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Lekking in Birds and Mammals: Behavioral and Evolutionary Issues

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I. INTRODUCTION

Of all animal societies perhaps the most bizarre are leks. These aggregations of displaying males are visited by females solely for copulation. To some they have represented the vindication of Darwin's theory of sexual selection (Darwin, 1871; Selous, 1927). To others they have seemed simply baffling. "Leks . . . challenge the whole enterprise of behavioral ecology. There are no answers as yet . . ." to questions about their evolution (Gould, 1982). Generalities in our understanding of leks have been slow to emerge. As a consequence of this challenge, a great deal of research has focused on leks in the past two decades. This review attempts to organize the results of this work in a way to suggest directions for the future.

Even the problem of what species to include in a discussion of lekking has no simple answer. Criteria for leks (Wiley, 1974; Bradbury, 1981) focus on three features: (1) lack of any parental care by males, as well as any direct contributions of males to feeding or protecting their mates; (2) lack of any association of displaying males with resources, such as food, shelter for young, or nesting substrates, that affect female reproductive success; and (3) aggregation of displaying males. Females visit leks solely for copulation and then leave to raise their offspring without any association with a male. Males contribute nothing except sperm to their offspring. In all known cases that fit the above criteria, the males in any one aggregation differ markedly in their mating success.

These features of social organization, however, do not occur as an invariant syndrome. Extremely unequal distributions of matings among males recur in many species that lack male parental care, and the features of leks mentioned above occur in various combinations in other species (Table I). In particular, some closely related species or even populations of the same species that share the first two features differ in the dispersion of displaying males, which may be

TABLE I
CLASSIFICATION OF MATING SYSTEMS WITH LITTLE OR NO MALE
PARENTAL CARE^a

Mating locations	Receptive females	
	Aggregated	Dispersed
Associated with resources	Colonial resource-defense polygyny	Dispersed resource-defense polygyny
Not associated with resources	Leks	Dispersed display sites

^aExcluding mating systems in which males defend individual females or groups of females (harems) for relatively long periods of time.

either aggregated in leks or dispersed on solitary display sites. Although this review focuses on species that fit the three criteria given above for leks, there are allusions to species with dispersed display sites where appropriate.

Lekking has evolved independently in many groups of birds (Payne, 1984; Höglund, 1989) and mammals (Bradbury, 1977; Gosling, 1986; Clutton-Brock *et al.*, 1988a), and mating systems that fit the three basic criteria also appear among frogs, fish, and insects. This review, however, focuses on birds and mammals, groups for which the most intensive studies of lekking are available (scientific names of species mentioned in the text can be found in Section XIII).

The current interest in leks arises from the restriction of males' reproductive contributions solely to sperm. This situation distills the complexities of sexual selection. Females get nothing but genes from mates; so any choice of mates by females evolves without complications introduced by males' associations with resources used by females or by males' contributions to the survival or reproduction of offspring or mates. The interest of lekking species for the study of sexual selection, first recognized by Darwin (1871), was emphasized near the turn of the century by the pioneering English naturalist Edmund Selous (1927). The term "lek" derives from ordinary Scandinavian words meaning play and, by extension, courtship.

Despite the continuing interest in the evolution of leks, I emphasize in this review a distinction between behavioral and evolutionary mechanisms. Previously, I have argued that social organization of any sort requires investigation on three levels (Wiley, 1981). The lowest level of investigation, one that attempts no explanation, produces a description of the patterns or structure in individuals' social relationships throughout their lives, a step analogous to anatomy in other branches of biology. The next level of investigation identifies the genetic, physiological, and behavioral mechanisms that produce these patterns in social relationships. These mechanisms, operating throughout an individual's life, of

course, amount to the epigenesis of the individual's social behavior. Ultimately, any complete biological understanding requires an investigation of the evolutionary mechanisms that have produced the present genetic composition of the population.

In the case of mating systems, including leks, this hierarchical approach separates, in particular, female choice from sexual selection. The first is a behavioral mechanism that can generate patterns of mating between individuals; the second, often a consequence of differences in mating success produced by particular behaviors, is a mechanism of the propagation of genes in a population. In some cases these approaches are conflated and in others pursued almost in isolation. In the end, however, structural, behavioral, and evolutionary approaches are no doubt mutualistic in advancing our knowledge. Each suggests issues for those interested in the others.

To clarify the relationships of these approaches in studies of leks, in this review I first consider some general patterns in the social structure of leks, in particular the constancy and variability in the locations of leks and the non-uniform distribution of matings. Then I examine the behavioral interactions that could produce these patterns. Next I turn to general evolutionary issues raised by lekking species, including possibilities for sexual selection, and finally to evolutionary scenarios, complex hypotheses for the evolutionary origins of lekking.

II. PATTERNS IN LEK BEHAVIOR

As a first step in understanding leks, this section examines two patterns described repeatedly for lekking birds and mammals: constancy in the locations of leks and nonuniform distributions of matings among males.

A. CONSTANCY IN LOCATIONS OF LEKS IN SUCCESSIVE YEARS

Almost every investigation of a lekking species has noted that leks tend to recur from year to year in similar locations. To establish how much locations vary, however, it is necessary to determine the locations of leks over large areas and spans of years. In one such study, Patterson (1952) mapped the locations of all leks of sage grouse in 526 km² in Wyoming for 3 years. In the first year, there were 28 leks, with 14 to 400 males each (mean, 78 males). In the second and third years, all leks recurred in locations occupied the preceding year. In the third year, after the population declined by 26%, leks included 2 to 295 males. Because annual mortality of male sage grouse is high (Section IX), probably 75% of the males at leks in the third year had not been present 2 years earlier. Bradbury *et al.* (1989a) also reported that leks of this species recurred from year to year in the same locations, with significant rank correlations between numbers of males

present at each lek in successive years. Likewise, 20 leks of sharp-tailed grouse in Alberta all recurred on the same sites in three successive seasons (Rippin and Boag, 1974a). In other populations of this species, however, more change has occurred. In North Dakota, only 73 of 178 leks remained active more than 5 years (F. R. Henderson and W. W. Jackson, cited by Bergerud and Gratson, 1988), and in Wisconsin 14 of 25 leks remained active on the same site in 3 successive years (Gratson, 1988). Constancy in locations of leks evidently varies among populations of the same species, but often a substantial majority of leks remain in the same locations from one year to the next.

The appearance of new leks and disappearance of former ones often accompany marked increases or decreases in populations (Schwartz, 1945; Dalke *et al.*, 1963). Those leks that disappear and those that appear in new locations also tend to include few males. Tropical lekking species rarely undergo major changes in population densities within periods of a few years, and locations of most leks are correspondingly stable (Lill, 1974a,b, 1976; Snow, 1974; Stiles and Wolf, 1979).

Mammalian leks also show constancy in locations. Fallow deer, with a rutting season confined to about 1 month each year, usually form leks at similar locations in successive years (Clutton-Brock *et al.*, 1988a; Appollonio *et al.*, 1989a,b). In Uganda kob, reproduction occurs year-round. A male holds his position on a lek for periods of several weeks, during which he has little opportunity to feed, and then is replaced by a male from outside the lek. Individual males thus cycle between periods of lekking and periods away from leks when they forage and regain their condition (Buechner and Roth, 1974). Of 15 leks, 10 remained active in the same locations for at least 14 years (Buechner and Roth, 1974). These leks thus clearly exemplify constancy of location with continual turnover of male membership.

Species with dispersed display sites also show constancy in the locations of sites with successive males in occupation. In these species, since often only one male is regularly associated with a display site, stable locations might result entirely from each male's faithfulness to a site. For example, in most tropical species, longevity of males are high enough that display sites are often occupied by one male for several years in a row, longer than the durations of most field studies (Snow, 1970; Vellenga, 1980b; McDonald, 1989a,b). Nevertheless, in both satin bowerbirds and several genera of manakins display sites can have a succession of different males in residence (Snow, 1962a; Lill, 1974a,b; Vellenga, 1980b; McDonald, 1989a,b). In species with high annual mortality, like forest grouse, it is easier to determine the proportion of display sites occupied by a succession of different males. In both ruffed grouse and blue grouse, about a third of all display sites are occupied perennially by successions of males; another third are occupied intermittently, and the remainder in any one year have had no previous occupation (Gullion and Marshall, 1968; Gullion, 1967, 1981; Lewis and Zwickel, 1981; Lewis, 1981).

A prerequisite for constancy in the locations of leks is a stable habitat and thus, stable spatial patterns of resources and movements of individuals (Bradbury *et al.*, 1989a). Leks are often associated with particular features of habitats, such as sparse or short vegetation (de Vos, 1983; Gosling, 1986; Gosling and Petrie, 1990), streams (Stiles and Wolf, 1979), steep slopes (Snow, 1970), low ridges (Schwartz, 1945), or depressions (Wiley, 1973a; Bradbury *et al.*, 1989a). Yet, even though leks often occur in locations with particular vegetational and microtopographical features, no report has ever concluded that these tendencies completely explain the locations of displaying males in any lekking species (Section VII,C).

B. MOVEMENTS OF LEKS WITHIN A SEASON

A number of studies have documented that the males on a lek have moved to new locations (Stiles and Wolf, 1979; Gibson and Bradbury, 1987; Gratson, 1988; Appollonio *et al.*, 1990). In some cases, these movements were temporary relocations during a single morning's activity (Lumsden, 1965, 1968; Koivisto, 1965); in other cases, they involved permanent relocations that occurred either abruptly or by stages from day to day. In some cases, such moves suggest an attraction of males to females in new locations (Section IV). In other cases, these shifts occur in response to changes in habitat near leks, as when lekking grouse move from sites with relatively tall grass or shrubs to recently burned areas (Anderson, 1969; Sexton and Gillespie, 1979; Cannon and Knopf, 1981; Gates, 1985). Black grouse in Finland often form leks on frozen lakes in early spring, only to move to nearby openings on shore as the ice thaws (Koivisto, 1965). These cases emphasize again that a stable habitat is necessary for constancy in locations of leks.

C. VARIATION IN AGGREGATION OF MALES

Another source of variation in lekking species results from differences in dispersion of males within or between populations. Among ruffs in a population in Finland, males switched between attending leks, waiting in areas used by females for feeding, and actively pursuing females (Lank and Smith, 1987). The number of males at leks was higher on days with higher temperatures, and thus lower energy requirements, and on days following those with greater numbers of females copulating. Males on leks copulated 4–5 times more frequently than those away from leks. Male buff-breasted sandpipers in Alaska shift from aggregation at leks early in the season to dispersed display later, in accordance with changes in the dispersion of females (Pruett-Jones, 1988). In Lawes' parotia about 30% of males display solitarily and have about the same success in mating as aggregated males (Pruett-Jones and Pruett-Jones, 1990). Solitarily displaying

males occur in small numbers in many species that regularly form leks (Hamerstrom and Hamerstrom, 1973; Lill, 1974a; Rolstad and Wegge, 1987) and in some cases copulate successfully (Kruijt *et al.*, 1972; Sexton, 1979; de Vos, 1983).

Intraspecific variation in sizes and spacing of leks often correlates with differences in population density. Thus, the sparse population of black grouse in the Netherlands, before its extirpation, formed smaller leks with greater average spacing of males within a lek than in denser populations in Scandinavia (de Vos, 1983). The same contrast applies to white-bearded manakins in Suriname and Trinidad. The less dense populations in Suriname average fewer males at a lek, wider spacing of leks and greater distances between males within leks (Olson and McDowell, 1983). In two antelopes, Uganda kob and topi, clustering of male territories into leks occurs in areas with dense populations (Leuthold, 1966; Montfort-Braham, 1975; Gosling, 1986; Gosling and Petrie, 1990). Fallow deer have especially plastic mating systems, including harems, groups of mixed sex with several males in a dominance hierarchy, solitary territories, and leks (Langbein and Thirgood, 1989). These variations are in part related to the densities of males and females in a population, as well as to the synchrony of females' estrus and perhaps to habitat (Schaal, 1986; Langbein and Thirgood, 1989). For many species, there is no information on the nature of the differences in males' and females' behavior that produce differences in the sizes and spacing of leks. Yet, these intraspecific variations could provide insights into the advantages and disadvantages of lekking for individual males and females.

D. MATING CENTERS

Sage grouse, perhaps the species with the most extreme development of lekking, is remarkable both for the very large numbers of males that congregate at some leks, 400 or more (Scott, 1942; Patterson, 1952), and for the compact groups of females, sometimes over 40 at a time, that gather at particular places within a lek. The latter feature of this species has occasioned substantial disagreement among observers. Scott (1942), in his report on sage grouse, noted that both the location of a lek itself and the sites where copulations occurred within a lek remained constant during any one season and from year to year. Subsequent observers of sage grouse have included those agreeing that mating tends to recur in the same locations within leks (Patterson, 1952; Wiley, 1973a) and those denying this pattern (Lumsden, 1968; Gibson and Bradbury, 1986; Hartzler and Jenni, 1988).

The evidence against stable mating centers comes in part from observations that some leks themselves move in the course of a single season (Section II,B). In addition, there is evidence that copulations on sage grouse leks do not always occur at a single site during a season (Lumsden, 1968; Hjorth, 1970; Hartzler,

1972; Wiley, 1973a; Bradbury and Gibson, 1983; Hartzler and Jenni, 1988). Three of these reports, however, come from a single lek, Ford's Creek Lek, near Grass Range, Montana. In 1965, Lumsden used cannon-nets to capture males and females on this lek; others had trapped birds here in preceding years (Lumsden, 1968). Lumsden noted that this lek was unusual in having two clusters of males about 800 m apart. During his observations following cannon-netting, marked males used broadly overlapping areas on the lek and females gathered at 20 different locations. He also noted that males moved their positions in response to his activities following netting or trapping on the lek. In 1968, I found that males on this lek occupied largely exclusive territories (Wiley, 1973a). Females likewise favored particular sites, but one such site was discontinued and another initiated in the course of the 2 weeks of frequent mating. Hartzler, who observed Ford's Creek Lek for the three seasons 1969–1971, again found that males had territories and that copulations did not occur at a single location on the lek during any one season (Hartzler and Jenni, 1988). There were some striking differences in locations of copulations between years, although the locations of some concentrations of matings corresponded between years. Hartzler trapped males on this lek in the first year of his study and reported that several which he could identify before trapping returned to their previous locations.

Thus, both observers after Lumsden agreed that males defended territories on this lek, and all three observers agreed that copulations were not restricted to a single location within a season. Gibson and Bradbury (1986) have cited Hartzler's data as their primary evidence against stable mating centers. In addition, Hjorth (1970) reported that matings occurred in four males' territories on a lek in Montana with only six regularly attending males. In contrast, at larger leks not subjected to netting or trapping, Scott (1942), Patterson (1952), and Wiley (1973a) observed that mating occurred predominantly, although not exclusively, in a small area within a lek. Maps of the locations of copulations indicated that these areas, about 10 m in diameter, approximated the size of a central male's territory but did not necessarily coincide with any one male's boundaries nor with the geometric center of the lek (Wiley, 1973a). The conclusion seems inescapable that leks of sage grouse vary in the stability of mating centers, at least within any one season.

There are two possibilities, not mutually exclusive, for explaining these differences in the stability of mating locations. First, the disturbance of a lek by cannon-netting or trapping might disrupt the birds' behavior, perhaps that of both sexes (Section II,F); such disruption might carry over for a number of years, if males and females tend to return to similar locations in successive years or to follow more experienced individuals (Section V). Mating centers have shifted locations when disturbed (Wiley, 1973a) or when covered by a snow drift (Scott, 1942). Second, it seems likely that leks might vary in the stability of individuals' locations, both those of males and those at which females copulate, regardless of

possible disturbances. It is plausible, for instance, that smaller leks might be less stable than larger ones (Section VI).

As for the locations of copulations on sage grouse leks in successive years, most evidence is anecdotal. Results of mapping the locations of copulations in successive years have so far only been published for Ford's Creek Lek (Hartzler and Jenni, 1988); there is no similar comparison between years for a lek in which mating locations have remained stable within a season.

In other species as well, few studies have mapped the locations of copulations, as well as males' display sites or boundaries, in successive seasons. On one lek of common capercaillie, two mating centers each shifted location once in the course of 4 years (LeClerq, 1988). In one population of sharp-tailed grouse, mating centers recurred at the same locations within several leks for 3 years (Kermott, 1982; p. 34), but in another with exceptionally high annual mortality mating centers shifted 10–20 m between years (Landel, 1989). Within a large lek of Guianan cock-of-the-rock, individual display courts varied in mating success from year to year, but the most successful courts were clustered in the same part of the lek in each of 4 years (Trail, 1984; p. 159). In lekking fallow deer, copulations also tend to recur in the same locations in successive years (Clutton-Brock *et al.*, 1988a; Appollonio *et al.*, 1989b). On topi leks, worn patches in the most successful territories persist from year to year (Gosling and Petrie, 1990).

Sage grouse sometimes form extremely large leks, with as many as 200–400 males. On such leks, females have several sites at which they congregate and copulate (Scott, 1942; Patterson, 1952; Wiley, 1973a). Roughly one such focus for females occurs for each 50–70 males present by the end of the mating season. This arrangement suggests that such a large lek actually constitutes a "superlek," an aggregation of aggregations, with each basic unit having a maximum of 60 or so males. Such superleks have also been reported for other species (Bradbury, 1977).

E. DISTRIBUTION OF COPULATIONS AMONG MALES

A pattern reported universally by observers of leks is the nonuniform distribution of matings among males. While widely recognized in a qualitative way, there is relatively little quantitative information. To obtain the necessary data requires unbiased observation of a random or representative sample of males. For species in open habitats with brief mating seasons, it is possible to obtain nearly complete observation of behavior, and to examine the possibility that scattered copulations are more often overlooked than clustered ones. For species with prolonged mating seasons and those with leks in dense habitats, it is necessary to plan focal-individual observations on a schedule that avoids suspected biases.

Only for a few species are there adequate data to compare different leks, years, or populations. To present these distributions in a uniform format, it is useful to

graph them as cumulative proportions of copulations against cumulative proportions of males attending a lek (Figs. 1–4). These graphs make it clear that within any one season the distribution of copulations among males on a lek is highly skewed. They also suggest the possibility of inter- or intraspecific variations in the distribution of mating on leks. The greater skew in sage grouse than in black grouse agrees with a proposal that mating distributions might be less uniform in grouse with greater sexual dimorphism or larger leks (Wiley, 1974).

Distributions of matings within one season would not be reflected in distributions of lifetime mating success, if a male's success varied from year to year (Clutton-Brock, 1983). However, successful male black grouse tended to remain successful from year to year, at least until near the ends of their lives (Kruijt and de Vos, 1988). Consistent success in mating from year to year has also been reported for male common capercaillie (Wege and Larsen, 1987; LeClerq, 1988) and Guianan cock-of-the-rock (Trail, 1984, p. 91). The distribution of lifetime mating success in these cases might not differ markedly from that within a single season.

A further issue in interpreting these distributions is the contribution of genetic and environmental influences on mating success (Sutherland, 1985a,b, 1987; Hubbell and Johnson, 1987). One aspect of this issue is particularly relevant to lekking species. Distributions of matings within one season are based on an assortment of males of different ages. If mating success varies with age (Section

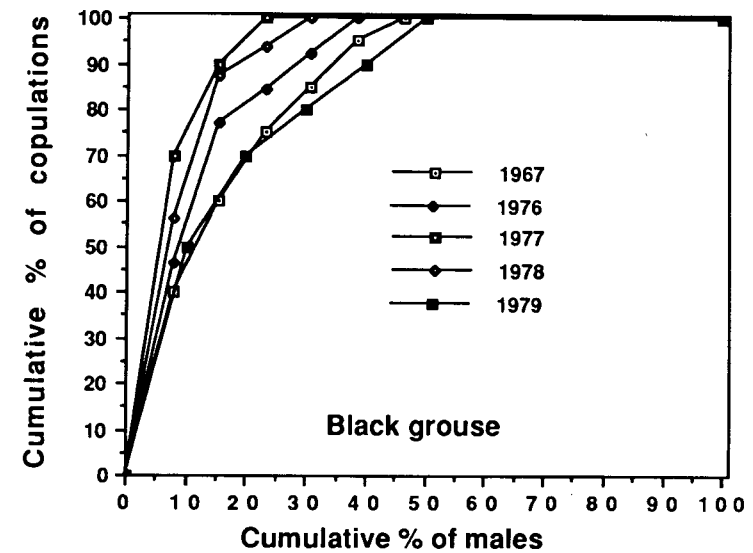


FIG. 1. Distributions of matings among males at one lek of black grouse in 5 years (Kruijt and de Vos, 1988).

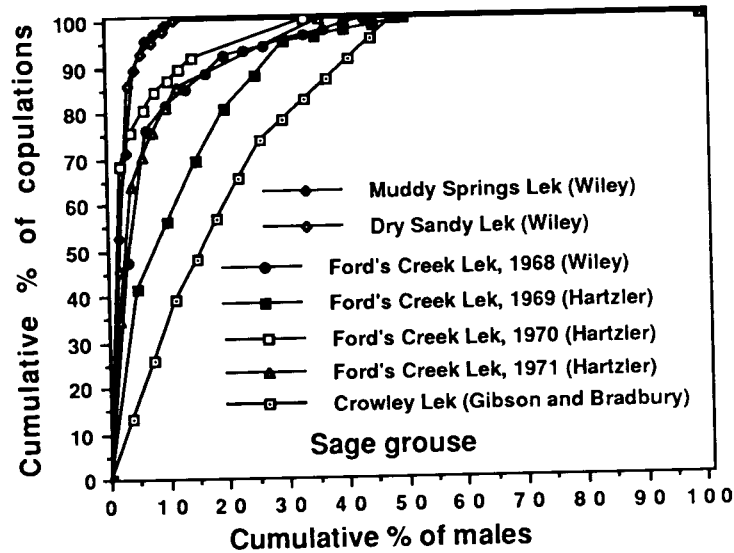


FIG. 2. Distributions of matings among males on leks of sage grouse (Wiley, 1973a; Gibson and Bradbury, 1985; Hartzler and Jenni, 1988).

