may be difficult to document (e.g., Beehler 1983b) because they are subtle, confined to specific (prebreeding) seasons, or episodic, occurring only when the composition of the lek is altered. Certainly, the amount of conflict should diminish once neighbors or group members become familiar with one another, especially in species that defend the courts as territories. Thus, males in small leks with a few faithful members should be disrupted less frequently than males in large leks with higher turnover (see Trail 1985b). The best measure of frequency of disruption is simply the mean number of disruptions per female visit.

In a tight lek, the level of disruption reflects the stability of the mating hierarchy, as a function of the absolute age of the male-male arena association or of the relative mating equality of the members of the lek. When relative equality exists (i.e., reduced mating skew), we believe disruption by subordinates is most common. We contend that the lek that has "exploded" is the product of accommodation between males in a lek in which behavioral dominance has broken down (perhaps in conjunction with a shift in female mating habits). Thus, high levels of disruption promote wider spacing (i.e., "explosion") of males originally clustered in a small arena; males remain clumped in space but maintain a "safe" distance between courts (Foster 1983). We predict that mating among males in a lek that

has exploded is more equitable than that in a tight lek. A useful counter example is that of the cock-of-the-rock (Trail 1985b), in which males exhibit high levels of disruption but maintain a tight lek. We suggest that this exception has arisen because leks of this species are always situated adjacent to a resource required by females, that is, the restricted cliff-face nesting sites.

We suggested above that females in species with solitary-court systems might use quality of the display court or "dominance area" as an index to male quality. Once clusters form, the lek can serve only as an index to group quality.

We have already expressed our dissatisfaction with models that stress the importance of female choice based strictly on male phenotype. The conservative mating rules discussed for mating systems of dispersed males apply equally well to the lek situation. Females could visit any number of arenas but would continue to select the same male, or arena, within and between years, and naive and unsuccessful females would tend to imitate choices of older, successful individuals. We now offer a nonexclusive alternative to "choice-by-phenotype" that may operate in at least some vertebrate lekking species (see Foster 1977a, 1981; LeCroy 1981). We suggest that with the formation of male clusters, especially in tight leks, 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. Whereas before, male quality was manifest as the quality of the territory held, it is now manifest as the position of dominance held over rival males. This may explain the observation that females of some species seem receptive to any male in a hierarchy as long as he is the highest-ranking individual present at the time she visits (Foster 1981, 1987). We suggest that female-default mating and conservative mating rules may be manifested to differing degrees in different taxa. Too little effort has been invested in documenting patterns of female behavior in the lek.

In contrast to Bradbury (1981), we believe that the intra-demic variation in mating patterns produces leks of varying size. Thus, we do not believe that an ideal lek size exists for a particular species in a particular habitat. Nonetheless, we predict that the number of males present in an arena is a positive function of two factors: (1) the mating skew within the local population; and (2) the number of females that copulate in the arena (i.e., the success of the hotshot[s]). The interaction of these two factors should produce a within-deme range in size of lek units comparable to that observed in nature (e.g., Beehler and Pruett-Jones 1983; Pruett-Jones 1985). The greater the mating inequality, the greater the likelihood that an unsuccessful male will settle near a hotshot rather than displaying solitarily. The particular hotshot that a male joins is a function of the number of females that visit the arena and the number of satellite males already present. In contrast, under a regime of reduced mating skew, some males should leave the arena (or fail to join one) in order to form solitary courts or smaller arenas, which, under these conditions, might be visited by females. With a lowered mating skew, a hotshot would have to be relatively more dominant to elicit or maintain a joining response from his younger or less successful rivals. Life history parameters would influence the form of the relationship in each species, producing general inter-taxonomic differences.

If mating potential for a satellite were low, risks associated with arena occu-
pancy could outweigh benefits, and selection would favor delayed breeding. Such
males should remain floaters. The greater the mating skew, the larger this floater
population would be. Such a system would have a few large leks, many floaters,
and many subordinate lekking males.

We agree with Bradbury and Gibson (Bradbury 1981; Bradbury and Gibson
1983) that inter-arena distance is probably some function of the size of female
home ranges. As we stated earlier, however, we do not believe that this parameter
can be measured in a way meaningful for this issue. An additional, and to us
critical, factor in determining spacing and size of arenas is the degree of mating
skew. As skew decreases, more and smaller arenas appear in the habitat, reducing
inter-arena distance. As skew increases, fewer and larger arenas remain. We also
suspect that hotshot males (and their attendant cluster of subordinates) distribute
themselves through the environment as evenly as possible so as to minimize
competition for the wide-ranging females. Such regular distributions are charac-
teristic of many court species (Bradbury 1981; Beehler and Pruett-Jones 1983;
Foster, unpubl. data) and contradict the hotspot model.