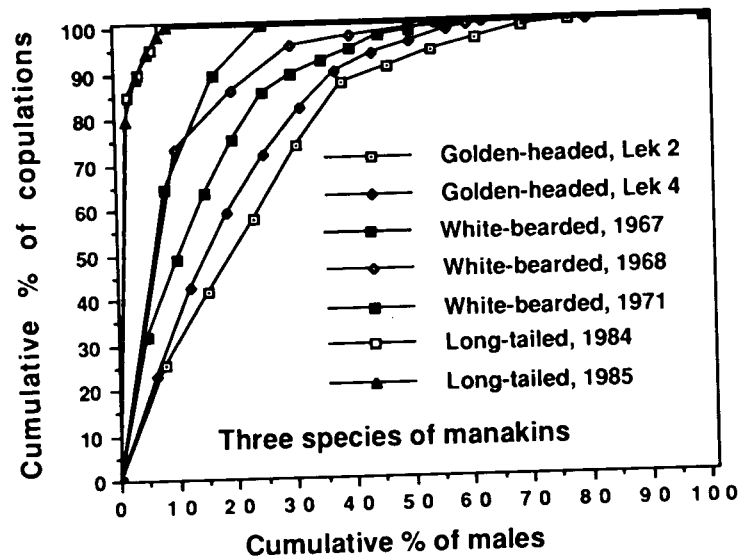


FIG. 3. Distributions of matings among males on leks of three species of manakins (golden-headed, Lill, 1976; white-bearded, Lill, 1974a; long-tailed, McDonald, 1989b).

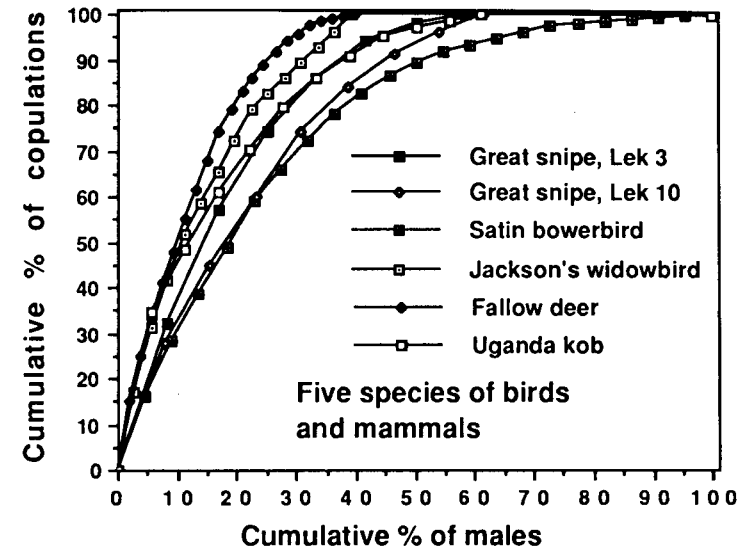


FIG. 4. Distributions of matings among males on leks of four species of birds and mammals and in satin bowerbirds, a species with dispersed display sites (great snipe, Höglund and Lundberg, 1987; satin bowerbird, Borgia, 1985b; Jackson's widowbird, Andersson, 1989; fallow deer, Clutton-Brock *et al.*, 1988a; Uganda kob, Floody and Arnold, 1975).

III,B), lumping males of different ages will exaggerate the deviation from uniformity in lifetime reproductive success. Comparisons of different species or populations might reflect the degree to which young males attend leks and thus are included in the totals for lekking males.

It is not clear to what extent lekking is associated with unusually skewed distributions of male mating success. Polygynous species in general have greater variance in male mating success than do monogamous species (Clutton-Brock, 1983; Payne, 1984). To assess the effect of lekking itself, as opposed to polygyny in general, would require a comparison of distributions of male mating success in lekking species and in species with resource-defense polygyny, harem polygyny, or dispersed display sites. In a comparison of male black grouse, red deer, and northern elephant seals (Kruijt and de Vos, 1988; Clutton-Brock *et al.*, 1988b; LeBoeuf and Reiter, 1988), among those surviving to reproductive age, the proportion failing to mate at least once is lowest in red deer and highest in elephant seals. Thus, nonuniformity in distributions of matings among males of lekking species might not be exceptional among polygynous species overall.

Sexual differences in size, coloration, and elaboration of secondary sexual characters also tend to be associated with polygamy, although exceptions are numerous (Clutton-Brock *et al.*, 1977; Payne, 1984). On the other hand, lekking species seem not to have greater sexual dimorphism in comparison to species

with other forms of polygyny. Höglund's (1989) comparative review showed no association of sexual dimorphism in size or coloration with lekking, but his study only classified species into two categories of dimorphism and lumped all species without leks regardless of other distinctions in mating system. Among species of grouse, sexual dimorphism in size is allometric: the ratio of male to female mass increases with increasing female mass. The smallest and least dimorphic species include those that are usually monogamous. The two largest and most dimorphic have leks, but species with leks and those with dispersed display sites do not differ clearly in either mass or dimorphism (Wiley, 1974). Some lekking species lack any notable sexual differences either in mass or secondary sexual characters (Stiles and Wolf, 1979; Payne, 1984; Trail, 1990; Höglund *et al.*, 1990). In conclusion, it remains unclear whether or not lekking species stand out from related species with dispersed display sites, or other forms of polygyny, in distributions of male mating success and in sexual dimorphism.

F. GENERAL METHODOLOGICAL PROBLEMS IN STUDYING LEKS

Studies of leks, like other behavioral studies, involve some intrusion of the observers, but leks present some special problems not often explicitly discussed. For example, many studies have used small blinds erected within or near leks. Males often appear reluctant to shift their locations and eventually accept a blind on a lek, even to the extent that they walk within 1 m or perch atop it (Schwartz, 1945; Hamerstrom and Hamerstrom, 1973). Females, on the other hand, shift their locations more readily and, in any case, have less time during their few visits to habituate. Females have been found to avoid a newly erected blind (Wiley, 1973a) and might avoid permanent ones as well. Clearly, even subtle reactions of females could alter the locations of matings on leks.

Capturing individuals for marking is often most easily accomplished on or near leks (Lumsden, 1968; Robel, 1966, 1967; Gibson and Bradbury, 1985). Studies of leks are exceptional among field studies of behavior in the temptation to capture individuals near locations with such significance for the subjects' social behavior. In some cases, it has been possible to capture and mark individuals away from leks during the nonbreeding season, and this is probably the optimal procedure (Lill, 1974a,b, 1976; Hamerstrom and Hamerstrom, 1973; de Vos, 1983; Kruijt and de Vos, 1988). Recognition of individuals for behavioral studies can sometimes instead rely on minor natural variations in appearance (Hjorth, 1970; Wiley, 1973a; Hamerstrom and Hamerstrom, 1973; Gosling and Petrie, 1990).

There are few studies of the effects of disturbing individuals on their leks. Dalke *et al.* (1963) reported that less than half of the male sage grouse returned to a lek after cannon-netting. Although older males were more likely to return than yearlings, even some of them disappeared. For black grouse, radio packages

increased mortality of both sexes for a week following capture. Survivors beyond this time, however, appeared to fare as well as controls (Angelstam, 1984). Some male black grouse caught on leks in the Netherlands did not return for 1–2 days; those with central positions lost all or parts of their territories while those with peripheral positions did not (Kruijt *et al.*, 1972).

The difficulties of studying leks without disturbance, in conjunction with variation in the patterns of lekking within any one species, create a basic conundrum that all students of leks must confront. There is an unavoidable choice between intensive investigation of one or a few leks, on the one hand, and extensive but less thorough assessment of variation among leks, on the other. In the end, we need both kinds of information.

III. BEHAVIORAL INTERACTIONS OF MALES

Any social structure is generated by individuals' responses to each other. Of course, each of these responses invites further explanation in terms of physiological, ontogenetic, and genetic mechanisms. The first step, however, in understanding the social structure of leks is to examine the responses of the individuals involved: the responses of males to each other, of males to females, of females to males, and of females to each other.

A. TERRITORIALITY AND DOMINANCE

The interactions of males attending leks typically include elements both of territoriality and of dominance relationships. Different investigators studying the same species have often emphasized one or the other aspect of males' interactions, without clear indications that they actually observed different behavior. An example comes from studies of greater prairie chickens by two groups. Hamerstrom and Hamerstrom (1960, 1973) discussed males' relationships almost entirely in terms of territoriality. They described males defending small areas with well-defined, but flexible, boundaries at which neighbors engaged in ritualized encounters and sometimes escalated fights. In contrast, Robel and colleagues (Robel, 1964, 1966, 1967; Robel and Ballard, 1974) described the relationships of males in terms of differences in aggressiveness. In 2 years, the males most successful in mating also ranged over the largest areas on the lek. Although Robel referred to these areas as "territories," they were in fact ranges determined by plotting the males' locations at 15-min intervals.

These differences are resolved by considering the males' behavior in the presence and absence of females. When there are no females visiting a lek, males occupy small discrete territories with definite boundaries from which all intruding rivals are normally evicted. On the other hand, when females are present,

males often leave their territories to approach the females. In these conditions, relationships more closely resemble those of a dominance hierarchy without clear reference to location. Despite these movements of males, copulations usually occur within males' territories as defined by boundary encounters (Hamerstrom and Hamerstrom, 1960, 1973). Robel (1967, p. 113) described successful males "escorting females to the center of activity [of the lek] prior to copulation."

Greater prairie chickens seem to represent an extreme among grouse in movements of males on a lek, although movements of displaying males away from their territories occur in other lekking grouse as well (Koivisto, 1965; Lumsden, 1965, 1968; Moss, 1980). As in prairie chickens, dominance relationships among male sage grouse become clearer after they move away from their previously established territories (Gibson and Bradbury, 1987).

The combination of dominance and territoriality applies to males of other lekking species as well. A territory is often defined as an area within which an individual dominates its rivals and has nearly exclusive access to resources (Waser and Wiley, 1979). Even without exclusive use of an area, dominance relationships can vary with individuals' locations (Brown, 1963; Piper and Wiley, 1989). Furthermore, in some cases not all territorial locations are equal. When better competitors defend better locations, the result is an "ideal despotic distribution" (Fretwell, 1972) or "polarized territoriality" (Wiley, 1973a). In this case, individuals are ranked in the end by the value of their locations, even though they interact primarily with immediate neighbors. Thus the questions are, To what extent do lekking males show evidence of ranking, even when they maintain nearly exclusive areas? and To what extent does location influence interactions, even when males' movements overlap?

Evidence for dominance relationships without respect to location comes from several tropical lekking species. Male long-tailed manakins use overlapping sets of display sites so that each display site is visited regularly by 3–15 males (McDonald, 1989a). At each site, dominance is clearly established between the two or three most frequent males. The top-ranking (alpha) male at one site tends also to dominate opponents at 1–3 nearby sites. In this case, individual males rise in dominance at the sites they use as more dominant males disappear (McDonald, 1989b). Male capuchinbirds also congregate for display without indications of territoriality; one male in each group dominates the others in access to the perch used for copulation (Snow, 1972; Trail, 1990). Limited observations of Goldie's bird of paradise, a species restricted to several small islands at the eastern end of New Guinea, suggest similar dominance relationships among males sharing a display site (LeCroy *et al.*, 1980; see also Snow and Goodwin, 1974).

Clear indications of dominance relationships also appear among male satin bowerbirds, which construct bowers of woven sticks at their dispersed display sites. Males steal bright decorations and sticks from each others' bowers, and

some males are much more successful at defending their bowers and stealing from neighbors than are others (Borgia, 1985a,b; Borgia and Gore, 1986). In addition, at artificial food sources away from their display sites, supplantations indicate a dominance hierarchy among males (Borgia, 1985a, 1986). It remains unclear, however, whether or not dominance at feeding sites is related to success in protecting bowers from rivals. Males' relationships might also influence the locations of their display sites, as males sometimes take over more successful individuals' sites when the latter disappear (Vellenga, 1980b). Bowerbirds, like manakins and capuchinbirds, have low annual mortality, so even studies extending over a number of years have obtained little information on turnover of males.

Studies of lekking grouse have also revealed that males continue their social relationships away from leks and during seasons with little activity at leks (Lumsden, 1965; Koivisto, 1965; Robel, 1969; Angelstam, 1984). The clearest description of this behavior pertains to male black grouse from a lek in the Netherlands (Kruijt *et al.*, 1972; de Vos, 1983; Kruijt and de Vos, 1988). These males tended to associate with each other elsewhere as well. When feeding, males seldom interacted, but they regularly interrupted any responses of other males to females. These interruptions were performed mostly by those males with peripheral territories at the lek, as if their zones of dominance over rivals extended radially outward from the lek. Furthermore, this site-dependent dominance or territoriality was polarized, as males took central positions on leks when they were available (Section III,B). Male common capercaillie also have large ranges that extend radially outward from leks, but the relationships of males in these areas is unknown (Hjorth, 1970; Wegge and Larsen, 1987; LeClerq, 1988).

Continuity in the relationships of males is also indicated by the observation that male grouse often maintain their spatial arrangements to some extent even when they move away from a lek to approach nearby females (Sections II,B and IV; Koivisto, 1965; Lumsden, 1968; Gibson and Bradbury, 1987). Continuing relationships of males throughout the year might also lead to low levels of aggression among males early in the season, as often observed (Wiley, 1973a; Moyles and Boag, 1981; Hartzler and Jenni, 1988; but see Koivisto, 1965).

Territorial relationships of males within leks are clearest when all males, even those generally unsuccessful in mating, can copulate successfully provided they get a chance at locations within their territories (Buechner, 1961; Buechner and Schloeth, 1965; Hjorth, 1970; Wiley, 1973a; Floody and Arnold, 1975; Bradbury, 1977; Beehler, 1983b; Kruijt and de Vos, 1988; Hartzler and Jenni, 1988; Andersson, 1989). In these cases, males generally adhere to territorial boundaries even in the presence of receptive females. In sage grouse, territorial boundaries often remain stable for periods of weeks, and males dominate all intruders in their territories even when females are on the lek. Males with little overall success in mating nevertheless copulate without interruption at locations inside their territories, provided females stay away from boundary zones one to a few

meters wide (Wiley, 1973a; Hartzler and Jenni, 1988). Within the boundary zone between territories, neighboring males interrupt each others' copulations reciprocally. Males with high overall success tend to have many females that solicit well inside their territories. Less successful males either have few females solicit inside their territories or attempt most of their copulations near their boundaries with more successful neighbors and thus have higher probabilities of interruption (Wiley, 1973a). In black grouse as well, copulations near territorial boundaries are more likely to be interrupted by neighbors (Kruijt *et al.*, 1972).

Success in interrupting copulations has been taken as evidence of a male's dominance on a lek (Scott, 1942; Lumsden, 1965; Foster, 1983). The preceding discussion, however, indicates that asymmetries in interruptions do not necessarily reflect dominance relationships in a simple way. If females tend to mate within particular males' territories, the neighbors of these males would have the greatest opportunities for interruptions. In Guianan cocks-of-the-rock, it is indeed the neighbors of the most successful males that interrupt the most copulations (Trail and Koutnik, 1986). The neighbors of successful males might also attempt most of their copulations near their territorial boundaries, where they would have a higher risk of disruption by neighbors (Wiley, 1973a).

Even when males can copulate without challenge within their territories, there are often indications of overall dominance relationships among those on a lek. The tendency of males to move their positions on leks toward the center, where most matings take place, recurs in a number of lekking species (Section III, B). In addition, boundary encounters when females are present on a lek are often asymmetrical. Those males farther from females tend to encroach on the territories of their neighbors closer to females, so that the former more often provoke encounters to which the latter respond and the latter more often terminate encounters in order to return to the females (Wiley, 1973a; Kruijt *et al.*, 1972; Kermott, 1982, p. 110). These patterns suggest that males in locations nearer females prevent other males from occupying those positions, so that males are in fact ranked by their territorial positions.

Hartzler and Jenni (1988) argued that polarized territoriality of this sort could not apply to the Ford's Creek Lek. The shifting locations of females on this lek make stable polarity in territorial relationships unlikely. Nevertheless, their maps indicate that some males did move their boundaries from one year to the next to include parts of areas where frequent copulation occurred the preceding year. Hartzler and Jenni (1988) also emphasize the relatively slow reoccupation of vacancies on grouse leks (Kruijt *et al.*, 1972; Wiley, 1973a). However, the settled relationships of neighboring males could also explain why interactions do not increase markedly when a vacancy appears. It would pay peripheral males to wait before they leap, if, as in black grouse, central males easily evict intruders after absences from the lek (Kruijt *et al.*, 1972; see also Snow, 1962a).

In conclusion, in most species males' relationships on leks do not conform

completely either to dominance, without influence of location, or to territoriality, without indications of ranking. The combined influences of ranking and location on males' relationships have rarely been considered explicitly. In particular, more information is needed on asymmetries in the territorial relationships of males on a lek and on site-dependent dominance among males away from leks.

B. AGE AS A FACTOR IN THE SOCIAL RELATIONSHIPS OF MALES

In most lekking species, as in many other polygynous species (Selander, 1972; Clutton-Brock *et al.*, 1977; Clutton-Brock, 1983; Alatalo *et al.*, 1988), young males have less developed secondary sexual characteristics than do older males. Male manakins retain a drab, female-like plumage for 3 years before attaining full development of bright male plumage (Snow, 1962a,b; Lill, 1974a, 1976; Foster, 1977a, 1981, 1987; McDonald, 1989a,b). Similar sequences of male plumages occur in many cotingas, both in species with leks and those with dispersed display sites (Snow, 1982). Male birds of paradise with leks and bowerbirds with dispersed display sites retain immature plumage even longer (Gilliard, 1969; Vellenga, 1980b). Male fallow deer and reduncinine antelope, including the lekking species, require several years to attain full body mass and antler size (Buechner and Roth, 1974; Clutton-Brock *et al.*, 1988a). Although female hammer-headed bats can breed at an age of 6 months, males do not attain full development of their enlarged larynx and active sperm until 18 months (Bradbury, 1977).

Among lekking grouse, males in their first year often have less developed tail feathers and other secondary sexual characters, although these distinctions are sometimes subtle or unreliable (Patterson, 1952; Eng, 1963; Dalke *et al.*, 1963; Koivisto, 1965). They are also smaller on average than older males (Beck and Braun, 1978). In common capercaillie, the largest grouse, growth to full size takes at least 2 years (Moss, 1987a,b). In addition, in sage grouse the esophageal sac used to produce characteristic sounds does not develop as rapidly during a male's first spring as in later years, so that first-year males attain full development only after the females begin to appear regularly on leks (Eng, 1963; Lumsden, 1968; Wiley, 1973a,b).

A similar delay in seasonal development applies to second-year male blue grouse, a species with dispersed display sites (Bendell, 1955). On the other hand, sexually monomorphic lekking species, such as hermit-hummingbirds (Stiles and Wolf, 1979), lack any age-related differences in males' morphology. For these species, it is not known whether or not young males' seasonal development lags behind that of older males.

In those species with delayed development of full size or secondary sexual characteristics in males, recognizably younger males often visit leks but do not participate fully in lekking activities. In manakins, males retaining some female-

like plumage briefly visit older males' display sites at leks (Snow, 1962a; Lill, 1974b, 1976; Foster, 1981; McDonald, 1989a). They sometimes claim these sites when the older males vacate them during the annual molt, but they are evicted quickly when the older males return (Snow, 1962a). In black grouse, yearling males intruding on a lek often evoke little attention from established males, unless they begin to display (Kruijt *et al.*, 1972; de Vos, 1983). Young male sage grouse often join groups of females visiting leks and thus temporarily escape notice by territorial males (Wiley, 1973a). Young male fallow deer infiltrate leks in the interstices of older males' territories (Clutton-Brock *et al.*, 1988a).

In sage grouse, younger males do not usually establish territories on leks until after females begin to visit regularly (Patterson, 1952; Eng, 1963; Emmons and Braun, 1984). They display for brief periods at first and do not occupy any one area consistently (Wiley, 1973a; Hartzler and Jenni, 1988). Seasonal delay in regular attendance of yearling males at leks has not been well documented in other lekking grouse, although it has been noted for common capercaillie (Dement'ev and Gladkov, 1967). In Norway, males of this species do not establish stable territories until the end of their second spring (Wegge and Larsen, 1987).

Young males of lekking species often have less stable locations for display than do older males. In several species of grouse, yearlings are known to visit several leks while older males with few exceptions attend only one (Dalke *et al.*, 1963; Koivisto, 1965; Robel, 1967; Robel *et al.*, 1970; de Vos, 1983; Emmons and Braun, 1984; Wegge and Larsen, 1987). First-year males normally establish territories at the peripheries of existing leks (Robel, 1967; Robel and Ballard, 1974; Koivisto, 1965; Wiley, 1973a; Kruijt *et al.*, 1972; de Vos, 1983; Moyles and Boag, 1981). Although yearling male black grouse in the Netherlands sometimes established territories late in the season in the central parts of leks, these males had all lost their territories by the following season, so that all 2-year old males held peripheral territories (de Vos, 1983). In lekking species other than grouse, young males also visit more than one lek before establishing stable positions (Buechner and Roth, 1974; McDonald, 1989a,b) and display from peripheral positions (Beehler, 1983b; Trail, 1984, p. 160). In Trinidad, immature male white-bearded manakins displayed at a "practice lek" separate from the leks used by older males where copulations occurred (Snow, 1962a). In sage grouse, yearling males also sometimes display near groups of females at locations away from leks (Dunn and Braun, 1986).

In species with solitary display sites, like the bearded bellbird and several forest-inhabiting grouse, yearling males also display either less than older males or not at all and often tend to take positions near the peripheries of established older males' territories (Snow, 1973; Gullion, 1967, 1981; Bendell and Elliott, 1967; Bendell *et al.*, 1972; Zwickel, 1972; Hannon *et al.*, 1979; Ellison, 1971). Yearling male blue grouse preferentially settle near those display sites of older

males visited more frequently by females (Lewis and Zwickel, 1980, 1981; Jamieson and Zwickel, 1983).

In studies of lekking grouse, first-year males either have never copulated successfully (Koivisto, 1965; Robel, 1967; Wiley, 1973a; Moyles and Boag, 1981; Hartzler and Jenni, 1988) or have only copulated infrequently (de Vos, 1983; Hjorth, 1970; Hartzler and Jenni, 1988). Hamerstrom and Hamerstrom (1973) found that 18% of copulations by male greater prairie chickens during a 22-year study were performed by yearling males. Their extensive data on the age structure of this population based on marked individuals suggest that on average 34% of males were yearlings. Assuming that yearling and older males were observed equivalently, copulation rates/male averaged about 2.3 times higher for older males. This pattern of little or no copulation by males in their first breeding season, and sometimes even later, recurs in all lekking species: in fallow deer and kob (Buechner and Roth, 1974; Clutton-Brock *et al.*, 1988a; Appolonio *et al.*, 1989a,b), in ruff (Hogan-Warburg, 1966), in manakins and cock-of-the-rock (Snow, 1962a; Lill, 1974a, 1976; Trail, 1985a), and in hermit-hummingbirds (Stiles and Wolf, 1979; Snow, 1974). It also applies to species with dispersed display sites (Snow, 1973; Payne and Payne, 1977; Borgia, 1986).

The possibility that young males' behavior is simply an alternative tactic for copulation seems unlikely, although the tendency of some yearling males to mingle with groups of females might suggest this possibility. In sage grouse, yearling males that join groups of females on leks have never been seen to copulate. The current evidence suggests that young males in these species instead make less commitment to competition for territories and mates. Nevertheless, a male should in general take any adventitious opportunity for copulation; infrequent copulations by first-year males probably need no other explanation.

Do behavioral interactions with older males control the development of reproductive physiology and morphology in younger males? Social interactions with older, dominant males might inhibit reproduction by younger subordinates (see Vandenberg, 1971); alternatively, young males might fail to develop full reproductive behavior and physiology regardless of interactions with older males (see Wiley and Hartnett, 1976). An investigation of this behavioral and physiological question would involve comparisons of first-year males subject to interactions with older males and others not subject to such interactions. Removals of older males from leks would also provide relevant information, but no fully satisfactory experiments along these lines are available for lekking species. Systematic removal of older males from leks of the common capercaillie suggested that the seasonal development of young males was to some extent independent of their interactions with older males (Kirikov cited by Dement'ev and Gladkov, 1967, p. 97). This experiment, however, did not preclude interactions between age classes away from the lek.

Interactions with older males might have more influence on where, rather than when, younger males establish themselves. Two studies that removed central males from leks of greater prairie chickens and sharp-tailed grouse showed that additional males established themselves on these leks primarily at peripheral locations, while nearby undepleted leks did not acquire additional males (Ballard and Robel, 1974; Rippin and Boag, 1974a,b). It is probable that the recruits in these studies were previously unestablished yearling males, although they were not examined in the hand as required to determine the ages of males in these two species. Radio-tracking, however, showed that young males often visited several leks at this time (Robel *et al.*, 1970), and no males previously established on nearby leks moved to the experimentally depleted ones (Rippin and Boag, 1974a). In grouse, the formation of new leks in response to increasing populations can also involve mostly yearling males (Cannon and Knopf, 1981).

It seems plausible that young males of lekking species prospect for optimal locations to establish themselves. For instance, yearling male sharp-tailed grouse are attracted to leks used by large numbers of females, even when male mortality on these leks is higher than elsewhere (R. L. Brown, reviewed by Bergerud and Gratson, 1988, p. 503). Male black grouse tend to establish territories at locations where they interact with females or other males (de Vos, 1983), and the same might apply to yearling male sage grouse (Emmons and Braun, 1984).

These patterns in the behavior of immature males in lekking grouse are remarkably similar to extensively documented patterns in blue grouse, a species with dispersed display sites. Yearling males' testes develop later in the season and never reach the same size on average as do those of older males, although yearlings do produce viable sperm (Bendell, 1955; Hannon *et al.*, 1979). Yearlings also arrive in breeding areas later than do older males, at about the same time that females arrive, and preferentially localize their activities at the periphery of older males' territories, particularly those territories that most frequently have females nearby (Bendell and Elliott, 1967; Bendell *et al.*, 1972; Zwickel, 1972; Lewis and Zwickel, 1980, 1981; Jamieson and Zwickel, 1983). When older males are removed from their territories, yearlings occupy the vacancies, although some yearlings remain nonterritorial despite the persistence of vacancies (Bendell and Elliott, 1967; Bendell *et al.*, 1972; Zwickel, 1972). Nevertheless, these territorial yearlings do not develop gonads any larger than those of nonterritorial yearlings collected at the same time (Hannon *et al.*, 1979).

Age-related differences in behavior might continue even after males have reached full adult development. Long-tailed manakins provide a clear example (McDonald, 1989a,b). Males with fully developed plumage become regular attendants at display sites of more senior, dominant males, which perform nearly all the copulations. Only after persisting in subordinate status until the dominant male disappears can a younger male acquire dominance at a small zone with 1–3 display sites. Survival is high in this species, so that males of known age have

never become dominant at display sites before age 8. Band-tailed manakins have a similar succession of males from subordinate to dominant status in a display territory; final stages of courtship are again performed only by dominant males. In this species, however, one of two cases of succession involved a reversal of the relationships of the two top-ranking males in a territory; in the other case, succession of the second in rank followed disappearance of the dominant male (Robbins, 1985). In these two species, succession to mating status occurs among males ranked in a dominance hierarchy.

Alternatively, succession could occur by movements of males from less to more advantageous locations. In species like some lekking grouse, in which first-year males establish territories at the peripheries of leks and established males tend to retain their territories from year to year (Kruijt *et al.*, 1972; Evans, 1969; de Vos, 1983; Hartzler and Jenni, 1988), young males might well have to wait for vacancies to obtain better locations. In some cases, social interactions at leks might produce a stochastic progression of males toward central locations where most copulations occur (Kruijt *et al.*, 1972; Wiley, 1973a, 1978). Such a process would generate a correlation of mating success with seniority and age. This correlation, however, would presumably not be strong, because the irregular geometry of most leks and the stochastic nature of mortality would create considerable variation in the progression of males. In addition, individual differences in males' capabilities and physiological condition would introduce further variation.

Seventeen years of data on marked black grouse at one lek in the Netherlands showed that males were progressively more likely to occupy central territories and to have higher mating success with increased age at least through age 5; thereafter males appeared to lose vigor, so that they often lost their territories and declined in mating success. The mean rate of copulation for males in their third through fifth years was 2.8/year, approximately a 4-fold increase over that for males in their first or second years. The former were also nearly twice as likely to hold central territories (42 and 23%, respectively) (Kruijt and de Vos, 1988), where most copulations occurred (Kruijt and Hogan, 1967). Males in fact were four times more likely to shift territorial boundaries toward the center of a lek than toward the periphery (de Vos, 1983). Males that moved had always been unsuccessful in their previous locations. In confirmation of the greater competition for central positions, vacancies of central territories were filled more quickly than vacancies of peripheral territories (Kruijt *et al.*, 1972).

For the common capercaillie, Wegge and Larsen (1987) reported that males only exceptionally moved to fill vacancies. The areas involved, however, are ranges extending 0.5–1 km from the lek. Because the ranges of different males regularly visiting a lek were, for the most part, exclusive, Wegge and Larsen (1987) called them territories, although evidence of defense or dominance was not obtained. The spatial organization of males within the lek was not investigat-

ed. On the other hand, they reported that 3-year-old males had larger ranges located farther from the lek than did older males (mean areas 61 and 26 ha, respectively); the youngest male known to have mated was 4 years old. These findings suggest the possibility of succession in status, but perhaps not associated with changes of location.

On relatively large leks of sage grouse, males have been found to move their territories into vacancies closer to a mating center. In each of four instances, a neighboring male located farther from females moved its territory into a vacancy over periods of several days (Wiley, 1973a). In contrast, at the Ford's Creek Lek, which lacked a stable mating center (Section II,D), there was no clear movement of territories toward positions frequented by females and no improvement of mating success with age after a male's second year (Hartzler and Jenni, 1988). The question of territorial succession in sage grouse cannot be answered without more observations on vacancies and movements of territories on a number of leks.

Movements of territories to fill vacancies closer to the center of a lek have also been observed in hermit-hummingbirds (Stiles and Wolf, 1979), white-bearded manakins (Snow, 1962a), and Uganda kob (Floody and Arnold, 1975). On leks of kob and topi, mating tends to occur in central territories (Floody and Arnold, 1975; Fryxell, 1987; Gosling and Petrie, 1990). In Guianan cock-of-the-rock, males progress from being intruders on leks, to holding peripheral and eventually central territories (Trail, 1984, pp. 157–158). Among mature males, individuals tended to move their small territories around a display court closer to successful males, but these moves were not restricted to occupation of neighboring vacancies. Males that moved their territories, whether previously successful or unsuccessful, were less likely to mate in the following year than were comparable males that did not move. However, once a male mated successfully, he became much less likely to move again. In this species it thus seems probable that a male's success in mating depends both on the location of his court within a lek and on his occupation of it for several years during which females become familiar with him. Mating success of marked males increased on average with age (Trail, 1984).

The clearest evidence for territorial succession in lekking species comes from experimental removals of central males. In greater prairie chickens, for instance, after removal of 2–3 males in central positions on leks with 7–9 established males, the remaining birds that previously had peripheral positions shifted their ranges to more central positions where copulations occurred (Ballard and Robel, 1974). This study, however, failed to collect information on the boundaries of males' territories, as revealed by aggressive interactions, as opposed to their ranges on the lek. On a lek of white-bearded manakins, when two successful males were removed, neighbors occupied the vacancies, either immediately or eventually, and copulated successfully (Lill, 1974a).

Removals of central male sharp-tailed grouse from two leks induced similar changes (Rippin and Boag, 1974a,b); vacancies created in the center of a lek were first filled by males originally located adjacent to the center and then, after these were removed, by males originally in peripheral locations. Evans (1969) provides a clear illustration of the movement of a male sharp-tailed grouse's territory toward the center of a lek; in this case, the movement consisted of a partial withdrawal from the male's original territory during the autumn and complete withdrawal by the following spring. Hjorth (1970) also illustrates a shift in territorial boundaries, in which two yearling neighbors divided an area vacated by a 2-year-old male after he was trapped on the lek. In this case, the two yearlings both copulated in their newly acquired areas. In general, copulations tend to occur near the centers of leks in this species (Lumsden, 1965; Hjorth, 1970, p. 412; Kermott, 1982).

This pattern of territorial succession in sharp-tailed grouse was confirmed by Moyles and Boag (1981). Males began to establish territories in the first autumn, although some were not permanently established at a lek until their second autumn. These young males first took peripheral positions on leks, where they displayed little aggression or constancy in attendance at first. They then moved their positions to occupy vacancies toward the center of a lek, so that mating success depended in part on seniority at a lek. By mapping males' territories on a lek in three successive years, Kermott (1982) also documented this process. In five cases, males with peripheral territories acquired central territories in adjoining locations in subsequent years; no transitions from central to peripheral territories occurred.

An increase in aggressiveness is not usually sufficient to change the territorial locations of male sharp-tailed grouse. Trobec and Oring (1972) implanted testosterone pellets in five males on one lek in May, late in the breeding season. Although the implanted males engaged in more aggressive interactions, predominantly with more centrally located males, none managed to evict an opponent or to enlarge its territory. Trobec and Oring's finding thus suggests that current behavioral interactions do not alone explain social relationships and the distribution of mating success on leks. Leks evidently exhibit "social inertia" (Guhl, 1968).

Hormonal manipulations of males on leks would bear further investigation. In birds with relatively large, all-purpose territories, males implanted with testosterone in some cases increase the sizes of their territories and in some cases do not (Watson and Parr, 1981; Wingfield, 1984). In sharp-tailed grouse, there is one well described case of an unusually aggressive yearling male that obtained a central territory and mated successfully (Kermott, 1982, p. 66). It seems possible that hormonal manipulations would have the greatest effect early in the season before territorial boundaries are set.

In some species with dispersed display sites, males also move to occupy sites

vacated by successful males (Payne and Payne, 1977; Shaw, 1984). For instance, in village indigobirds, following removal or disappearance of five successful males, less successful males relocated to claim the vacated sites (Payne and Payne, 1977). In three cases, their subsequent mating success was not followed. In the other two cases, respectively, a newcomer copulated successfully within a few days and a series of males all failed to copulate. Future experiments of this sort, with adequate replication, might compare removals of successful and unsuccessful males.

This review of the behavioral interactions of males on leks shows how sparse the available evidence remains. We lack a study that incorporates all of the following: (1) observations of several leks, (2) mapping of territorial boundaries and copulations based on complete observations or unbiased sampling, (3) permanently identified individuals followed for most of their lives, and (4) adequately replicated experimental manipulations.

C. COOPERATION AND COORDINATION OF MALES

Perhaps the most striking form of male–male interaction on leks occurs in those species in which two or more males coordinate their efforts. The unique case of the ruff apparently involves cooperation of two male morphs, those with predominantly white ruffs and head tufts and those with any of various darker colors. When white males, termed “satellites,” visit leks, they display submissive behavior to resident territorial males (Hogan-Warburg, 1966). Although a resident attempts to drive away satellites once females are present on his territory, satellites nevertheless obtain some copulations (Hogan-Warburg, 1966; van Rhijn, 1973). Individual satellites seem to form associations with particular territories on a lek, but these associations might result simply from their attraction to territories in which females gather. Because the coloration of the breeding plumage is retained throughout life and thus presumably has a genetic basis, the persistence of this polymorphism requires some form of balancing selection (Hogan-Warburg, 1966; van Rhijn, 1973, 1983, 1985). Hogan-Warburg (1966) argued that satellites on small leks are more successful and contribute more to the success of resident males. It has also been proposed that the presence of a satellite on a resident’s territory increases the chances that a female will copulate (Hogan-Warburg, 1966; Shepard, 1975). van Rhijn (1973) could not confirm these suggestions and instead proposed that the presence of a satellite male enhances the attraction of females to a resident’s territory (van Rhijn, 1973, 1985). Although there is little quantitative evidence to evaluate any of these points, there are indications that residents and satellites might interact cooperatively to enhance mating success by both males and also that competition occurs between them as well.

No other lekking species has comparable male polymorphism. Coordination of

displays, however, raises similar issues of cooperation and competition. In the long-tailed manakin (Foster, 1977a; McDonald, 1989a,b) and its congeners with similar displays (Snow, 1977; Foster, 1981), the strikingly coordinated efforts of two males are related to succession of males in dominance at display sites. In these species, two males produce a loud call in unison when females are not present nearby. In long-tailed manakins, the rate of coordinated calling correlates with female visits to a display site (McDonald, 1989a). When a female arrives, the two males engage in a coordinated dance, which consists of alternating performances of similar actions. The subordinate male of the pair, however, always retires before the final preliminaries to copulation, which is always performed by the dominant male. The subordinate might realize some eventual benefit, because when a dominant male disappears, the subordinate becomes the new dominant at the same site (McDonald, 1989a,b). This succession, however, does not necessarily result in immediate benefits for the new dominant, as visits by females in one case decreased markedly in the first year. These birds have such low mortality, however, that data are slow to accumulate on the consequences of takeovers. The possibility of eventual benefits from inheriting a display site could help to explain a subordinate’s assistance in attracting and stimulating females by means of coordinated vocalization and display.

In several other tropical lekking birds, males also coordinate displays (Snow, 1963; Foster, 1977, 1981; LeCroy *et al.*, 1980; Robbins, 1983, 1985; Prum, 1985, 1986; Prum and Johnson, 1987). Some of these cases involve two males performing similar displays in stereotyped alternation, as in the wire-tailed manakin (Schwartz and Snow, 1978), and in other cases performing synchronized or alternating calls, as in the calls of some birds of paradise of the genus *Paradisaea* (Gilliard, 1969, p. 410; Dinsmore, 1970; LeCroy, 1981). Male capuchinbirds time their loud calls to avoid overlap with other males on their lek (Snow, 1972). Remarkable coordination also occurs in sharp-tailed grouse, although it is not emphasized in reports on this species (Lumsden, 1965; Hjorth, 1970; Kermott and Oring, 1975). Males have specially modified tail feathers that are scraped together to produce a staccato rattle. At intervals all males on a lek cease and stand in place; after a pause of several seconds, they resume abruptly, producing a dramatic acoustic effect.

These instances of coordination might represent males’ attempts to outdo each other in competitive display, or they might represent collective signals that attract females, or both (Avery, 1984). The brief synchronized silences during tail-rattling by sharp-tailed grouse are difficult to interpret solely in terms of competitive display by individual males. Instead, these coordinated displays might represent cooperative efforts to attract and stimulate females. Since male sharp-tailed grouse tend to move their territorial locations toward the center of the lek, where most copulations occur, cooperation in display might have evolved in conjunction with succession of social positions, as in long-tailed manakins.

Less striking forms of coordination occur in other species in the form of contagious display. This possibility has again received little attention, although observers occasionally note its occurrence (Snow, 1962a; Snow and Goodwin, 1974). Display by one male tends to stimulate display by nearby males. This form of coordination in display is easily explained by competition among individual males. No male would do well to be outdone by its neighbor, if it could help it. Nevertheless, it is not inconceivable that the collective aspects of simultaneous display by aggregations of males might also have some influence on females that displays by individual males would not (Section V,D).

If coordinated or contagious display represents a form of reciprocal altruism (Avery, 1984), all males involved must realize some increased expectation of mating success in the long run. In addition, there must be some means of denying advantages to noncooperators (Axelrod and Hamilton, 1981). Territorial succession or succession in dominance could provide both of these essentials, if noncooperators were less likely to improve their locations or status (see Wiley and Rabenold, 1984). These possibilities for lekking species have not received attention.

IV. RESPONSES OF MALES TO FEMALES

An aspect of the behavioral mechanisms of lekking that has received little systematic attention is the response of males to females. In part this neglect results from observations that males congregate and establish territories in the absence of females.

Almost every report on lekking species, as well as on species with dispersed display sites, indicates that males visit leks both earlier and later in the season than do females. In nonmigratory lekking species, males often visit leks throughout the year except during periods of molting and physiological stress. Thus, males of lekking grouse visit their leks from the earliest mild days in late winter or early spring until their period of molt in late summer and then, in most species, again during the autumn until severe weather begins (Patterson, 1952; Lumsden, 1965; Koivisto, 1965; Hammerstrom and Hammerstrom, 1973; de Vos, 1983; Vehrencamp *et al.*, 1989). In tropical species, males also visit their leks almost throughout the year except during molt (Snow, 1962a,b; Trail, 1984). Attendance at leks, however, drops or ceases during periods of short food supply (Snow, 1962a), which can be an annual occurrence in seasonal climates (Foster, 1977b; Worthington, 1982). Male fallow deer, which occupy their territories on leks continuously during the brief rut, nevertheless attend both several days earlier and later than do females (Clutton-Brock *et al.*, 1988a; Appollonio *et al.*, 1989a). Males of tropical lekking antelope also visit their leks throughout the year, except during seasons of sparse food in highly seasonal environments

(Buechner and Roth, 1974; Schuster, 1976). The pattern thus suggests that males of many lekking species spend as much of their time as possible at their leks and leave only as necessary for food or during periods of increased susceptibility to predators such as during molt.

The same principal applies to daily attendance as well. Males of lekking deer and reduncinine antelope continuously occupy their territories at leks for periods of several weeks, with little food (Buechner and Roth, 1974; Floody and Arnold, 1975; Fryxell, 1987; Clutton-Brock *et al.*, 1988a). Males of lekking birds, hammer-headed bats, and topi leave their leks daily in order to feed (Bradbury, 1977; Gosling and Petrie, 1990). Nevertheless, in all species, males attend their leks for longer periods each day than do females. Once again, males appear to spend as much time as possible on their leks and leave primarily when necessary for feeding and drinking.

Although males interact with each other for long periods in the absence of females, they respond in several obvious ways to females. These responses include (1) movements toward females, (2) changes in tactics and rates of display, and (3) copulation.

The first of these responses is clear when males on leks move as a group to approach nearby females (Section II,B). This tendency to approach females is confirmed by responses of males to groups of taxidermic mounts of females. Male sharp-tailed grouse were attracted to sites as much as 100–200 m away from established leks by mounted females, although no information was provided about the ages or previous territorial histories of the males that responded (Bergerud and Gratson, 1988). According to Bergerud and Gratson (1988), R. L. Eng found that taxidermic mounts of females also attracted male sage grouse away from an established lek. In three experiments with black grouse in the Netherlands, de Vos (1983, pp. 38–42) showed that nonterritorial and yearling males in particular were attracted to taxidermic mounts of females or to caged decoys. Displaying to a female appeared to stimulate a male to establish a territory that included the female's location. There were indications, however, that a male's attachment to the site waned gradually in the absence of further interactions with females.

The result might differ when taxidermic mounts of females are placed within territories on a lek. In an experiment in 1969, I found that four mounted females in normal postures inside a territory on the periphery of a large lek, about 50 m from an active mating center, resulted in no clear attraction of other males. On a lek of sharp-tailed grouse, Kermott (1982, p. 115) also found that a taxidermic mount, although energetically courted when placed within a male's territory, would not induce neighboring males to leave their territories even when the resident male was temporarily absent.

The way in which groups of males approach females depends on the responses of individual males. In lekking grouse, males with no females in their territories

spend most of their time displaying on the sides of their territories closest to females elsewhere on the lek (Kruijt *et al.*, 1972; Wiley, 1973a). These males tend to encroach across their boundaries with neighbors that are closer to females. Each male thus spends most of his time displaying as close as possible to the females and at intervals interrupts his displays to dash across his territory to encounter encroaching neighbors also trying to approach the females (Wiley, 1973a; Kermott, 1982, p. 110). Similar tendencies evidently also apply to black grouse and Uganda kob, in which aggressive interactions are most frequent along territorial boundaries nearest locations where females gather and copulations occur (Kruijt *et al.*, 1972; Floody and Arnold, 1975). These tendencies could easily result in a group of males moving as a unit away from their usual locations to approach nearby females. The nearest peripheral male only needs to move outward away from the other males and toward the females; the immediate neighbors could then also move toward the females, and so forth.

Lekking males often change their tactics of display depending on the presence of females on the lek or even their distance from females' locations within a lek. Many species have displays that in part permit accurate location of a lek or display site by nearby females, such as the various jumps and short flights performed by some species of lekking grouse (Lumsden, 1965; Hjorth, 1970; Kruijt *et al.*, 1972), ruffs (Hogan-Warburg, 1966; van Rhijn, 1973), buff-breasted sandpipers (Myers, 1979), and Jackson's widowbirds (Andersson, 1989) and certain calls or mechanical sounds produced by tropical lekking birds and bats (Bradbury, 1977; Snow, 1973; McDonald, 1989a). The "flutter jump" displays of several species of lekking grouse are released particularly by females flying near a lek or by their calls (Hamerstrom and Hamerstrom, 1960; Koivisto, 1965; Kermott, 1982, p. 25). The performance of these displays decreases once females have arrived near a male. Sometimes males on a lek at a distance from females continue these displays after other males closer to females have desisted.