Tests and Predictions of the Hotshot Model

A number of predictions that devolve from the hotshot model distinguish it from
those of the models of Bradbury and Gibson. Several practical manipulative
experiments might be used to test the predictions and to evaluate the models.

1. *Dominance test.*—Remove the top hotshot(s) from a focal lek and observe
the resulting lek activities. The hotshot model predicts reduction in number of
females visiting and mating, and loss in attendance of some of the subordinate
males. Both the female-preference and hotspot models predict no change in
female visiting, female mating, or attendance by subordinates. The well-docu-
mented results of the removal experiment of Robel and Ballard (1974) support the
hotshot model.

2. *Local culling of hotshots.*—Remove the top hotshot male(s) from all of the
leks within an experimental study plot. The hotshot model predicts that within-lek
disruptions will increase, male mating inequality will decrease, and some large
leks will break up into two or more small leks. Female-preference and hotspot
models predict no change in disruption, no shift in female preference between
leks, and no breakup of the larger leks. This experiment has not yet been per-
formed.

3. *Subordinate culling.*—Focusing on two neighboring leks of equal size, leave
one a control and repeatedly remove a percentage (e.g., 15%–25%) of male
subordinates from the second (experimental) lek, thus reducing the total size of
the lek without disturbing the activities of the dominant males. The hotshot (and
also the hotspot) model predicts no change in female visiting or mating patterns,
whereas the female-preference model predicts that females begin to shift to the
control (larger) lek. Although such a manipulative experiment has not yet been
reported in the literature, data of Pruett-Jones (1985) for Lawes' parotia provide
indirect support for the notion that females do not seem to be using lek size as a
cue when making mating decisions.

4. *Female mating patterns: default versus choice.*—The hotshot model pre-

dicts that mating success is more closely correlated with within-lek dominance (as measured in appropriate male-male interactions, such as the fewest received disruptions of mating, the most successful aggressive displacements, etc.) than with male morphology. The models of Bradbury and Gibson predict a predominance of phenotypic correlations (vocal characteristics, dance rate, plume length, etc.). The data collected to date are equivocal, although some seem to support the hotshot model (e.g., Trail 1985a), whereas other data support the female-preference model (e.g., Gibson and Bradbury 1985). As indicated earlier, attempts to show a cause-and-effect relationship between phenotypic traits and mating success fail, in our view, because of the inability to tease apart phenotype from within-lek dominance (a difficult, though feasible, task for the field researcher). Significantly, nearly all phenotypic traits cited as important for female choice are male behaviors that could be correlates of dominance status (e.g., see especially Borgia 1985a,b; Borgia and Gore 1986).

5. *Within-deme variation in lek size.*—The hotshot model predicts great variation in lek size within a sample study area and a positive correlation between lek size and the length of tenure of the dominant male(s). The female-preference model predicts an optimum lek size and the extinction of smaller leks as a result of competition from larger leks. The hotspot model predicts that lek size will depend solely on the number of females using a patch of habitat, not on the tenure and the experience of the dominant male. Data on variation in lek size in the ruff (Hogan-Warburg 1966) and observations of lek "budding" in *Paradisaea minor* (Beehler, unpubl. data) support the hotshot model, although we lack auxiliary information on the relationship between long tenure of the hotshot and size of the lek. The female-preference model provides no mechanism for the initiation of a lek at a new site. Likewise, although the hotspot model links male court concentrations to "female hotspots," it provides no mechanism for explaining why males cluster into tight display groups.

Although we believe that controlled removal experiments, as suggested above, may provide ready answers to many of the behavioral underpinnings of lek organization, long-term field observation on marked populations of lekking species are required for adequate testing of the more-recondite aspects of the competing hypotheses.

SUMMARY

We critically review the female-preference and hotspot models, the two most widely accepted recent explanations of lek organization. On the basis of what we believe are the inadequacies of these models—too great a reliance on the presumed acuity of female discrimination, the assumption that females have full freedom of choice within the lek, and insufficient recognition of the importance of male-male interactions—we develop an alternative set of hypotheses, which we call the *hotshot model*, to explain the development and maintenance of lek behavior. Our model attributes strong male mating skew to the interaction between (1) simplified and conservative mating rules of females and (2) social dominance among males. We demonstrate the importance of male-male domi-

nance relationships in lek and non-lek court mating systems. We then argue that a strong mating skew among males forces novice males entering a population to adopt a long-term mating strategy that involves delayed breeding (floating) and subordinate lek behavior. The structure of leks is created by a complex of male-male interactions, with conflict between hotshots (who attempt to control lek mating) and subordinates, who may benefit from disrupting lek activities. Explanations for the number of males in an arena and inter-arena distances are based on modifications of the hotspot and female-preference models. We suggest specific field tests to help distinguish which hypothesis best models the behavioral interactions that produce lek mating.

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