Proximity to females in general tends to increase rates and intensity of display. During the 2 hrs. following sunrise, when females are most numerous on leks, male sage grouse with females in their territories usually performed "strut" displays at rates of 6–6.5/min; in comparison, males with no females in either their own or neighboring territories usually displayed at rates of 1–1.5/min (Wiley, 1973a). Males with females in neighboring territories, but not in their own, displayed at intermediate, and highly variable, rates. During the middle of April in 2 years, Hartzler and Jenni (1988) report 21 and 22% increases in rates of display when male sage grouse had females within 3 m (6.6 and 6.2 displays/min) in comparison to when they did not (5.4 and 5.1 displays/min). As territories were roughly 5–10 m in diameter, females within 3 m would be either within the male's own territory or near the boundary of a neighbor's territory. Although few measurements are available, many other observers note in passing that lekking males increase their rates of display when females are nearby (Snow,

1962a; Robel, 1964; Hogan-Warburg, 1966; Kruijt *et al.*, 1972; Lill, 1974a, 1976; Beehler, 1983b; Trail, 1984, p. 223; LeClerq, 1988).

Once females have approached closely, males of lekking species generally switch to a series of intricate movements around the females and sometimes different vocalizations or sounds. These close-range tactics have been particularly well described for several species of manakins (Snow, 1962a; Lill, 1974a, 1976; McDonald, 1989a), ruff (Hogan-Warburg, 1966; van Rhijn, 1973; Shepard, 1975), and black grouse (Kruijt *et al.*, 1972). Male ruffs crouch and freeze when females enter their territories. The act of rising from this position seems to trigger solicitation for copulation in females (Shepard, 1975). In black grouse, males repeatedly perform "rookooing" displays while moving in circular or semicircular paths around the female. These movements sometimes appear to herd females farther into the male's territory and sometimes appear to represent a gradual testing of the female to determine whether or not she will hold still for mounting and copulating. When a female leaves a male's territory, the male often performs a characteristic movement of turning directly away from her, presenting his undertail coverts and "rookooing" toward locations of previous copulations in his territory, a tactic that sometimes appears to attract the female back (Kruijt *et al.*, 1972).

Quantitative study of these movements has proved difficult, as a consequence of their complexity, but would repay more effort. Kruijt (1967) adopted the innovation of placing a taxidermic mount of a female in normal walking posture on a small sled that could be pulled back and forth with a simple rope and pulley. During my work with sage grouse, borrowing Kruijt's idea, I filmed four males as they interacted with a stuffed female on a small, moveable sled. The subjects were all in their second year or later, and they occupied neighboring territories but had different levels of mating success. The tests were conducted on days when females had visited the lek but at times during the morning after all females had left the subjects' territories and all neighboring territories. These experiments showed that male sage grouse have tactics for display that closely resemble those described for black grouse, although they are not often so apparent in the birds' normal behavior because females so frequently associate in groups. All males in this small sample responded vigorously to the model without any major differences in tactics.

The ultimate response of a male to a female on a lek is copulation. Males of lekking birds, like males of many other birds, eventually attempt to mount and copulate with any motionless female and probably virtually any motionless object of approximately the correct size (Lill, 1974a). More interesting are the apparent restraints on males' copulatory responses to females, in view of the enormous time and effort spent obtaining a chance to copulate. Forced copulations, in which males aggressively subdue resisting females, are not reported for any lekking species. Many investigators emphasize that the decision to copulate

is the female's (Selous, 1927; Wiley, 1973a; Lill, 1974a, 1976; Bradbury, 1977; Beehler, 1983b, 1987a; Kruijt and de Vos, 1988; Clutton-Brock *et al.*, 1988a; McDonald, 1989a; Trail and Adams, 1989). In all lekking species, copulation is invariably preceded by the female adopting a special solicitation posture. Any female that is not ready to copulate simply scoots away when approached too closely by a displaying male. When this happens, males do not pursue but instead resume display. Even males that never copulate within a season refrain from aggressive attempts at copulation.

It is interesting to note that there are two reports of abnormal female sage grouse that have aggressively attempted copulation with other females (Scott, 1942; Wiley, 1973a). These females matched others in plumage and size and joined groups of females on the lek. Unlike other females, they repeatedly attacked nearby females, especially soliciting ones, grabbed their necks, mounted, and attempted to copulate like a male. The victims, some of which lost beakfuls of feathers to the assailant, struggled away from these attacks as quickly as possible.

This abnormal behavior illustrates two points: attempts at forced copulation are within the realm of possibilities for at least this lekking species, and even aggressive attempts at copulation in these circumstances are not successful without the partner's cooperation. For ducks, it has been argued that females eventually submit to forced copulations to avoid physical injury (McKinney *et al.*, 1983). In contrast, male sage grouse, even those that are otherwise unsuccessful in mating, do not attempt forced copulations, and females apparently do not submit. In general, males of lekking species, despite strong responses of other sorts to nearby females, normally act with restraint in attempting copulation.

V. RESPONSES OF FEMALES TO MALES

Much attention in investigations of lekking species has focused on the responses of females to males, in order to identify the mechanisms for female choice of mating partners. Most of these studies have sought correlations between measures of males' morphology or behavior and their mating success or visits by females. Before considering these findings, it is useful to examine the behavior of females in approaching and visiting leks.

A. INTRODUCTION TO THE BEHAVIOR OF FEMALES AT LEKS

In all lekking species, females usually visit a lek on several days before copulation (Lumsden, 1965; Kruijt and Hogan, 1967; Clutton-Brock *et al.*, 1988a; McDonald, 1989a; Pruett-Jones and Pruett-Jones, 1990). Furthermore, during

these visits to a lek, a female often visits more than one male's territory. Even in the case of a lek of fallow deer, in which the most successful males held territories on the side from which females approached in their regular daily movements, most females visited several males before mating (Apollonio *et al.*, 1989b).

The manner in which females approach a lek in some cases suggests that they obtain an overview before making any close approaches to individual males. Thus, female manakins, cocks-of-the-rock, and birds of paradise in tropical forests usually first perch in trees above or near the congregation of males' display perches and then visit several males in succession (Gilliard, 1962; Lill, 1974a, 1976; Trail, 1985a; Beehler, 1983b; Trail and Adams, 1989). Female sage grouse often arrive at a lek in dim light before sunrise, at a time when males display almost continuously. In typical approaches, females fly directly over the aggregation of displaying males (Wiley, 1973a). While in flight over the lek, they utter a distinctive call. Female sharp-tailed grouse approaching a lek also utter a distinctive call, which appears to stimulate male display (Lumsden, 1965). Female black grouse tend to land in central territories on a lek or, if they have landed in the periphery, to walk immediately toward the center (Kruijt and Hogan, 1967).

After landing near the periphery of the lek, female sage grouse proceed, as it becomes light enough to see well, to walk toward the center and to join other females (Wiley, 1973a). While thus walking, females tend to avoid displaying males; they are less likely to stop walking near a displaying male than near another female (Wiley, 1973a). Female black grouse also walk slowly among the displaying males and avoid those that approach them (Kruijt and Hogan, 1967). Aside from the evidence of their presence on the lek, the females appear superficially indifferent to the males, until they begin to adopt solicitation postures. Female kob and topi entering a lek likewise tend to avoid males and to approach other females (Gosling and Petrie, 1990; Balmford, 1990).

Females of lekking grouse usually mate only once before laying a clutch (Lumsden, 1965; Kruijt and Hogan, 1967; Robel, 1970; Hamerstrom and Hamerstrom, 1973; Robel and Ballard, 1974; Wiley, 1973a). Kruijt and de Vos (1988) reported that about 20% of females mate two or three times in a season, usually with the same male. This usual equivalence of one copulation with one clutch allows easy interpretation of the mating success of lekking male grouse. In ruffs, on the other hand, females often copulate with more than one male during a single visit to a lek (Hogan-Warburg, 1966; van Rhijn, 1973), and in golden-headed manakins females copulate up to 6 times over a period of 1–3 days for each clutch (Lill, 1976).

Studies of marked or radio-equipped females have often revealed that some of them visit more than one lek in a season. In golden-headed manakins over a third of known females were observed visiting two leks less than 200 m apart, al-

though observations at each lek covered only half of the time; nevertheless, 98% of females seen at two leks mated at only one of them and 94% of females showed strong or absolute preferences for single males (Lill, 1976). Female grouse and birds of paradise also often visit more than one lek in a season (Robel *et al.*, 1970; Kruijt *et al.*, 1972; Pruett-Jones and Pruett-Jones, 1990). Radio-tracked female sage grouse have home ranges large enough to include an average of 2.2 leks (Bradbury *et al.*, 1989b).

On the other hand, some females show remarkable faithfulness to a particular male or location when copulating more than once (Kruijt and de Vos, 1988; Lill, 1974a, 1976; Trail and Adams, 1989; Pruett-Jones and Pruett-Jones, 1990; Balmford, 1990). In white-bearded and golden-headed manakins, females often returned directly to the same display site and partner and copulated with few preliminaries when they were reneesting within any one season. Future work must address questions about possible differences in the behavior of females at the different leks they visit and in the age or previous experience of females that visit more than one lek or male and those that do not. Nevertheless, it is clear that females visit a number of males and often more than one lek before mating.

The highly unequal distribution of matings among males on leks and the absence of forced copulations indicate that females must in some way largely concur in decisions about mating. There are four possibilities for the mechanism of this concurrence: (1) females could use similar criteria in selecting males with particular individually distinctive features; (2) females could use similar criteria based on the overall distribution of males or stimulation on a lek; (3) females could use similar criteria in choosing a location with particular environmental features, such as microtopography or vegetation; and (4) females could copy each other. Individual females might use a combination of these mechanisms, perhaps in some hierarchical order; concurrence in choice would be preserved if all females combined these mechanisms in the same way.

The first and second possibilities are considered in the immediately following sections. The third possibility has no support: even though leks tend to occur in locations with certain topographic or vegetational features (Section II,A), no report has ever suggested that these features were sufficient to specify the locations of leks or of copulations within leks. Nevertheless, it remains possible that females are not completely inattentive to vegetational or other environmental features in their mating decisions. The fourth possibility is the subject of Section VI.

B. RESPONSES TO THE OVERALL ARRANGEMENT OF MALES

There is circumstantial evidence that females might use the overall spatial arrangement of males in choosing a place to copulate. Females in many lekking species copulate more often in central than in peripheral portions of a lek, although not necessarily at its geometric center (Koivisto, 1965; Robel, 1966;

Wiley, 1973a; Lill, 1974a; Floody and Arnold, 1975; Kermott, 1982; Trail, 1984; Fryxell, 1987; Hartzler and Jenni, 1988; Clutton-Brock *et al.*, 1988a; Gosling and Petrie, 1990). In black grouse, central territories (those with neighbors on all sides) attract more females, and males with central territories are more likely to copulate (Kruijt and Hogan, 1967; Kruijt *et al.*, 1972). On leks of greater prairie chickens, records from a 22-year study showed that copulations occurred over twice as frequently in central as in peripheral territories, although there were more males with peripheral territories (Hamerstrom and Hamerstrom, 1973). Hogan-Warburg (1966) found examples of successful males located near the peripheries of leks of ruffs, but Shepard (1975) reported a tendency for females to solicit for copulations in central territories on two of the three leks she studied. However, the small numbers of resident males on these leks made it difficult to identify central and peripheral territories. These correlations of mating with central locations on leks could, of course, result either from aggregation of males around sites where mating occurred or from females' preferences for central locations.

Central territories on leks tend to be smaller than peripheral ones, as reported in numerous studies. It is thus also possible that females might be attracted to dense congregations of males, rather than to central portions of a lek as such. In leks of golden-headed manakins, densely clustered males have higher mean mating success than more dispersed males nearby (Lill, 1976). As these clusters remained in similar locations from year to year, however, it was not possible to exclude the preference of females for the location of a cluster. Female black grouse and village indigobirds also appear attracted to places with more densely clustered males (Kruijt *et al.*, 1972; Payne and Payne, 1977).

Despite the tendency for females to copulate in central or denser portions of a lek, it is usually clear that not all males in these locations have equal mating success (Kruijt *et al.*, 1972; Wiley, 1973a; Lill, 1976; Payne and Payne, 1977; Hartzler and Jenni, 1988). Because males on neighboring territories often differ markedly in success and because leks often have somewhat irregular shapes, mating success of males on leks usually lacks any fixed relationship with distance from particular locations. Gibson and Bradbury (1985), for instance, found no significant correlation between mating success (numbers of copulations) of individual males and the distances of the centers of their territories from the geometric center of copulations. Mating status (whether or not each male mated at least once) also had no significant relationship, in a logistic regression, with distance from the center of copulations. In addition, two studies have found no indication of a significant linear regression of mating success on distance from the geometric center of males' territories (Gibson and Bradbury, 1985; Andersson, 1989). Nevertheless, it remains possible that females do respond, even if not linearly or symmetrically with distance, to the center of the distribution of males or to the greater density of central males in their initial orientation on a lek.

C. PREFERENCES FOR FEATURES OF INDIVIDUAL MALES

For lekking species, most evidence of female preferences for individual males' features comes from correlations between features of males' behavior or morphology and their mating success. There are two problems with these correlational studies: (1) any significant correlation between two variables might actually result from the influences of some third unidentified variable; and (2) the direction of causality is often difficult to resolve, even if we accept some causal relationship between the two variables. The first problem is minimized by multivariate analysis of the many possible influences on mating success, in order to control for correlations and interactions among the independent variables (Lande and Arnold, 1983; Gibson, 1987). The second problem is difficult to eliminate entirely without experimentation.

These two problems might differ in the degree to which they confound interpretation of correlations with male morphology and behavior, respectively. Correlations of male behavior with mating success could result either (1) because females approach and copulate with males that have particular features of behavior, or (2) because males alter their behavior when females, perhaps especially those receptive to courtship, approach them. A third alternative, perhaps the most realistic, is that both kinds of causality occur: females tend to approach and copulate with males that respond to them in particular ways. In contrast, correlations of male morphology with mating success or female visits do not in general face this problem of interpretation, as morphology remains essentially constant during the course of a female's visits before copulation. This correlation, on the other hand, often encounters the possibility of a third causative variable, in particular, age.

A final caveat in interpretation of correlations is a problem of any exploratory analysis: when large numbers of possibilities are considered, some statistically significant results are expected by chance. In the absence of some antecedent hypothesis about which correlations should prove significant and which should not, it can even prove difficult to specify exactly how many possibilities have been considered at some stage of the investigation.

Most correlational studies of male mating success or of female visits to males have uncovered significant correlations with some of the variables considered. Morphological variables are notably less frequent among the significant correlations than are behavioral variables (Table II), at least when analysis excludes immature males. Some of the behavioral correlates seem almost certainly the result of females' choices rather than their cause. For instance, the correlation of mating success with frequency of boundary encounters with neighbors (Kruijt *et al.*, 1972; Wiley, 1973a; Lill, 1976; Kermott, 1982, p. 109) is reasonably explained by the attraction of males toward the boundaries of, or even into, neighboring territories with females in them.

Some behavioral correlates of mating success, like display rates, seem es-

TABLE II
CORRELATES OF MALE MATING SUCCESS IN BIRDS AND MAMMALS WITH LEKS OR DISPERSED DISPLAY SITES

Species (ref.)	Attributes of males	
	Correlated with mating success	Not correlated with mating success
Black grouse (Kruijt <i>et al.</i> , 1972)	Circling-in movements	
Black grouse (Kruijt and de Vos, 1988)	Rookooing phrase duration ^a	
Sage grouse (Wiley, 1973b)		Strut displays ^a Boundary encounters ^a Fights
Sage grouse (Gibson and Bradbury, 1985)	Attendance Strut displays ^a Principal component of acoustic features Three separate acoustic features	Territory size Distance to geometric center of males Distance to geometric center of matings Body mass Two principal components of size
Sage grouse (Hartzler and Jenni, 1988)	Strut displays during peak of female visits ^a	Strut displays before females visited
Great snipe (Höglund and Lundberg, 1987)	Display fights ^a Central location	Attendance White tail feathers Principal component of size Mass Fights Principal component of acoustic features
White-bearded manakin (Lill, 1974a)		Mass Wing length Displays Fanning displays/female visit Snap-jump bouts/female visit Territorial defense Display court size Saplings used for display
Golden-headed manakin (Lill, 1976)	Territorial invasion by others Invading others' territories	Body mass Wing length Display fights Agonistic interaction Calls/display fight
Long-tailed manakin (McDonald, 1989a)	Toledo calls Butterfly displays ^a	Tail length Hops

(continued)

TABLE II
(Continued)

Species (ref.)	Attributes of males	
	Correlated with mating success	Not correlated with mating success
Satin bowerbird (Borgia, 1985b)	Blue feathers Two other kinds of bower decorations Size and density of sticks in bowers Quality of bower Display probability	Four other kinds of bower decorations
Lawes' parotia (Pruett-Jones and Pruett-Jones, 1990)		Display rate Vocalization rate Attendance Five measures of size
Jackson's widowbird (Andersson, 1989)	Tail length Jump displays	Jump height Attendance Display court quality Collar diameter Body mass Three measures of size Distance to geometric center of males
Village indigobird (Payne and Payne, 1977)	Songs ^b Attendance	Body mass Hovering displays or other displays
Fallow deer (Clutton-Brock <i>et al.</i> , 1988a)	Early start in rut Central territory Fighting success Groaning rate Antler length Hind foot length	
Fallow deer (Apollonio <i>et al.</i> , 1989a)	Attendance Territory position Age Fights Agonistic encounters	Fighting success Courtship duration
Uganda kob (Floody and Arnold, 1975)		
Uganda kob (Balmford, 1990)	Fighting Whistle bouts Ear length Body mass	Other measures of morphology

^aCorrected for effects of exposure to females, or evidence presented that stimulation by females has little effect.

^bCorrected for effects of copulation but not for effects of female visits.

pecially plausible as bases for female preferences; these correlations, however, are prime candidates for the reverse (or reciprocal) causation. As reviewed above (Section IV), a male sage grouse increases its rate of display markedly when there is a female in a neighboring territory and even more when there is a female within his own territory. As similar findings are reported for many lekking species, the problem for interpreting correlations is severe. Since most of the variance in measures of males' display rates is associated with differences in their exposure to females, detection of any residual differences in males' displays involves extraction of a small signal from a lot of noise.

In such cases, the exact procedures for removing the noise can prove to be critical. Even when it is reasonable to expect that behavioral differences among individual males on a lek would influence mating success, either directly or indirectly, the difficulty of identifying these differences on the basis of correlational studies suggests that special caution is required in reaching conclusions.

The sensitivity of such analyses to procedural details might explain the diverse results reported for sage grouse (Wiley, 1973a; Gibson and Bradbury, 1985; Hartzler and Jenni, 1988). At Ford's Creek Lek in Montana, Wiley (1973a) examined the rates of display of male grouse in 10-min periods during which a focal male had one or more females either within his territory, in a neighboring male's territory, or in neither, as determined by examining time-lapse films. The idea was to examine males' rates of display under conditions of comparable access to females. The study included 6 males with 4–20 samples each in which females were within the subject's territory. These males obtained 0–41 copulations during the entire season. There were no differences between males that successfully copulated at least once and those that did not, nor any correlations of display rates with total numbers of copulations among successful males, except that the most successful male displayed at a significantly lower mean rate when females were in his territory than did another male that never copulated. The lower mean rate of this successful male resulted from several outlying samples with much lower rates, perhaps a result of fatigue from continual display (see also Scott, 1942). There were no notable differences in display rates among these males in the other two conditions of access to females. The small sample size in this study would not, however, permit detection of small differences among males.

Hartzler and Jenni (1988) and Gibson and Bradbury (1985) reported significant correlations between display rate and mating success. In comparison to Wiley's study, their methods resulted in larger samples of males for comparison but less specific information about access to females. Instead of classifying males by the locations of females with respect to their territorial boundaries, they recorded the distance to the nearest female during 5- or 10-min samples of males' displays. Hartzler calculated display rates for each male when females were closer than 3 m and when females were farther away, during three periods in

April in each of 2 years; he then compared males that had copulated at least five times and those that had not. In five of the six periods, more successful males displayed at higher mean rates than less successful ones and in three of them the difference was statistically significant ($p < 0.05$, Mann-Whitney U Tests on data in their Tables 7.5 and 7.6; Hartzler and Jenni do not report statistical tests for these data). In four of the six periods, more successful males also displayed at higher mean rates less than successful ones when females were more than 3 m away. Among males that copulated at least once, there was no significant correlation of mating success with display rate.

Gibson and Bradbury (1985) controlled for proximity to females by obtaining the linear regression of display rates on distance to the nearest female and time of morning and then using the residual for each sample as a measure of the corrected display rate (145 total samples, 19 males). Whether or not a male copulated at least once was then taken as a dichotomous response variable and mean corrected display rate was taken as an explanatory variable in a logistic regression; statistical significance was high for an association of display rate with mating success. Attendance at the lek and the first principal component of acoustical measures of the display also had significant associations with mating, but three morphological measures did not. Only one variable, the third principal component of acoustical measures, correlated with number of copulations among those males that mated at least once.

Sage grouse provide a good example of how sensitive the results of such an analysis might be to the procedures for controlling males' exposure to females. In particular, arbitrarily categorizing distances to females or employing linear regression on distances to nearest females would not provide adequate controls for exposure to females if males' responses to females changed nonlinearly with distance. Consider, for example, the consequences of males responded especially vigorously to females inside their territorial boundaries. Male sage grouse consistently near females tend to be either those with high mating success or their immediate neighbors, which often display close to boundaries nearest females. These neighbors, although close to females, might both copulate much less frequently and display less, either because males respond more intensely to females within their territories, regardless of distance, or because males without females in their territories more often interrupt their bouts of display to defend their other boundaries.

Alternatively, consider the consequences of males' responses to females were an accelerating, rather than linear, function of proximity to the nearest female. In this case, those males that copulated most frequently and thus were consistently close to females would have high residuals in linear regressions of display rate on distance to females. In both of these hypothetical examples, nonlinear relationships between display rates and distances to females result in significant associations of display rates with mating success, in the absence of any real

differences in individual males' responses to females. A further confounding possibility is that males might respond more to receptive females than to others, as suggested by Lill's (1974a) finding that male white-bearded manakins display more to previous mates returning in the course of subsequent nesting attempts than to other females.

The ruff, another lekking species that has received some quantitative study by several investigators, provides a further example of disagreement on the determinants of mating success. When a female enters a male's territory, he often adopts a motionless squatting position, interrupted at intervals by partial rising and stereotyped turning. In the Netherlands, Hogan-Warburg (1966) reported that females often adopted solicitation postures when males rose from squatting. In Sweden, Shepard (1975) reported that the proportion of all solicitations on a lek obtained by any one male was related to the frequency of his actions while females were on his territory. van Rhijn (1973), on the other hand, presented evidence that females were significantly less likely to solicit for copulation when the territorial male's activity was high. These studies also fail to agree on whether or not the presence of a satellite male in a resident's territory stimulates a female to copulate, but none presents a quantitative analysis of this question. Although these studies all focus on the behavior of males with females inside their territories, they do not consider the possibility that males are more responsive to receptive females than to other visitors. Statistical analysis in the studies of Hogan-Warburg and van Rhijn is based on small samples, possibly unrepresentative, and in some cases involves repeated measures on the same individuals. The study by Shepard lacks statistical analysis of critical points.

Among species for which there is only one report on correlates of mating success, assessments of possible reverse, or reciprocal, causation have varied. In their investigation of village indigobirds, Payne and Payne (1977) reported a consistent correlation in 2 years between time spent singing and mating success. Time spent singing did not differ between hours in which a male copulated and those, at the same time but on other days in which he did not. There was no assessment, however, of the possibility that females' visits, not just copulations, affect a male's time spent singing. Such an effect might even extend over several days. At a lek of black grouse in the Netherlands, the male with the highest number of copulations in each of 3 years had significantly shorter durations (and thus higher rates) of phrases in the rookooing display when females were within 30 m than did other males (Kruijt and de Vos, 1988). When no females were present on the lek, all males averaged longer durations, but the differences among males remained. Furthermore, one male with lower copulatory success in later years also had longer phrases then. This study, like others discussed above, lacked a full assessment of the responses of males to females.

Other studies reporting correlations between display rates and mating success have taken no steps to determine the direction of causation (Höglund and Lund-

berg, 1987; Andersson, 1989; also probability of display, Pruett-Jones and Pruett-Jones, 1990). Andersson (1989) discounted the possibility that rates of males' flight displays varied in response to females, because all males seemed to display when females were nearby. Variation in males' display rates with proximity to females was not documented.

The trend for behavioral, rather than morphological, differences among males to correlate with mating success (Table II) alone suggests that males' responses to females might explain these correlations. Morphology, unlike behavior, does not change from moment to moment in response to females. Morphology on the other hand often correlates with age (Section III,B). In view of the major changes found in male behavior in response to females (Section IV), interpretation of correlations between behavior and mating success must include thorough investigation of the temporal and spatial aspects of males' responses to females, before conclusions are reached about females' responses to males.

In the end, correlations provide problematic evidence for females' response to males. The best approach to demonstrating these responses is experimentation (see Andersson, 1982a; Moller, 1988). In lekking species, a number of reports that females are attracted to playback of males' vocalizations suggest that experimental analysis of females' discriminations among individual males might be feasible. Gibson (1989) reported that female sage grouse are attracted to playback of the sounds of a male's displays presented inside the territory of an unsuccessful male. This experiment included no comparisons between displays of successful and unsuccessful males, nor between different species or types of sounds. Others have reported, with less documentation, attraction of female greater prairie chickens to playback or imitations of male vocalizations (Hamerstrom and Hamerstrom, 1960; Silvy and Robel, 1967). Female black grouse, on the other hand, were not attracted to playback at a location away from a current lek (Kruijt *et al.*, 1972).

Despite the difficulty of establishing the fact in the field, it remains plausible that a male's effort in displaying influences his mating success, either indirectly through influences on other males or directly through influences on females. Effort might include rates of display, intensity of display, and attendance at leks for longer periods during the day and the season instead of foraging. Attendance is one of the features of male behavior that recurs as a correlate of mating success (Table II; Kermott, 1982; Beehler, 1983b; Trail, 1984, p. 99; Gibson and Bradbury, 1985; Andersson, 1989). Another of Gibson and Bradbury's correlates of mating success in sage grouse, the first principal component of acoustical measures, depended on three features of the sounds that accompany the "strut" display, all of which correlated with whether or not a male copulated. These sounds might also reflect the effort expended in display. They result from the abrupt escape of air from the males' esophageal sac, which is compressed by the musculature of the overlying skin during the display (Clarke *et al.*, 1942; Honess

and Allred, 1942; Wiley, 1973b). The compression of the sac probably determines the velocity of the escaping air and thus the frequencies of the associated pops and whistle. This connection would make the frequency of the whistle an index of the effort of the displaying male, one that is less ambiguous, given uncertainty about the male's distance, than the intensity of the sound. These high frequencies are also absent from the displays of yearling males (Wiley, 1973b). Although much remains to be confirmed here, there is a possibility that these acoustical components provide an unbluffable index of the intensity of a male's display, just the sort of attribute that could provide a female with reliable information about a male's vigor.

D. RESPONSES TO COLLECTIVE FEATURES OF AGGREGATED MALES

If females respond to some collective features of aggregated males when approaching leks, then larger leks, or leks of some minimal size, might attract more females than smaller ones. Although larger leks in general do attract more females than smaller ones, the evidence that larger aggregations of males attract disproportionately more females is mixed (for example, see Cade, 1981). In Uganda kob, average rates of copulation increased with the number of males on a lek, but reached an asymptote at 10 or more males (Balmford, 1990). During a 12-year study of greater prairie-chickens (Hamerstrom and Hamerstrom, 1955), visits by females increased monotonically with the number of males on a lek, but the increase was not in proportion to the number of males. Copulations increased nearly in proportion to the number of visiting females, but only for leks with 15 or fewer males; on larger leks the number of copulations decreased with lek size. Thus, in this case, large leks attracted disproportionately few females and had an even smaller share of copulations. In comparisons of a large and a small lek of golden-headed manakins in 2 years, Lill (1976) found no consistent differences in numbers of copulations or visits by females in proportion to numbers of males.

It is not plausible that an aggregation of males could produce an advertising signal detectable over a disproportionately wide area (Bradbury, 1981). For instance, a long-range acoustic signal produced in exact unison by two males would be doubled in intensity (increased by 3 dB) at the source; this intensity would increase the distance at which it could be detected by a factor of $\sqrt{2}$ (assuming constant background noise and excess attenuation) and would thus exactly double the area over which it could be detected. Although males of some lekking species produce loud calls in unison (Section III,C), there is no evidence at present that these calls are in exact, phase-locked unison; anything less would result in less than proportionate increase in the area of detection for aggregations of males.

Additional males would also result in more continuous broadcast of signals

from a lek, particularly if males tended to avoid overlap with each others' calls (Section III,C). Greater continuity of display could result in greater probability of detection at long ranges, but detection by females is again not likely to increase in proportion to the number of males involved.

Even if there is no disproportionate increase in the effectiveness of advertisement by larger leks, the possibility remains that females respond to some collective aspect of the stimuli from a lek. The temporal or spatial patterns of the signals from an aggregation of males (Section III,C) might provide cues for females choosing leks. At the moment there is no clear information concerning this possibility. In addition, the numbers of males and females at leks do not provide a critical test of females' preferences for different sizes of leks. Despite such preferences, approximate equality of female/male ratios across leks could result from compensating adjustments in the settlement of males (Sections IV and VII,A). Experiments would provide clearer evidence for any preferences for larger leks.

VI. INTERACTIONS OF FEMALES

The strongly nonuniform distribution of matings among males on a lek is difficult to explain solely as a result of dyadic interactions of males with independently acting females. As Bradbury and Gibson (1983) and Bradbury *et al.* (1985) have demonstrated with simulations, the observed correlations of male morphological or behavioral features with copulatory success are not high enough to produce the observed skew in copulatory success, provided one assumes that each female independently chooses a mate on the basis of males' morphological or behavioral features.

Several possibilities might produce greater agreement in females' choices than that generated by these simulations (Bradbury *et al.*, 1985). Females might base their discriminations on extremely subtle but stable individual differences among males (for instance, 95% correct choices for much less than 10% differences in males' features), or the variance in the distribution of males' features might be greater than reported. These two possibilities seem unlikely, without new evidence. Females might also base their discriminations on multiple cues provided by males. If individual females combined separate assessments of several different features of males, then the redundancy provided by multiple cues could improve accuracy of discrimination. Finally, some females might copy choices made by others.

The problem of concordance in female choice is similar to the problem of linearity in dominance hierarchies (Landau, 1951; Chase, 1974; Bradbury *et al.*, 1985). Here, the observed correlations of individuals' morphological or behavioral traits with their rankings are not strong enough to produce hierarchies as

linear as those observed, on the assumption that each dyadic dominance relationship is settled independently. The fundamental problem is that the observed correlations between individuals' characteristics and their social status are inadequate to produce a high degree of concordance in the responses of individuals acting independently. On the other hand, interdependence of individuals' responses, such as by copying each other, can produce very high levels of concordance (Losey *et al.*, 1986).

In lekking species, interdependence of males–female associations for copulation could conceivably arise in two ways. First, interactions among the males could ensure that only one male in an aggregation could successfully mate, regardless of any preferences of females. If, for instance, only one male on a lek had opportunities to mate without interruption, as a result of males' interactions with each other, then only this male would copulate successfully. Such a situation might arise particularly in those species with frequent interruptions of copulations. It must be recognized, however, that overall rates of interruptions are not directly relevant to the issue here. The question is whether or not all males have exclusive areas in which they could copulate without interruption provided females gave them the chance.

When two or more males sharing a display site establish clear dominance relationships, as in long-tailed manakins and capuchinbirds, then copulations at this site are monopolized by the top-ranking male without interruptions by subordinates (Foster, 1977a; LeCroy *et al.*, 1980; McDonald, 1989a,b; Trail, 1990). In these cases, the high concordance among females in mating partners at any one site results from the males' relationships. Differences in mating success among sites, however, require other explanations.

In greater prairie chickens and some manakins, interruptions might contribute to nonuniform mating distributions (Robel, 1966; Lill, 1976; Foster, 1981, 1983). In golden-headed manakins, for instance, mating success was found to correlate with rates of disrupting other males' interactions with females (Lill, 1976). In Guianan cock-of-the-rock, on the other hand, males' success in copulation was not related to the proportion of their copulations disrupted; the proportion of females' visits disrupted was in fact greater for those males that received more visits (Trail and Koutnik, 1986). Persistent disruption in this species was directed against more successful neighbors. Yet only occasionally did a male succeed in copulating with a female he had disrupted. As a rule, females in lekking species appear to have control over where and with whom they copulate (Section IV). In such cases, male–male interactions would have little if any influence on the concordance in females' choice of mates.

Alternatively, this concordance could result from interactions among females, in particular copying. In the extreme case of no errors in copying, if each female copulated only with a male that she had seen copulate previously, then all females would select the same partner (provided both that any one female might

start the process when she had seen no other female copulate for a long time and that females had opportunities to observe others' copulations).

Copying of mating partners might occur either immediately or after a delay. For long-tailed manakins, anecdotal observations suggest that a female observing another copulate tended to return to copulate at the same site, and thus with the same male, within a few days (McDonald, 1989a). At lek of fallow deer in England, such effects were immediate. Females often moved into the territory of a male while he was mating; as a consequence, a male sometimes mated several times in quick succession (Clutton-Brock *et al.*, 1988a). In the ruff, females usually form groups on leks; a soliciting or copulating female attracts other females and stimulates them to solicit in the same territory (Hogan-Warburg, 1966).

Less direct copying of other females could also tend to produce concordance in mating associations. For instance, females might simply follow or approach other females (Kruijt and Hogan, 1967; Balmford, 1990). In sage grouse, females on leks are likely to stop walking close to other females (Wiley, 1973a), an attraction that would contribute to the formation of compact congregations of females in one or a few males' territories (Scott, 1942; Patterson, 1952; Wiley, 1973a; Lumsden, 1961, 1968; Moss, 1980). In golden-headed manakins, about 20% of females' visits to males' territories occurred simultaneously with other females and 48% of females were observed to engage in at least one simultaneous visit. This latter figure might actually be low, as observations were conducted on alternate days at each of two leks. Although only a minority of copulations occurred during simultaneous visits, Lill's (1976) data do not indicate whether observing a copulation might affect a female's subsequent behavior. Female Lawes' parotias also often visit leks in groups (Pruett-Jones and Pruett-Jones, 1990). Copying of females could also occur indirectly, if females attended persistent cues, such as odors or trampled spots left by previous females (see Wiley, 1973a; Clutton-Brock *et al.*, 1988a; Gosling and Petrie, 1990; Balmford, 1990).

Copying by females could affect mate choices in two ways. Females might tend to copy others indiscriminately on each occasion they choose a mate. Alternatively, younger or less experienced individuals might selectively copy older or experienced ones, while experienced females repeated previous choices of particular males or locations. In the case of lekking birds, there are some suggestions that opportunities exist for females' preferences to pass from older birds to younger ones. In lekking grouse, younger females tend to visit leks somewhat later than, but overlapping with, older females. In sage grouse, in which large numbers of females often congregate at leks during a 10 to 15-day period (Wiley, 1973a; Hartzler and Jenni, 1988), and females tend to visit leks on one or more days before mating, females that are at least 2 years old begin to arrive 4–5 days

earlier than yearlings and have started mating by the time yearling females begin to visit (Dalke *et al.*, 1963; Gates, 1985; Petersen and Braun, 1990). Yearling females are also more likely to visit more than one lek (Petersen, 1980). In long-tailed manakins as well, younger females visit more display sites than older ones (McDonald, 1989a,b).

There are also suggestions that females making return visits to a lek move more directly to the location at which they copulate than do females with less experience on the lek (Kruijt and Hogan, 1967; Lill, 1974a). Female Guianan cocks-of-the-rock returning in a subsequent year visited fewer males on fewer days than did females not known to be returning, perhaps an indication that they acted more on their previous experience. In only 33% of cases, however, did they actually return to the same male for copulation (Trail and Adams, 1989). The majority of female Lawes' parotias mate with the same male both within and between seasons (Pruett-Jones and Pruett-Jones, 1990). On the other hand, in golden-headed manakins, three of four females observed mating in 2 successive years switched to a different lek (Lill, 1976). These data are too few for any general conclusions about the proportions of females that return to the same male or location for mating in successive years.

If older females tend to rely on previous experience in selecting mating partners, rather than to copy, while younger females tend to copy, then traditions of female preferences could persist across years. Such a process would be analogous to "oblique" cultural transmission (transmission from older to younger individuals, other than parent-offspring) as modeled by Cavalli-Sforza and Feldman (1981). Variation among groups of individuals as a result of sampling or transmission error is enhanced by oblique as opposed to vertical (parent-offspring) transmission, and especially by "teacher/leader" transmission (one-to-many oblique transmission). Could switches in successful males on leks, within or between seasons, result in part from such fads in female preferences, as Trail (1984, pp. 109–110) suggested for Guianan cocks-of-the-rock? Such switches might occur with greater frequency on smaller leks.

It is clear from this discussion that much remains to be learned about the behavior of females on leks. Many possibilities need further investigation. Copying, immediate or eventual, between females could help to explain the concordance in mating associations on a lek and perhaps also generate correlations between male features and mating success. If older females relied relatively more on previous experience and younger females more on copying, these patterns might also persist from year to year on a lek. On the other hand, copying between females within a lek would not guarantee high concordance in associations of male features with mating success between different leks. This is another possible explanation for differences in correlational studies of mating success on different populations of the same species (Section III,C).

VII. LOCATIONS OF LEKS

Recent discussions of leks have raised the question of whether it is males or females that determine the spacing and locations of leks. One suggestion is that males take positions allowing maximal access to females, whose movements are determined by considerations other than the locations of potential mates (Emlen and Oring, 1977; Parker, 1978; Bradbury, 1981; Gosling, 1986). Females might also prefer large aggregations of males, in order to increase their choice of mates (Alexander, 1975). Other proposals include aggregation of unsuccessful males around successful ones so that they can intercept some females attracted to the preferred males (Bradbury and Gibson, 1983; Beehler and Foster, 1988; Gosling and Petrie, 1990), and aggregation of males in locations that offer maximal protection from predators both for themselves and visiting females (Koivisto, 1965; Wittenberger, 1978; Gosling, 1986). Males or females might also prefer traditional locations. For each of these possibilities, locations of leks, like social relationships within leks, depend on interactions of individuals and their responses to the environment.

A. FEMALE CHOICE MODELS

Females could influence the sizes and spacing of leks if each simply chose her mate from the largest aggregation of males within her range. Simulations of this process show that, if males adjust their locations to maximize access to females, they are forced into leks separated by approximately the diameter of females' ranges (Bradbury, 1981). Recent studies indicate, however, that leks are usually more closely spaced than predicted by this model. Radio-tracked female sage grouse have ranges considerably larger than the distances between leks in the same population (Gibson and Bradbury, 1986; Bradbury *et al.*, 1989b). Three of seven radio-marked females did not visit the leks nearest their nests sites but did visit ones farther away (Bradbury *et al.*, 1989b). In other species as well, females appear to have ranges substantially greater than the spacing of leks (van Rhijn, 1983; Wegge and Rolstad, 1986; Svedarsky, 1988). Modifications of this model to include a female's costs of travel and delays before mating, however, result in distances between leks that are less than the diameters of female ranges (Gibson *et al.*, 1990).

Bradbury *et al.* (1989b) report that, in comparison to a Poisson distribution for random settlement of males at leks, the distribution of lek sizes in three populations of sage grouse consistently showed an excess of very large and very small leks. This tendency to aggregate could result from females' preferences for larger leks, but any attraction of individuals to members of the same or opposite sex could also have the same effect. More direct evidence that females prefer larger leks is lacking (Section V,D).

B. HOT-SPOT MODELS

Another mechanism for the location of leks involves aggregation of males at hot spots for access to females. These models assume overlapping ranges of females, which mate with any males that they encounter, and settlement of males in positions with maximal access to mates (Bradbury and Gibson, 1983; Bradbury *et al.*, 1986). As a result of this process, the concentration of males at a site can exceed the concentration of female traffic there, because males settling at sites with high female traffic reduce the availability of unmated females at nearby locations with less traffic. Various alternatives (ideal free or ideal despotic settlement of males, random or uniform distributions of females' ranges) generate quantitatively different results, but all lead to predictions that aggregation of males, as measured by the sizes and spacing of leks, should correlate with the diameters, and hence overlap, of females' ranges. A critical test of this prediction would require information from a series of populations of the same or similar species. Even then, an observed correlation between the sizes of females' ranges and the sizes or spacing of leks could have two interpretations. Either leks increase in size with overlap in females' ranges as predicted by the model, or females' ranges expand when leks are larger and farther apart for other reasons.

There is, however, more direct evidence that movements of females influence the locations of leks. First, in some species lekking males on occasion leave their positions and move as a group to approach nearby females (Section II,B). Second, when females have well-defined routes of travel during daily or seasonal migrations, leks are often located along these routes (topi, Montfort-Braham, 1975; Gosling, 1986; Gosling *et al.*, 1987; hammer-headed bats, Bradbury, 1977; fallow deer, Schaal, 1986; Appollonio *et al.*, 1989b; sage grouse, Patterson, 1952; Dalke *et al.*, 1963; Bradbury *et al.*, 1989a,b; ruff, van Rhijn, 1983, 1985). Leks of topi tend to occur where females congregate to rest at midday (Gosling and Petrie, 1990). In the case of Kafue lechwe, leks shift location progressively as the population withdraws from alluvial areas during the peak of the rainy season (Schuster, 1976). Indirect evidence suggests that some male sage grouse likewise change leks as females move from wintering to nesting areas (Bradbury *et al.*, 1989b). White bellbirds apparently also shift their display sites in response to females' movements to higher elevations at the start of the breeding season (Snow, 1973). Perhaps the most convincing evidence for the importance of female traffic comes from a lek of fallow deer that moved to a new location in response to a change in the movements of females (Appollonio *et al.*, 1990). After parts of the forest were cut, females followed a different route in their daily travels to feeding grounds. A lek located on the former route gradually disbanded, as the males moved to a previously unoccupied location on the new route. This example illustrates the fundamental principle that males cease to visit a lek to which no females come, although not necessarily immediately.

Attraction to females probably also influences male recruitment to leks. Young males in lekking species often visit several leks before establishing stable positions (Section III,B), and it is not improbable that these prospectors might assess the number of females attracted to a lek in relation to the number of previously established males. Attendance of males at leks of sage grouse sometimes shifts markedly with changes in the presence of females nearby (Bradbury *et al.*, 1989b). It would be instructive to compare such data for yearling and older males.

Of course, where males go to find females depends strongly on where females go when ready to mate. Simulations of hot-spot models have assumed that females make no special movements in seeking mates (Bradbury *et al.*, 1986). In some species, however, females are known to undertake movements specifically to visit leks or display sites, although not necessarily over great distances (Beehler, 1987b; van Rhijn, 1983; Wegge and Rolstad, 1986; Clutton-Brock *et al.*, 1988a; Balmford, 1990).

C. HOTSHOT MODELS AND SITE-SPECIFIC PREFERENCES OF FEMALES

The hotshot model proposes that males intrinsically less successful in attracting females congregate around more successful males in order to intercept arriving females. It can thus explain why males display in aggregations, rather than at dispersed sites, even if females lack any preference for groups of males or particular locations. A necessary assumption, of course, is that females choose mates on the basis of individual differences among males.

The aggregation of unsuccessful males as satellites around successful ones could result either (1) from each male's own experience in attracting females or (2) from an evolved response by intrinsically inferior males. In the first case, males would be expected to try first to attract females on their own before moving close to a successful male. Solitary males are reported for a number of lekking species, and they sometimes copulate as frequently as lekking males (Kruijt *et al.*, 1972; de Vos, 1983; Pruett-Jones and Pruett-Jones, 1990). Although there are no reports that males first display solitarily and then move to a lek, males often first take positions at the periphery of a lek and move if they are unsuccessful (Section III,B).

In the second case, males would be expected to establish either solitary display sites or ones near successful males in accordance with stable differences in their intrinsic abilities to attract females, which could depend on size, vigor, or ornamentation. Effects of age on mating success would complicate this picture: males temporarily likely to be unsuccessful because of age might initially take positions as satellites near successful males; once they reached an optimal age for attracting females, they should then, depending on their intrinsic abilities, either estab-

lish their own display site (which in some instances might involve replacing a successful male) or remain a satellite of a successful male. Some aspects of lek behavior provide circumstantial evidence for such mechanisms, including the usual pattern of higher mating success by central males (Section III,B) and even the traditional locations of many leks with a succession of successful males (Section II,A; Beehler and Foster, 1988). On the other hand, reports of newly established leks suggest that young males predominate (Section III,B).

It is difficult to establish, as hotshot models predict, that less successful males on leks obtain matings as a result of parasitizing the attraction of females to more successful males rather than as a result of variation in females' preferences. For instance, forced copulations do not generally occur on leks (Section IV). It is possible that females might lose patience as a result of having to wait too long or being interrupted too often while attempting to mate with their preferred partner and might thus mate with other males on the lek. In Guianan cocks-of-the-rock, some males appear to obtain a few copulations in this way, although unsuccessful males, despite their interruptions of copulations by successful neighbors, are more often persistently rejected by females (Trail and Adams, 1989). It is also possible, in those species like sage grouse in which 20–40 females sometimes gather in one or two males' territories, that neighboring males obtain some copulations while a more successful rival is preoccupied elsewhere in his territory.

An alternative explanation for the aggregation of males would require that females have a preference for mating in particular locations, as a result either of individual preferences or of copying other females (Section VI). The constancy in locations of leks and, in some cases, of mating centers within leks (Section II,A and D) might arise because (1) females prefer to mate at particular locations, (2) females are consistently attracted to a particular male, as long as he survives, or (3) preferred males tend to succeed each other at a particular site.

Experimental removals of males can separate female preferences for locations as opposed to individual males (see Warner, 1987, 1988). Two limited experiments along these lines with lekking birds have resulted in individual cases of females that returned to the same site to copulate, even in the temporary absence of any male (Lill, 1974a; Payne and Payne, 1977). Female Uganda kob tend to return to the same territory in successive visits to a lek, despite changes in the resident males (Balmford, 1990). These cases suggest that females in lekking species can develop site-specific preferences for mating without reference to particular males. On the other hand, at a lek of Guianan cocks-of-the-rock, experimental obliteration of one successful male's display court resulted in no apparent decrease in his mating success following a shift in his location to an adjacent unoccupied position (Trail, 1984, pp. 162, 231).

If females tended to mate at particular locations, males would be expected to congregate there either to compete individually for females or to await succession to an optimal location (Section III,B). In either case, less successful males

should try to obtain as many copulations as they can. This behavior would prove difficult to distinguish from that predicted by hotshot models.

D. HABITAT PREFERENCES AND PREDATION

Leks tend to occur in particular topographic locations or habitats. In some species, the habitat associations might result from females' preferences either for areas relatively safe from predators or near feeding grounds or routes of travel. Female fallow deer apparently prefer to mate at sites away from feeding grounds where interference with copulations by subordinate males is less frequent (Clutton-Brock *et al.*, 1988a). Females might also prefer to mate at locations away from feeding grounds in order to reduce competition with males for food (Brown, 1964; Crook, 1965; Wrangham, 1980). Black grouse, although often occupying habitats along the edges of woodland, prefer locations as open as possible for leks, perhaps for protection from predators (Koivisto, 1965) or to reduce attraction of predators to nesting areas (Kruijt *et al.*, 1972; Bergerud, 1988). Leks of sage grouse, topi, and Uganda kob are also characteristically located in areas of sparse vegetation (Patterson, 1952; Wiley, 1973a; Bradbury *et al.*, 1989b; Balmford, 1990; Gosling and Petrie, 1990).

Several reports have suggested that predation occurs very infrequently on leks (Berger *et al.*, 1963; Hamerstrom *et al.*, 1965; Lill, 1974b, 1976; Oring, 1982; Kruijt and de Vos, 1988). However, studies in areas with little human disturbance suggest that predation on leks is not insignificant (Patterson, 1952; Koivisto, 1965; Wiley, 1973a; Hartzler, 1974; Trail, 1987; Bradbury *et al.*, 1989a). On a lek of the Guianan cock-of-the-rock, Trail (1987) observed two kills by raptors and two by snakes in about 250 days of observation, although attacks by raptors occurred on average about once every 5 days. This lek averaged 55 males, which maintained year-round territories on it, so the annual mortality of displaying males on this lek amounted to approximately 10%, about a third of total annual mortality.

Lekking males of many species exhibit sudden, dramatic escape behavior at the appearance of major predators and often apparently spontaneously as a result of false alarms (Patterson, 1952; Koivisto, 1965; Wiley, 1973a; Hartzler, 1974; Beehler, 1987a; Trail, 1987; Bradbury *et al.*, 1989a), an indication that risks of predation have affected the evolution of males' behavior. In addition, certain predators, like golden eagles preying on sage grouse, goshawks on black grouse, and ornate hawk-eagles on Guianan cocks-of-the-rock, make highly specialized attacks on leks. It was my impression that golden eagles knew the locations of sage grouse leks in advance; they attacked suddenly over a nearby ridge, flying at full speed close to the ground in the dim light at dawn (Wiley, 1973a). Accounts of other lekking species suggest similarly purposive behavior by major predators (Koivisto, 1965; Trail, 1987).

Although predation seems to influence the behavior, including habitat preferences, of individuals on leks, there is little evidence that aggregation of males in itself provides protection from predators. For instance, in populations of sage grouse in California, attacks by predators were disproportionately frequent on larger leks, although there was no significant relationship of male mortality with size of lek (Bradbury *et al.*, 1989a). The crucial comparison, however, might be between solitary males and groups of even a few. In Uganda kob, leks attract more predators than do solitary males, but again there is no difference in male mortality (Balmford, 1990; but see Fryxell, 1987). Enhanced detection of predators by males on leks apparently compensates for attraction of predators. There seem to be no reports of females falling to predators on leks; in some species, most females' visits and copulations occur at times when attacks by predators are less frequent than at other times (Koivisto, 1965; Wiley, 1973a; Hartzler, 1974).

One difficulty with all studies of predation at leks, however, is the possibility that an observer's presence might alarm or distract predators and reduce the rates of predation. Nevertheless, although particular features of vegetation or topography might attract one or both sexes because they provide protection from predators, this process seems not to provide a complete explanation for aggregation at specific sites.

VIII. SEXUAL SELECTION IN LEKING SPECIES

This review has made a point of distinguishing behavioral mechanisms from evolutionary ones. Female choice and sexual selection illustrate the complexity in the interactions of these two levels of analysis well. Female choice refers to individual females' behavioral preferences for copulating in particular circumstances; sexual selection refers to differences in transmission of genes that influence males' copulatory success (Borgia, 1979; Wade, 1979; Wade and Arnold, 1980; Arnold, 1983).

The relationships between female choice and sexual selection constitute the central interest of lekking species, inasmuch as the sexes do not interact, in general, except during the chain of events leading to copulation. The following sections identify some general issues in the study of sexual selection and apply them to lekking birds and mammals.

A. PASSIVE ATTRACTION

The first consideration concerns the nature of female choice. Parker (1982, 1983) has proposed that "passive attraction" of females could produce sexual selection without female choice. Attraction is "passive" when receptive females approach the most salient males, those that females perceive, for instance, to

have the loudest calls or most noticeable coloration. Of course, signals that appear loudest to a female at a particular time do not necessarily have high intensity at the source, since the loudest male could by chance simply be the closest to the female. Nevertheless, assuming random or uniform distributions of females, any male that produced more intense calls at source would be perceived loudest by a disproportionate number of females. "Active choice," on the other hand, requires that females reject some males regardless of the salience of their signals (Parker, 1983).

The strength of a particular stimulus for a female depends on the capacities of her sense organs (Halliday, 1983; Sullivan, 1989) and her processing of sensory input. Although the terms suggest some essential distinction, "active" rejection and "passive" attraction both involve sensory filtering or discrimination. Acceptance of the most intense stimulus (or one above some threshold) necessarily involves rejection of other, less intense stimuli. Redefining passive choice as mating with the closest male or the first one encountered (Searcy and Andersson, 1986) does not avoid the problem. Imagine, for instance, that choice of a mating partner involved no more than copulation with the first male detected following onset of receptivity (at some time not affected by exposure to males). Even in this case, the properties of male behavior and female sensory mechanisms would determine which males were detected (produced stimulation above some threshold) and which were not. Regardless of whether her behavior depended on peripheral or central sensory filtering, a female's responses would involve discrimination among males' traits.

Female discrimination among potential mates, by whatever mechanism, is reducible to a problem in signal detection (Wiley, 1983). In its simplest form, a mechanism for detecting a signal receives an input, in the form of a signal with noise (either from random variation or masking energy), and then either responds or does not according to some criterion. Any response of a female involves a criterion for acceptance or rejection of a stimulus. A criterion might be relative for simultaneously compared signals (such as loudest call or longest tail), or absolute for sequentially processed signals (such as a call meeting certain frequency specifications or a tail exceeding a definite length). A criterion could be simple or complex, stringent or lax. The mechanism might involve only the properties of the peripheral sense organs or also the cognitive properties of the central nervous system. The issue to which Parker's (1983) argument draws attention is not whether or not females choose mates, but whether or not they necessarily have exacting criteria for their choices. In all cases, a females' responses have evolutionary consequences for males' traits.

Natterjack toads provide a case of relatively nonspecific criteria for mate choice by females (Arak, 1983, 1988). Larger males with louder calls and larger defended areas in breeding ponds obtain more mates. However, females do not make discriminations based on the acoustic attributes of calls; instead, they evidently

accept any conspecific male they encounter once they reach the breeding pool, usually a male with a large defended area. Loud calls and large size presumably contribute to defending a large area.

Do leks of any birds or mammals resemble this situation? In one report that might suggest it, Robel (1967) showed that male greater prairie chickens with larger ranges on leks obtained more matings. Most copulations occurred within the males' much smaller territories, however (Section III,A). Evidently successful males ranged more widely over the lek to approach females and then accompanied them back to their territories for copulation. Another presumptive case for females' mating with the first males they encounter is provided by a lek of fallow deer in Italy, in which the most successful males occupied territories where females entered the lek; females, however, visited several males before mating (Appollonio *et al.*, 1989b). In general, females of lekking birds and mammals visit a number of males on a lek before mating (Section V,A).

B. DIRECT AND INDIRECT FEMALE CHOICE

Even when mating opportunities are determined mostly by interactions among males, as in Natterjack toads, the behavior of females would always, perhaps even in the case of forced copulations, affect how male-male competition influences mating. Female tendencies to mate in particular locations, in groups, or in synchrony, could all influence which males would have access to them for copulation. This point suggests a distinction between direct and indirect female choice. In the case of direct choice, females mate with particular males because of their preferences for particular features of stimulation produced directly by individual males. In the case of indirect choice, females mate with particular males because of other aspects of their preferences for situations in which to mate.

Three possibilities for indirect choice seem particularly relevant to lekking species: preferences for mating in aggregations of males, for mating in particular locations, and for copying other females. Females' tendencies to mate in aggregations of males, as a result of responses to collective properties of aggregates rather than to features of individual males (Section V,D), would allow male competition to determine mating opportunities. Females might also prefer to mate near the centers of aggregations, which would further restrict mating as a result of male competition. If females preferred to mate at a particular site (Section VII,B), this preference would create male competition to occupy that site. Preferences either for aggregations or for particular sites could result from females' copying more experienced females (Section VI).

All of these possibilities for indirect female preferences could lead to sexual selection for male characteristics that is just as intense as that from direct preferences. Indirect preferences could also lead to exaggeration of collective or coor-

dinated display in aggregations and male competition within aggregations. Yet, none of these consequences would require differences in females' responses to stimulation produced by individual males.

C. INTER- AND INTRASPECIFIC CHOICE

Considering female choice as a form of signal detection tends to weaken the distinction between inter- and intraspecific aspects of female choice. Instead, these apparent alternatives represent points on a continuum of criteria for responses. Consider a varying stimulus, as a result of a signal plus noise, along a dimension of stimulus parameters. It is reasonable to assume that, along most stimulus dimensions, differences between hetero- and conspecific males are greater than those among conspecific males. Suppose a female solicits copulation when stimulation meets some criterion (Real, 1990). Her discrimination between hetero- and conspecific males is then analogous to discrimination among conspecific males, except that the signal/noise ratio is likely to be higher.

When females have only brief associations with males before copulating, as in most lekking species, the possibility of error in discriminating between suitable and unsuitable mates increases (Wiley, 1983). A relatively high probability of errors in recognition of conspecific mates is suggested by the high frequency of hybrids reported for species with ephemeral associations of mates (Sibley, 1957; Gilliard, 1969). Consequently, particularly in lekking species with brief mating seasons, sexual dimorphism in species-specific courtship signals might evolve in part to reduce errors in females' choices of conspecific mates.

The interpretation of frequencies of hybrids, however, is problematic, because strong sexual dimorphism might make hybrids more noticeable to ornithologists. Further tests of this hypothesis might compare frequencies of both female and male hybrids in species with brief as opposed to prolonged associations of sexes prior to mating and in species with monomorphic as opposed to dimorphic plumage. It is perhaps significant that manakins, with their prolonged breeding seasons and repeated visits by females to leks over periods of months, do not seem to have high rates of hybridization (Parkes, 1961). Experimental studies of females' responses to features of conspecific and heterospecific males might well complement studies of their responses to variation in features of conspecific males.

A clear case of two sympatric lekking species with unusually high levels of hybridization is provided by greater prairie chickens and sharp-tailed grouse in central North America (Johnsgard and Wood, 1968). Overlap of their ranges has increased as a result of human activities in the past 150 years. The two species lack bold plumage patterns, but they differ distinctly in the coloration of the large bare patches of skin over the esophageal pouch, in overall size, in the development of specially modified feathers, and in their sounds and actions during dis-

play (Hamerstrom and Hamerstrom, 1960; Lumsden, 1965; Hjorth, 1970; Ker-mott and Oring, 1975; Sparling, 1983), differences great enough that the two species were long classified as belonging to separate genera. In zones of overlap, however, hybrids often represent 10% of all individuals and, in some populations, even higher proportions (Johnsgard and Wood, 1968). Mixed leks are more common (as much as 17% of leks) in populations with more nearly equal proportions of the two species, but the proportion of mixed leks is far below that expected by random assortment of males. There have been no reports of copulations by hybrid males. A high incidence of hybridization between lekking species suggests that some females either lack precision in their discrimination of suitable mates or rely on indirect mechanisms of mate choice.

D. COSTS AND BENEFITS RELEVANT TO SEXUAL SELECTION

The possibility of errors in females' choices implies that some preferences are better (more likely to propagate to subsequent generations) than others. The costs and benefits of females' preferences, and of males' features affected by these preferences, are at the heart of current theoretical work on sexual selection. Fisher's (1915, 1930) verbal argument for sexual selection proposed that female preferences for traits that were initially advantageous for males could lead eventually to the evolution of disadvantageous exaggeration in an accelerating, or run-away, process. Eventually, this exaggeration would be halted by compensating reduction in survival of males and perhaps by a switch in female preferences to other features of males. To crystallize issues, however, recent discussions have identified Fisherian evolution with the spread of traits disadvantageous for male survival as a result of arbitrary female preferences, ones with no effect on the female's own reproductive success or survival. In his discussion of females' "aesthetic" sense in the evolution of bird song, Darwin (1871) also indicated that sexual selection might result from arbitrary female preferences.

Mathematical analyses of Fisherian evolution, based either on two-locus models (O'Donald, 1980; Kirkpatrick, 1982) or on models of polygenic traits (Lande, 1981; Heisler, 1984, 1985), have shown that the run-away process occurs as a result of (1) the enhanced mating success of males with the preferred traits and (2) the genetic correlation between genes for the female preference and the male trait, a consequence of the assortative mating between individuals with these genes. In general, evolution of such traits results in a line of equilibrium frequencies of alleles for the male trait and the female preference (or, in the polygenic models, a line of equilibrium values for the male and female phenotypes). Along this line, the disadvantages of decreased survival by males are just balanced by the advantages of increased mating success (Arnold, 1987; Kirkpatrick, 1987).

Both the polygenic and the two-locus haploid models suggest that genetic drift is important in the evolution of exaggerated male traits. In both models, popula-

tions at stable equilibria evolve only by perturbations away from equilibria by genetic drift. In polygenic models, unstable equilibria occur under conditions of strong genetic covariance between the male trait and the female preference (Lande, 1981). The result is rapid evolution of both phenotypes toward extreme values. Such strong covariance could normally arise only in the course of sexual selection or by drift in small populations. Instability is also more likely when females prefer male features not directly subject to selection for viability (Heisler, 1985). In all cases, aside from any effects of genetic drift, female preferences are most likely to evolve when they reinforce directional selection for viability (Heisler, 1984, 1985).

In two-locus haploid models, when females sample males sequentially and when the preference for the male trait is not absolute, genetic drift must overcome a threshold in the frequency of the female preference allele before the frequency of the male trait allele exceeds zero (O'Donald, 1980; Kirkpatrick, 1982; Seger, 1985). This threshold decreases, so that chances for the spread of disadvantageous male traits increase, (1) when females prefer a less disadvantageous trait (Kirkpatrick, 1982; Seger, 1985) and (2) when females' preferences are more nearly absolute (females with the preference allele more often mate with males carrying the trait allele).

When females with the preference allele sample a group of males simultaneously and choose the best, the line of equilibria in the two-locus haploid model is in part unstable (Seger, 1985). In this best-of- N model, rapid evolution becomes possible. This situation appears superficially to apply to leks. However, the model indicates that unstable equilibria are most likely when samples of males are very small (in general less than 10) and randomly assembled. Systematic assembly of males, so that preferred males were overdispersed, would tend to stabilize the line of equilibria. Leks seem unlikely to represent random assemblages of males.

Fisherian evolution thus appears to depend primarily on genetic drift in small disjunct or colonizing populations to accomplish large changes in disadvantageous male traits. In these conditions, any one deme might have constantly shifting behavioral mechanisms of female choice, fluctuations that could even lead to premating reproductive isolation and speciation (Lande, 1981, 1982). This situation could well have occurred in the evolutionary history of many species. Species groups like the birds of paradise provide likely examples, but speciation by this process could just as well occur in species without leks. There is also no indication yet that leks themselves represent genetic subdivision of populations (Dunn and Braun, 1985). Consequently, it is not clear that lekking in itself predisposes species to Fisherian evolution.

A female preference for a male trait would spread without genetic drift if it reinforced directional selection for increased viability in both sexes (Heisler, 1984), or even only in females. Thus, a preference for vigorous males might

result in female offspring that would survive or reproduce more successfully (Andersson, 1986). Increased viability of female progeny increases the chances for female preferences to spread, because it counteracts any disadvantages arising from lower survival of male progeny or from immediate costs to females (Pomiankowski, 1987a). Conceivably, the opposite might also obtain: genes for male vigor might in some cases reduce female viability. Preferences for "good genes" for female descendants are often contrasted with Fisherian arbitrary preferences (Borgia, 1979, 1987; Kirkpatrick, 1987; Maynard Smith, 1987).

This review of current thinking about costs and benefits relevant to sexual selection suggests that these fall into three categories: (1) those expressed in males with genes for the preferred trait, (2) those expressed in females with genes for the male trait, and (3) those expressed in females with genes for the preference. These effects can be distinguished clearly in mathematical models. As a result of the genetic correlation between genes for the preference and those for the male trait, however, the latter two categories would prove difficult to separate in the field, since their effects would appear, in the absence of detailed knowledge of genotypes, as summed effects on females expressing a preference. Fisherian evolution represents one extreme, in which only costs of type 1 are considered. "Good genes" models emphasize benefits of type 2. "Polygamy threshold" (Orians, 1969; Davies, 1989) and "sexy son" models (Weatherhead and Robertson, 1979) emphasize, respectively, benefits and costs of type 3. In reality, all three kinds of these effects are likely to occur, to different degrees, as a consequence of female choice in any mating system. With this background, we can consider the situation as it is now understood in lekking species.

E. COSTS TO SUCCESSFUL MALES

If some aspect of female behavior results directly or indirectly in increased mating success for some males on leks, it is important to determine the costs in terms of reduced survival, if any, associated with these benefits of increased mating success. No study has yet demonstrated changes in survival as a result of experimental manipulations of males' behavior or morphology. Nevertheless, costs seem plausible for lekking males, since they do little or no feeding for substantial proportions of the year and of each day they are present on a lek (Section IV). The consequences of attendance are perhaps greatest in the least favorable seasons of the year, rather than during periods when females are present, which tend to coincide with more favorable seasons. Thus, for grouse, attendance during late winter mornings, long before females arrive, might represent a considerable metabolic sacrifice. Males also spend considerable effort in displaying while on leks, particularly during periods when females are visiting or likely to visit. Because males usually display at higher rates when females are

nearby, successful males should incur greater metabolic costs than unsuccessful ones (for example, Given, 1988).

These expectations based on behavioral observations have recently been confirmed for sage grouse by Vehrencamp *et al.* (1989). By using doubly labeled water, they found that metabolic energy expenditure was twice as high for males attending leks as for those not attending and that successful males (those observed to copulate at least once) had metabolic energy expenditures twice as high as unsuccessful males. On the other hand, they found that successful males lost less mass/day between captures during the mating season than did unsuccessful males. Thus, increased energy expenditure by successful males was more than completely compensated for, possibly as a result of their feeding strategies when away from the lek. Although male sage grouse have maximal reserves of lipids just preceding the breeding season, these reserves can provide only a small fraction of the energy required for display throughout the season (Hupp and Braun, 1989). The decrease in their lipid reserves and body mass during the breeding season suggests that these reserves might nevertheless provide the margin for especially demanding effort (Beck and Braun, 1978; Hupp and Braun, 1989).

Although Vehrencamp *et al.* (1989) also state that they found no differences in mortality between successful and unsuccessful males, a power test would be necessary to establish the precision of this negative conclusion. In addition to any increase in mortality as a consequence of the time and energy required for persistent display, conspicuous display would often increase a male's risks of predation (for example, Ryan *et al.*, 1982). For black grouse in the Netherlands, data are available for the mortality of mature males (at least 3 years old) during March through August in relation to their territorial status and positions. Males with central territories ($n = 27$), which were more likely to mate successfully, had 11% mortality, those with peripheral territories ($n = 47$) 17%, and those that had never had a territory ($n = 13$) 15%; none of these differences is statistically significant (de Vos, 1983). Peripheral males on sharp-tailed grouse leks also had higher disappearance rates, although some of this effect might have resulted from movements of young males to other leks (Moyles and Boag, 1981). Among male Guianan cocks-of-the-rock, males that mated successfully had annual mortality of 24%, compared to 20% for those that did not mate, again not a statistically significant difference (Trail, 1987). On leks of Uganda kob, peripheral males have higher mortality than central males, but there is no correlation between predation rate and mating success on individual territories (Balmford, 1990). Even when mortality of fully adult males is not clearly related to their mating success, lower mortality in younger males (Section IX) suggests that full commitment to display incurs increased mortality.

Males of species with extreme sexual dimorphism in size might also face higher costs as a result of greater metabolic demands for growth. Presumably,

these costs explain the finding that juvenile males of the two most sexually dimorphic grouse, sage grouse and common capercaillie, suffer higher mortality in the first months of life than do females in habitats or in years with poor conditions for growth (Wegge, 1980; Moss, 1980; Swenson, 1986).

The finding that successful adult males on leks do not always have higher mortality would be expected if these males were more vigorous to begin with (Parker, 1983; Andersson, 1982b, 1986; Zeh and Zeh, 1988). Parker suggests that males differing in vigor might adjust their allocations of effort in order to maintain constant mortality and variable commitments to display. Alternatively, they might maintain constant commitment to display but have variable mortality. The best indication of overall vigor is thus, as Andersson (1986) proposed, the product of survival and mating success. Sage grouse appear to adjust mating effort while holding survival constant, although imprecision in information about survival makes it difficult to reach a firm conclusion (Vehrencamp *et al.*, 1989). Constant mortality across a range of mating effort does not imply that display and attendance at leks do not influence mortality, since each individual male would presumably survive better if it did not attend a lek or display as much as it did.

Another difficulty in properly assessing the costs of male mating effort comes from the extremely nonuniform distributions of matings. Most of the variation in mating success occurs among "successful males," those that copulate at least once. How closely any costs correlate with mating success among these males is not clear. One relevant measure here is the correlation between display rates and mating success, uncorrected for proximity or access to females (Hartzler and Jenni, 1988; Kruijt and de Vos, 1988; Andersson, 1989). Although such measurements are often statistically significant, the correlations are not particularly high.

F. COSTS AND BENEFITS TO FEMALES

Costs to a female mating on a lek are not likely to be high. Predation on leks is low (Section VII,D) and, although difficult to compare, perhaps no higher than away from leks. Although females in some cases go out of their way to visit leks, the distances traveled for these visits tend to be relatively short (Section V). Females spend little time visiting leks. They rarely fight seriously or engage in strenuous activity there, although females at leks sometimes supplant or threaten each other (Lumsden, 1965, 1968; Hogan-Warburg, 1966; Kruijt and Hogan, 1967; Wiley, 1973a; Kermott, 1982, p. 28). Robel (1970) proposed that these interactions prevented or postponed copulation by some female greater prairie chickens and thus might regulate populations. This possibility seems unlikely. On grouse leks, aggressive behavior toward other females is usually performed by females that have solicited for copulation (Kruijt and Hogan, 1967; Lumsden, 1968; Wiley, 1973a; Robel's report also suggests that aggression by females is

associated with readiness to copulate). Since females ready to copulate initiate aggression, rather than receive it, aggression among females probably does not prevent or postpone copulation.

By mating at a lek, a female gives up any possibility of male parental care. This situation does not necessarily impose costs on females. Reducing the frequency of parental visits to nests might have benefits if predation were thereby reduced. For tropical birds that feed their young with fruit, the relationships between predation rates, clutch sizes, and frequencies of parental visits to the nest could favor a shift to single parental care, although this possibility needs more analysis (Snow, 1962a; Snow and Snow, 1979; Willis, 1979; Ricklefs, 1980; Beehler, 1983a, 1987a; Beehler and Pruett-Jones, 1983). For monogamous grouse, the presence of a guarding male appears to have no influence on a female's survival or reproductive success, except possibly when predator densities are high (Martin, 1984; Hannon, 1984; Martin and Cooke, 1987).

In the absence of any advantage from male parental care, females of lekking species might benefit by mating in locations separated from nesting areas, so that displaying males cannot attract predators to themselves and their nests (Kruijt *et al.*, 1972). In support of this idea, Bergerud (1988) provides evidence that most nests of lekking grouse are located approximately half-way between leks, but this result would be obtained if females simply distributed their nests uniformly or randomly and visited the nearest lek for mating. Phillips (1990) instead proposes that females should nest at an intermediate distance from leks, a prediction based on untested assumptions about predators' movements. Data from one of three species of grouse provide tentative support for this idea, but more information is needed for a definite conclusion.

These potential immediate consequences of choosing to mate at a lek have little relevance to a female's choice of a mate within a lek. Since a female's subsequent reproductive activities always occur away from the lek, her choice within a lek could directly influence her immediate reproductive success only if males differed in their ability to fertilize eggs. This possibility might apply, especially to female grouse, which usually mate only once for a clutch, but there is little evidence on this point (Avery, 1984). Perhaps a more important consequence of choosing a mate within a lek is exposure to infectious diseases or parasites during copulation (Section X). Even when slight, immediate costs for female preferences have the important theoretical consequence of drastically reducing the possibilities for Fisherian evolution (Pomiankowski, 1988).

Increased viability for a females' offspring represents another potential benefit from choosing mates. If females' preferences result, directly or indirectly, in mating with vigorous males, the viability of their female, as well as male progeny might increase. Indirect choice for vigorous males could result from female preferences for mating in aggregations of males, particularly near the centers of aggregations, or in particular locations (Section V,B). Such preferences could

lead to competition among males and result in matings with the most vigorous among them. Direct choice of individual males' features has received much more attention in recent investigations of leks. In some cases, these features might correlate with male vigor, as secondary sexual features, morphological or behavioral, seem more sensitive to male condition than other traits (Andersson, 1986). Examples of such condition-dependent male traits could include long feathers, the growth of which might depend on nutritional state (Alatalo *et al.*, 1988), synthesis of substances for bright coloration (Hamilton and Zuk, 1982), antlers (Clutton-Brock *et al.*, 1982; Clutton-Brock, 1982), higher display rates, or indications of greater display intensity.

These male features, however, raise problems for the evolution of female preferences. Since commitments to display and survival presumably involve trade-offs for any one male, females with brief exposure to males before making direct choices among them could be deceived by males making short-term adjustments in these trade-offs (Andersson, 1986; Zeh and Zeh, 1988). Indirect, rather than direct, female preferences might provide more reliable mechanisms to produce benefits for female descendants. Any direct preferences for features of individual males might focus on traits necessarily related to overall, long-term viability (Kodric-Brown and Brown, 1984). It is perhaps significant that correlates of high mating success often include attendance at leks, rates of display, and features of displays that might provide unequivocal indications of vigor (Section V,C).

A general problem in applying "good genes" models to lekking species arises from the divergent lives males and females in these species lead. One would expect that a similar genetic basis for male and female vigor would be most likely when the two sexes had the most similar ecology (Clutton-Brock, 1983). One aspect of female preferences that would often increase the viability of progeny of both sexes is avoidance of hybridization (Section VIII,C). A preference for conspecific males in fact represents an extreme form of a preference for "good genes," one in which the consequences of error are sometimes categorical.

G. HANDICAPS

"Good genes" models of sexual selection are in part a development of Zahavi's (1975) proposal that females should prefer males with "handicaps" to assure honest advertisement of male quality. Rather than simply choose the most vigorous displayer, females should prefer the most vigorous displayer in relation to a permanent disability, one that interferes with chances for feeding or avoiding predators. It is possible to imagine a variety of kinds of handicaps with different effects on the viability of males; in all cases, however, males of high viability (V) that lack the handicap (h) survive best, and those with low viability (v) that have the handicap (H) survive worst (Fig. 5). Different proposals for handicaps vary in

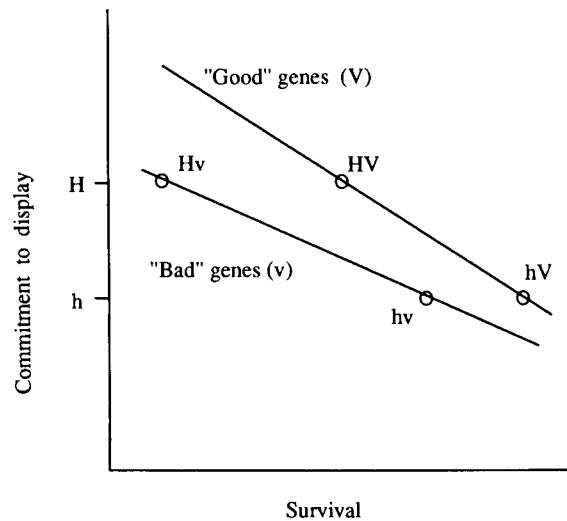


FIG. 5. Examples of the relationship of survival and display to illustrate the possibilities for males with "good" genes (genotype V) and those with "bad" genes (v) at two commitments to display, H and h. Hv males have the lowest survival, hV males the highest. HV and hv males have intermediate levels of survival; which of the two is higher depends on the shape, slopes, and positions of the lines in relation to the difference in commitment to display.

their ranking of HV and hv males between these extremes (Maynard Smith, 1987; Pomiankowski, 1987b, 1988).

Genes for male handicaps could of course spread, provided the frequency of a female preference for the handicap exceeded the necessary threshold for Fisherian evolution of disadvantageous male traits (Section VIII,D). The question therefore is, Can genes for a handicap spread even when the female preference is rare? Recent investigations of haploid genetic models have shown that, provided genetic variance for overall viability is maintained, the handicap gene either goes to fixation or is eliminated (Kirkpatrick, 1986a, b; Pomiankowski, 1987b, 1988). The line of equilibria for the preferred male trait (the handicap, in this case) and the female preference, as found in Fisherian evolution, is eliminated. This same result emerges when a handicap correlates with direct contributions by males to their mates' reproductive success, even when variation in these contributions is not heritable (Heywood, 1989). More reliable and less costly handicaps are more likely to spread (Pomiankowski, 1988). Nevertheless, a handicap still cannot spread unless the frequency of the female preference exceeds a threshold.

All males, regardless of overt handicaps, must make trade-offs in their commitments to mating success and survival. If these trade-offs differ among males, so that some males have lower survival for a given mating effort, these differ-

ences can be thought of as arising from covert handicaps. Because of the possibility of temporary adjustments of trade-offs, these covert handicaps do not allow a female with brief exposure to males to detect with much certainty those with high overall viability. An overt, permanent handicap improves her situation, by assuring that the consequences of successful display for survival were averaged over longer periods. The additional handicap means that fewer males could achieve any particular level of survival for a given commitment to display. As a consequence, errors in detecting males with "good" genes would decrease. If females had some criterion for commitment to display by a male before mating with him, then an overt, permanent handicap would increase a female's chances of detecting a male with high overall viability.

If we take a handicap in a general sense to be a male trait that increases a females' chances of detecting males with "good" genes, possibilities include long-term morphological commitments that require substantial investment of energy, skill in foraging, or vigilance against predators. Many of the morphological elaborations in males of lekking and other polygamous species might qualify. Some striking patterns, however, suggest that these features might not have high costs in many cases. First, in some species, secondary sexual morphology that increases conspicuousness, and thus might increase risks of predation, can be concealed for the most part when not actually in use for display. Prime examples are the three species of lekking grouse in North America. Away from a lek, males are, aside from overall size, hardly more conspicuous than a female, because most of the elaborate and conspicuous plumage is either on the lower side of the body or can be concealed with camouflaged feathers.

Second, modifications of beaks, jaws, legs, and wings are exceptional among secondary sexual characters in birds and mammals. Yet the clearest form of a handicap would involve modifications of those structures that directly contribute to collecting food or evading predators. In lekking birds, modifications of tail or body feathers are far more frequent and more extreme than modifications of wing feathers. One case of modified wing feathers, the stiffened secondaries of manakins in the genus *Manacus* (Snow, 1962a), does not result in a change in the shape of the wing. Sexual selection thus appears to have resulted in elaboration of male morphology in ways that tend to minimize direct impacts on males' abilities to evade predators and to forage. Exaggerated male traits thus seem not to have evolved solely because of costs that could improve a female's ability to discriminate males with high viability.

It is also worth noting that a female's discrimination of males that differ in genetic quality also depends on her criterion for mating. Thus, a female can reduce her errors in discriminating among males either (1) by attending to a signal, like a handicap, with greater variance in expression by males or (2) by attending to subtler differences in a signal with less variance.

H. CONCLUSION

Female choice of mates always involves some element of discrimination between males with "good" and those with "bad" genes, because mate choice, at a minimum, always requires species recognition to avoid dysgenic hybridization. The possibility of errors in female discrimination thus favors preferences for species-specific behavior or morphology. Simple considerations of signal detection suggest that, when the possibility of errors is high, females should prefer distinctive species-specific features of males. Since females of many lekking species, like those of other polygynous species, interact with conspecific males during relatively brief periods of their lives, advantages of female preferences for distinctive signals could explain, at least in part, the elaboration of morphology and behavior in males of these species. Furthermore, it seems probable that male traits preferred by females to permit species recognition would in general reduce male survival, since commitments to display and to survival must involve some trade-off for any male. Thus, selection for species recognition would fit models for the evolution of female preferences for male traits with immediate disadvantages for males but eventual advantages as a result of greater viability of progeny.

It is a bigger challenge to understand the evolution of female choice among conspecific males. Much recent work has focused on direct female preferences for particular features of conspecific males. There has been little attention to indirect female preferences. There is also no information from natural situations on the actual advantages or disadvantages of preferences to females and their descendants (Section X). On the theoretical side, models of Fisherian evolution suggest that arbitrary female preferences for disadvantageous male traits cannot usually spread in large populations. It remains a question for the future whether this result means that populations of lekking, and other polygynous, species are more subdivided than currently thought or that arbitrary preferences are the exception rather than the rule.

IX. EVOLUTIONARY CONSEQUENCES OF AGE STRUCTURE IN LEKING SPECIES

A tendency for older males to achieve higher mating success raises a number of issues in the evolution of mating systems. In lekking species, there are two aspects of age-related male mating success (Section III,B). First, it is a universal finding that males do not develop full adult morphology nor fully participate in activities on leks until an age later than that at which females begin to reproduce. Second, circumstantial evidence suggests that mating success might tend to increase with age to some extent, even after males have attained full morphological development. These patterns are also evident in other polygamous species, in-

cluding those with dispersed display sites and those with harem or resource-associated polygamy (Clutton-Brock *et al.*, 1988b; LeBoeuf and Reiter, 1988). For lekking species the evidence is generally stronger for the first of the above patterns than for the second, probably in part because the morphological distinctiveness of the youngest males makes this pattern easier to confirm. Regardless of the generality of the second pattern, the first in itself prompts all the essential questions.

One immediate consequence is that age-related trends in mating success of males in general reduce the variance in individuals' lifetime reproductive success (Clutton-Brock, 1983). In essence, it is inappropriate to extrapolate from the distribution of annual reproductive success in a sample of males of heterogeneous ages to a distribution of lifetime reproductive success (Section I,E).

Age-related mating success also raises questions about the use of lifetime reproductive success as a measure of the propagation of genes. The spread of genes in a population is fundamentally a question of differences in rates of propagation. Only by assuming constant generation times can one use lifetime reproductive success as a measure of rates of propagation of genes in a population. In general, comparisons of fitness require full calculations of differences in their Malthusian parameters. (Fisher, 1930; Charlesworth, 1980). Later onset of reproduction lowers rates of increase, unless there are compensating increases in survival or later fecundity. In order to attain a rate of increase matching that of genes associated with earlier reproduction, those associated with later onset of reproduction must have compensating advantages in eventual fecundity or early survival (Wiley, 1981). This problem arises for both of the patterns of age-related mating success noted above for polygamous and, in particular, for lekking species.

In discussing the evolution of these patterns, two points need emphasis. First, explanations for later onset of reproduction based on behavioral and physiological mechanisms are not adequate evolutionary explanations. Demonstrations that older males dominate younger males, or that they inhibit their physiological development, fit this category. In fact, proximate regulation of age-related reproduction by interactions among males of different ages varies among species (Section III,B).

Second, surprisingly minor demographic changes can favor later reproduction. To see this point, consider two populations, one in which males begin to mate at age one and another in which they begin at age three. Further imagine that, in both cases, females begin to reproduce at age one and that all males older than the age at onset of mating have equal probability of success. Genes affecting males in the two populations have the same rate of increase, because the population with later onset of mating also has a lower breeding sex ratio (breeding males/breeding females). The increase in eventual fecundity of males exactly compensates for their delay in breeding (Wiley, 1974). Notice, first, that a

population composed of males with later onset of reproduction would have a highly nonuniform distribution of matings across all males. Second, although males of any one age probably never have equal success in mating, an assumption of nearly equal expectations of mating success for males of a particular age is not necessarily unrealistic. Much variation in mating success presumably arises by chance or by environmental influences on development.

This simplified example suggests that small differences in the consequences of early or late reproduction can favor one strategy or the other. Thus, in a population of early breeders, a gene associated with a tendency to reproduce slightly later on average would spread if it resulted on average in a sufficient increase in survival or in fecundity once reproduction began; conversely, the opposite conditions would result in the spread of a gene for earlier reproduction in a population of late breeders. Males with genes for later reproduction at first must compete for mates with the more numerous males that begin reproduction earlier. As genes for later reproduction spread and a steadily greater proportion of males begin reproduction later, fewer males would compete effectively for mates in any one season. As a consequence, expected fecundity of males with later onset of reproduction would increase. In other words, selection for later onset of reproduction has positive frequency dependence, so that conditions for the spread of a gene for later reproduction improve progressively once started.

What could cause the evolution of such age-related behavior in lekking species? Female preferences are the crucial factor, in either one of two ways: (1) preferences for exaggerated, energetic display could create survival advantages for later breeding; or (2) preferences, direct or indirect, for older males as such would create fecundity advantages for later breeding.

Satisfactory evidence for either of these possibilities is currently lacking. It is worthwhile nevertheless to consider the requirements for obtaining such evidence. Consider the question of whether or not males might realize an advantage in survival by postponing full mating effort until later in life (Wiley, 1974). This suggestion was examined by Wittenberger (1978), who reasoned as follows: if males with late onset of mating survive better, then males should have higher survival than females and sex ratios should be skewed in favor of males. Late onset of mating is associated with sexual dimorphism in size in grouse (Wiley, 1974); hunters' bags provide an estimate of sex ratios in grouse populations; therefore, if late onset of mating in males increases survival, hunters' bags should show greater male-biased sex ratios in sexually dimorphic species. In fact, he shows that sex ratios in hunters' bags do correlate with sexual dimorphism in size, but in the direction opposite to the prediction. Hence, he rejects the hypothesis that advantages in survival explain delayed maturation in male grouse.

This analysis is flawed in two ways that illustrate the care needed in conducting this sort of demographic comparison. A superficial problem arises from

considering hunters' bags as random samples of populations. In fact, hunters appear to kill disproportionate numbers of males in highly dimorphic species of grouse, probably because they are easier targets and despite their inedibility (Helminen, 1963; Rajala, 1974; Lindén, 1981; Braun, 1984). The difference in overall survival of the sexes is thus even greater than sex ratios in hunters' bags suggest.

A more serious problem arises from comparing male and female survival in order to evaluate possible evolutionary advantages of the later onset of breeding by males. In fact, differences in survival between the sexes are not relevant to this question. Instead, we need to compare survival of otherwise equivalent males that begin reproductive effort at different ages. Since there are probably individual differences in vigor, stronger males might optimize the trade-off between survival and mating in different ways than weaker males (Section VIII, E and G). Nevertheless, there could well be some variation in age of full mating effort among males, not confounded completely by differences in vigor, that could serve for tests of the hypothesis. Better still, experimental manipulations of access to mates, mortality risks, or display effort might reveal the nature of trade-offs between survival and mating.

Studies of marked populations of lekking grouse, both in hunted and in unhunted populations, suggest that mortality of older males is higher than that of younger males, an indirect indication that full commitment to lekking behavior might in fact incur a cost in survival. In the protected population of black grouse in the Netherlands, 8% of males in their first and second years disappeared during spring and summer ($n = 88$), the period of most intense display and molt, while 20% of males in their third through fifth years disappeared in this season ($n = 138$) (de Vos, 1983). In boreal Sweden, territorial adult male black grouse suffered 31% mortality during spring, as determined by radio-tracking, while nonterritorial yearling males died in this period (total $n = 54$). The former but not the latter males also incurred rapid loss of weight during spring (Angelstam, 1984). A large sample of male greater prairie chickens marked during their first winter ($n = 398$) revealed that mortality, in this unhunted population, in the years following a male's first, second, third, and fourth or later springs was 49, 49, 61, and 71%, respectively (Hamerstrom and Hamerstrom, 1973). In contrast, the mortality of females decreased slightly with age, in keeping with the absence of major changes in reproductive effort by females. In sage grouse, the same patterns appear. Adult males have higher mortality than immature males (approximately 55 and 45%, respectively), despite a disproportionate kill of young males by hunters. Yearling females have slightly higher mortality than older females, but not significantly so (Zablan and Braun, 1990). Yearling males also lose proportionately less weight than do older males during the breeding season (4.7 and 2.2%, respectively; Beck and Braun, 1978). For white-eared kob, some

circumstantial evidence indicates that males in the age classes most active at leks suffer higher mortality than other age classes (Fryxell, 1987).

In blue grouse, a species with dispersed display sites, Lewis and Zwickel (1982) have estimated the consequences of delayed reproduction for both survival and breeding. Among 75 males of known age, none held display territories in their first year, but 78% did in their second year. Of the latter, 48% held territories on sites that were permanently occupied by a succession of males. Males on these permanent sites had slightly higher average annual survival, in comparison to males on transient sites (75 and 67%, respectively, although males on both kinds of sites had 86% survival as 2-year-olds). Of 2-year-olds without territories, 80% survived. Of those, 45% obtained permanent sites in their third year and the remainder took transient sites. Permanent sites, which are more likely to have females nearby, appear to offer advantages for mating. Using these figures, a 2-year-old postponing display could expect a 36% chance of obtaining a permanent site the following year (0.80×0.45) and a 44% chance of obtaining a transient site (0.80×0.55). Waiting would yield greater lifetime reproductive success in comparison to settling on a transient territory at age 2, provided the expected annual mating success on a permanent site was at least 28% greater than on a transient site. Although incomplete, this study provides an example of the kinds of information needed to assess the evolutionary advantages of waiting for advantageous situations for breeding (see also Wiley and Rabenold, 1984).

As this example illustrates, the evolution of later onset of mating could result from either increased survival or later fecundity. In lekking species, both of these effects are likely to depend on female preferences in mating. How should we view the evolution of later onset of full mating effort in males in relation to sexual selection? As reviewed in Section VIII,D, the consequences of female preferences divide into those that affect the survival and fecundity of males, those that affect the females making a choice, and those that affect female descendants. Female preferences for more energetic display, if arbitrary, would tend to increase the costs for displaying males; adaptive adjustments of age-related mating effort by males would then serve to minimize these costs.

In species with larger differences between the sexes in ecology and life history patterns, genes for male viability seem less likely to affect female viability although their effects in females are probably never completely lacking (Section VIII,F). In these species, preferences for older males as such, either direct or indirect, would thus have less influence on genetic quality of female descendants than in species with more similarities in the lives of the sexes. Yet, it is in those species with the greatest differences in the ecology and morphology of the sexes that a few older males are most likely to mate. These considerations lead to a tentative suggestion that age-related mating effort of males is more likely to have evolved as a consequence of female preferences for energetic commitment to dis-

play, either directly or indirectly, rather than as a response to female preferences for older males as such.

X. MAINTENANCE OF GENETIC VARIANCE: THE PARADOX OF THE LEK

A problem that confounds evolutionary explanations of lekking behavior in terms of female choice is the "paradox of the lek" (Borgia, 1979; Taylor and Williams, 1982). The problem is a general one for sexual selection. As with other forms of directional selection, genetic variance for the selected trait generally decreases (Williams, 1975; Maynard Smith, 1978; Jones, 1987). If enough females prefer males with certain traits, genes associated with those traits spread and eventually go to fixation, thereby removing any further selection for female choice, either as result of genetic advantages for offspring or as a result of assortative mating. For instance, O'Donald's (1980) simulations of sexual selection for disadvantageous male traits revealed that, as the frequency of the gene for the male trait approached 1.0, selection for the gene for female choice decreased to zero.

In O'Donald's (1980) simulations, only persistent back mutation of the gene for the male trait maintained the gene for female choice. Mutational variation at a single locus, however, does not produce significant selection for female choice (Taylor and Williams, 1982). For highly polygenic male traits, on the other hand, it is possible that deleterious mutations in any of numerous genes could provide slight, but effective, levels of selection for female preferences (Lande, 1976; Charlesworth, 1988). Mathematical models of sexual selection also show that genes for an arbitrary female preference and for the corresponding male trait can reach a stable equilibrium with polymorphism in one or both genes (Section VIII,D).

If females could discriminate among males on the basis of overall viability, then balancing selection for overall viability might maintain genetic variance despite the directional selection produced by female mating preferences. There are several possibilities (Felsenstein, 1976; Maynard Smith, 1989): (1) heterosis; (2) frequency-dependent selection, including selection on host-parasite interactions; (3) variation in intensities of selection in space or time; and (4) counteracting selection at different levels of organization, during different stages of life, or on different components of viability. Any of these possibilities might apply to lekking species.

Variation in selection in time or space can maintain genetic variance under special conditions. In the case of variation in space, maintenance of balanced polymorphism is sensitive to population subdivision and dispersal. So far, there

is no evidence that lekking species, or polygynous species in general, differ systematically in these regards from other species (Dunn and Braun, 1985). If so, species with strong sexual selection either (1) do not differ much from other species in overall intensity of directional selection or (2) have genetic variance maintained by some other mechanism.

In the case of selection varying in time, directional selection should usually lead to eventual fixation of alleles with the highest long-term fitnesses (Maynard Smith, 1989, pp. 65–76) and thus to loss of genetic variation. Nevertheless, if selection coefficients reversed in sign at intervals of one to a few generations, polymorphism could persist. Selection coefficients for genes affecting interactions with physical features of the environment or with some biotic features, such as competitors or predators, are perhaps unlikely to reverse in sign over intervals of a few generations. The effects of the physical environment, competitors, and predators simply do not often change that dramatically and rapidly.

Interactions with parasites might satisfy these conditions (Hamilton, 1982; Hamilton and Zuk, 1982), since parasites usually have much shorter generations than their hosts and thus might evolve rapidly to counteract their hosts' defenses. Host–parasite interactions could thus result in frequency-dependent selection: the most frequent adaptations of the host would be matched by rapid evolution of counteradaptations by parasites (Maynard Smith, 1989). Genes conferring resistance to parasites and disease might thus differ markedly over periods of a few generations. Their frequencies could either fluctuate or persist in a stable equilibrium determined by frequency-dependent selection. In either case, female preferences for males resistant to parasites, as indicated by vigor in display or elaboration of ornament, might evolve particularly in species with high morbidity from parasites (Hamilton and Zuk, 1982; Kirkpatrick, 1986b; Read, 1987).

The possibility that females might prefer males with signs of resistance to parasites has prompted investigations of parasite loads in relation to mating success in various species (Schall and Dearing, 1987; Kennedy *et al.*, 1987; Zuk, 1988; Clayton, 1990). Several studies have reported that heavily parasitized males display less than other males (Schall and Dearing, 1987; Kennedy *et al.*, 1987). In sage grouse, one study reported that attendance at a lek, display rates, and success in mating were lower for males with higher numbers of lice or a hematozoan parasite (Boyce, 1990; Johnson and Boyce, 1990; Spurrier *et al.*, 1990); another study found no relation between mating success and either a different hematozoan or hematocrit (Gibson, 1990). Numbers of hematozoan parasites in Lawes' parotias correlated negatively, but not significantly, with mating success, and more heavily parasitized males displayed for significantly shorter periods during the season (Pruett-Jones and Pruett-Jones, 1990). Male satin bowerbirds that mated successfully had fewer external parasites than those that did not, but there were no correlations between numbers of parasites and either quality of a male's plumage or his condition (as measured by mass/wing

length) (Borgia and Collis, 1989). Despite these erratic results, the persistent trends in lekking species for correlations among (1) mating success, (2) vigor or persistence of display, and (3) parasite loads (see also Section V,C) suggest that parasites might influence the evolution of female choice.

Comparison of males within a population, however, does not provide a strong test for the hypothesis that transient adaptation to parasites maintains genetic variance and female choice. Sufficiently ill males would presumably have low persistence and vigor in display and low attendance at leks. Infection is in essence a form of covert handicap that affects the trade-offs males make between mating and survival. Consequently, if female preferences, direct or indirect, for vigorous or persistent display evolved for reasons other than rapid adaptation to parasites, females would incidentally tend to avoid parasitized males. Even if selection favored preferences for males with genes conferring resistance to parasites, these preferences, like other preferences for good genes, would not avoid the paradox of the lek unless the genetic basis for resistance shifted over periods of a few generations.

Circumstantial evidence for transient adaptations to parasites might include shifts in the kinds of parasites affecting males from generation to generation. Johnson and Boyce (1990) report, for example, that the incidence of hematozoans in male sage grouse varies among populations and between years. For definitive conclusions, however, it is necessary to demonstrate that the sexes are similarly exposed to the parasites under study and to verify changes in the genetic basis for resistance.

Other possibilities for maintaining selection for female preferences do not require genetic variation for male traits at all. If females incurred a fixed cost for indiscriminate mating, then this cost could alone maintain selection for female preferences even when genes for the preferred male trait had reached fixation. Selection against dysgenic hybridization might provide a fixed cost of this sort (Sections VIII,C and H). Even after female choice had eliminated most or all genetic variance for species-specific morphology and displays, selection for female choice would persist. The significance of discrimination against hetero-specific males is that the "bad" genes persist, in the form of males of a separate species, even in the absence of genetic variance among conspecific males.

Immediate costs to females from indiscriminate mating could also maintain selection for female preferences, even though the preferred males' traits had no genetic basis. Possibilities include risks of copulation, such as predation, injury by males during competition for mates, and infection by parasitized males, as well as disruption of copulation and incomplete fertilization of eggs (Reynolds and Gross, 1990). For example, a female might realize higher immediate survival or fecundity by mating in the center of a group of males or with a dominant or vigorous male. Most of these possibilities, however, seem unlikely or remain unexamined for lekking species. For instance, injury of females is not reported,

and in many species disruption of copulations is not restricted to unsuccessful males (Sections III,A). Risks of predation on females at leks in comparison to elsewhere remain unknown (Section VII,D), but seem unlikely to explain the degree of skew in mating distributions within a lek. Selection on females to reduce the immediate risk of parasitism might explain the lower mating success of heavily parasitized males, particularly when parasite loads fail to correlate with either ornamentation or condition of males (Borgia and Collis, 1989).

The parasite loads of males at different ages have received little attention. In satin bowerbirds, older males have fewer external parasites (Borgia and Collis, 1989), but Gibson (1990) reported no differences with age for a hematozoan parasite in sage grouse. Age-dependent infection could result from acquired immunity or selective mortality. In either case, it could favor female preferences for older males, as a result either of obtaining good genes or reducing the risks of copulation.

It is important to emphasize that the persistence of selection for female preferences could depend on a combination of balancing or transient selection for viability and selection against risky copulation or dysgenic hybridization.

XI. EVOLUTIONARY SCENARIOS FOR THE ORIGINS OF LEKING

There have been many proposals for conditions that lead to the evolution of leks as opposed to other mating systems. Since these proposals in general aim to provide more or less complete explanations for the evolution of lekking, they are appropriately termed evolutionary scenarios. As complex hypotheses, each makes a number of assumptions about behavioral mechanisms and evolutionary processes.

Evolutionary scenarios raise a number of general problems. One is the difficulty of enumerating a mutually exclusive set of possibilities, in part because their complexity often leads to finely divided variants. More important, evaluation of any hypothesis requires attention to its assumptions as well as its predictions, a point more easily forgotten in evaluating complex scenarios than when dealing with simpler hypotheses. The following sections summarize current scenarios for the evolution of lekking in relation to behavioral mechanisms and evolutionary issues.

A. PREDATOR AVOIDANCE AND INTERSEXUAL COMPETITION

Protection from predation is the critical component in some scenarios for the origin of leks. In grouse, the association of lekking with display in open habitats and of dispersed display sites with display in forests suggests that aggregation at leks might reduce predation in open areas (Koivisto, 1965; Wiley, 1974). Protec-

tion from predators might benefit females near displaying males as well as the males themselves (Wittenberger, 1978; Gosling, 1986). Aside from the observation that predation occurs infrequently on leks, little is known about rates of predation on solitary and aggregated males or females in different habitats (Section VII,C).

Lekking in birds other than grouse is not clearly related to habitat or other conditions that might affect exposure to predators, although the presence of other males nearby might of course increase the chances of detecting predators in any habitat. It would be instructive to collect information on levels of vigilance and persistence of display by solitary males and males on leks of different sizes.

The tendencies for males in some species to move their positions toward the centers of leks (Section III,B) and of matings to occur in central portions of leks (Section II,D) suggest that leks might function in part as selfish herds (Hamilton, 1971). Critical evidence for this possibility would come from rates of predation at different positions on leks (Section VIII,E). Regardless of other influences on the evolution of leks, risks of predation merit attention, as they bear on the costs of male display and of female choice.

Another suggestion is the possibility that females prefer to mate in locations away from feeding or nesting areas in order to minimize their competition with males for food or their exposure to predators attracted to males (Section VII,D). This suggestion alone does not explain either the aggregation of males or the nonuniform distribution of matings.

B. DISPROPORTIONATE ATTRACTION AND MALE BUFFETS

This proposal explains the advantage of male aggregation by a disproportionate attraction of females to groups of displaying males. Some versions of this scenario propose that larger leks simply produce auditory signals that carry farther and thus attract females from a larger area, not in itself an adequate explanation for attraction of females (Section V,D). A more plausible scenario would involve female preferences for synchronized or coordinated displays (Section III,C).

Attraction of females to synchronized or coordinated displays might plausibly provide a means of choosing vigorous males either between or within leks. Age might also contribute, if developing coordinated displays required prolonged social interaction. Evolutionary stability of such cooperative relations between males would require either (1) kinship among males at a lek, for which there is no suggestion in lekking species, or (2) reciprocity based on individual recognition or age-related succession (Section III,B and C; Axelrod and Hamilton, 1981; Wiley and Rabenold, 1984).

Another possibility is that females choose to mate at aggregations of males because of responses to collective features of aggregated display, the spatial

density of displaying males, or the overall continuity of displays. These preferences might carry over to choices among males within a lek. The advantages of mating in a group of males might come from the ease of comparing males (Section IX,D), reduced waiting time for matings (Parker, 1978), or reliability of indirect choice of mates in obtaining optimal partners (Section XI,E). On the other hand, arbitrary preferences for mating in aggregations could in itself lead to Fisherian evolution of leks (Queller, 1987).

A related scenario, termed the female choice model, although perhaps "male buffet" is more descriptive, proposes that females prefer to mate in aggregations of males for convenience in choosing among individual males (Alexander, 1975; Emlen and Oring, 1977; Bradbury, 1981; Oring, 1982). This proposal thus requires mechanisms, not necessarily similar, for females' attraction to groups of displaying males and then for choosing, by direct or indirect means, among those assembled.

C. HOT SPOTS

In the hot-spot model for the evolution of leks, male aggregation results from males' displaying at locations that maximize their probable access to females. Simulations of this process have produced predictions for the spacing of leks, movements of females, and sizes of females' ranges, which in some cases agree with observed patterns (Section VII,B). More direct evidence from a number of species shows that leks often occur in locations with convenient access for females. In some cases, leks have disbanded and reformed elsewhere as a result of changes in movements of females (Sections II,B and IV). Furthermore, observations suggest that males in their first mating season might choose to join a lek as a result of experience with the numbers of females and males there previously (Section III,B). Thus, most of the assumptions of the hot-spot model seem plausible in modified form. One unrealistic assumption, however, concerns the movement of females. If females visit more than one lek or otherwise choose among them before mating, or if they follow other females to leks and then tend to return, females would not necessarily mate with the closest displaying male.

D. HOTSHOTS

The hotshot model proposes that females make direct choices among males and that unsuccessful males then move their locations near successful ones in order to intercept approaching females (Beehler and Foster, 1988; Gosling and Petrie, 1990). These mechanisms could lead to some constancy in location of leks, since, following the disappearance of the most preferred male, the next preferred is likely already to be established nearby. The optimal tactics for males in this case, however, are not clear (Section VII,B). In addition, a tendency of

females to find replacement mates nearby amounts to a partial constraint on preferences for mating, a significant modification of this model. Hotshot scenarios, in any form, confront the problem of explaining the near unanimity of female preferences on the assumption of independent, direct choices by females (Section V,A).

A variant of the hotshot scenario proposes that females base their preferences for mating partners on the chances of interruption during copulation (Foster, 1983). Either by trial and error or by observing other females, a female might thus choose the most competitive, vigorous male in a group. In some species, however, the most successful males are not necessarily those that are least likely to be interrupted (Section III,A). This scenario could explain the high uniformity observed in females' choices, either as a consequence of females' observing previous attempts at copulation or as a consequence of relationships among males.

E. MATING SUCCESSION

Another class of scenarios for the evolution of leks, appropriately termed mating succession models, could also generate high uniformity in females' preferences, in this case by indirect choice of males by females. In these scenarios, each female tends to return to one location to mate; she might identify this location initially in any of several possible ways, by following more experienced females, by observing other females copulating without interruption (Section VI), by attraction to collective features of displaying groups (Section V,B and D), or by preferences for vigorous display or other features of male display (Section V,C). The site-faithfulness of females might apply only within an individual female's life or might be transmitted by tradition from older to younger females (Section VI). As a consequence, it would pay for males to establish dominance or territories at these preferred locations. The tendencies for males to aggregate would presumably increase if females' preferences for locations were traditional. If females' preferences for locations were highly focused, males might also move their territories gradually toward preferred sites and thus eventually, provided they remained competitive and survived, succeed to mating positions (Section II,B). Alternatively, less specific preferences of females for locations might result in succession in dominance, rather than in territorial locations. In either case, the preferences of females for a location, whether traditional and highly focused or not, could result indirectly in matings with older or more competitive males and hence, perhaps, ones with higher overall vitality.

F. COMPARISONS OF SCENARIOS

All of the more complete scenarios, those explaining both the aggregation of display and the nonuniformity of matings within aggregations, are also complex

enough to admit a substantial number of variants. These variants, and the scenarios themselves, differ in their assumptions about the nature of mechanisms controlling the behavior of males and females. In some cases, scenarios grade into each other as the mechanisms become more complex. Thus, hotshot and mating succession models, in some of their variants, converge closely. Other scenarios, in some variants, are not mutually exclusive. Hotspot models, in the form of constraints on females' searches, and disproportionate attraction models could combine with hotshot or mating succession models. Predation reduction and intersexual competition models might combine with any of the others.

When expressed in simplistic form, each of these scenarios can probably be rejected for any lekking species; when expressed in realistic complexity, probably few or none can be rejected with current information. This conundrum arises from the complex variants each scenario can accommodate. The crucial distinctions are often the behavioral mechanisms that actually control the interactions of individuals. It is here that more research is needed. In addition to further investigation of female preferences for features of individual males, future work on the behavior of lekking species should include attention to (1) interactions between females, (2) female preferences for particular locations (including the spatial scale of such preferences), (3) female preferences for collective features of aggregated displays, (4) territoriality and dominance in relationships of males on leks and away from them, (5) age-related differences in the behavior of both males and females.

Recurring themes throughout this review suggest some general recommendations for further research on lekking species: (1) Quantitative analysis of social interactions is an essential base for any investigation. (2) Understanding behavioral mechanisms eventually requires experimentation. (3) Accurate understanding of behavioral mechanisms is essential for discussion of evolutionary issues and for comparison of evolutionary scenarios. (4) Age-related social behavior of males and females needs investigation. (5) Demography, in particular the demographic consequences of behavioral alternatives, also needs documentation. (6) Comparative studies should focus on variations in lekking behavior within species and also between related species. (7) Even wider comparisons are needed between lekking species and those with other mating systems, particular species with dispersed display sites lacking association with resources.

The many questions raised in this review result in part from the early stage of our current understanding of leks and in part from the complexity, both logical and logistical, of investigations of lekking species. In our push to find generalities, we should not neglect a fascination with the intricacies of lekking. We need to understand variations among and within species, as well as to identify general paradigms. Griffin (1976, p. 9) has cautioned against the "simplicity filters" that students of animal behavior sometimes adopt. While simple hypoth-

eses necessarily bear investigation first, we must move beyond them, if we wish to comprehend the complexities of animal behavior.

XII. SUMMARY

For species in which females have no associations with males except for brief periods preceding copulation, mating at leks probably enhances a female's discrimination of optimal mates, ones advantageous either for increasing the viability of her offspring or perhaps for reducing the immediate risks of copulation. The behavioral mechanisms by which this discrimination occurs are not yet well established for any species and might well differ among species or even among populations of the same species. These mechanisms might involve interactions among females, including learned traditions, as well as interactions among males and between females and males. Sexual selection could result from indirect, as well as direct, consequences of female preferences. The costs of display and ornamentation for males at leks are indicated by higher mortality of adult than younger males and greater energy expenditure by successful males. Advantages to females of choosing mates at leks remain mostly undocumented.

A general feature of mating at leks is a later onset of successful reproduction by males than by females. Age-related mating success of males on leks continues, at least in some cases, beyond the age at which fully developed morphology is attained and is, again at least in some cases, related to territorial succession or succession in dominance. Female preferences for mating at particular locations could provide the basis for either of these forms of mating succession and result indirectly in mating with older or more vigorous males.

Strong directional selection as a result of female preferences, either direct or indirect, tends to deplete genetic variation for the preferred male traits. This situation in turn reduces selection for the female preferences based on discriminations among conspecific males, the so-called paradox of the lek. Transient selection for resistance to parasites could maintain genetic variance for male traits, but evidence necessary to establish this possibility for lekking species is incomplete. The paradox of the lek does not arise when there are fixed costs of indiscriminate mating by females, such as immediate risks during copulation or dysgenic hybridization.

These generalities apply equally well to any species with brief interactions between the sexes and no associations of males with resources used by females. In particular, they apply to species with dispersed, rather than aggregated, display sites. In some taxa, the evolution of dispersed versus aggregated display appears related to risks of predation in different habitats; in others, this variation has no apparent explanation at present. All of these species in which copulation

occurs at display sites lacking resources, whether aggregated as leks or dispersed, isolate clearly the issues of evolution by sexual selection and thus merit our continuing attention.

XIII. SCIENTIFIC NAMES OF SPECIES MENTIONED IN THE TEXT

Bat, hammer-headed (*Hypsignathus monstrosus*)
 Bellbird, bearded (*Procnias avero*)
 Bellbird, white (*Procnias alba*)
 Bird of paradise, Goldie's (*Paradisaea decora*)
 Bowerbird, satin (*Ptilinorhynchus violaceus*)
 Capercaillie, common (*Tetrao urogallus*)
 Capuchinbird (*Perissocephalus tricolor*)
 Cock-of-the-rock, Guianan (*Rupicola rupicola*)
 Deer, fallow (*Cervus dama*)
 Deer, red (*Cervus cervus*)
 Eagle, golden (*Aquila chrysaetos*)
 Goshawk (*Accipiter gentilis*)
 Grouse, black (*Tetrao tetrix*)
 Grouse, blue (*Dendragapus obscurus*)
 Grouse, ruffed (*Bonasa umbellus*)
 Grouse, sage (*Centrocercus urophasianus*)
 Grouse, sharp-tailed (*Tympanuchus phasianellus*)
 Hawk-eagle, ornate (*Spizaetus ornatus*)
 Hermit-hummingbirds (*Phaethornis* spp.)
 Indigobird, village (*Vidua chalybeata*)
 Kob, Uganda (*Kobus kob thomasi*)
 Kob, white-eared (*Kobus kob leucotis*)
 Lechwe, Kafue (*Kobus leche kafuensis*)
 Manakin, band-tailed (*Pipra fasciicauda*)
 Manakin, golden-headed (*Pipra erythrocephala*)
 Manakin, lance-tailed (*Chiroxiphia lanceolata*)
 Manakin, long-tailed (*Chiroxiphia caudata*)
 Manakin, white-bearded (*Manacus manacus*)
 Manakin, wire-tailed (*Pipra filicauda*)
 Parotia, Lawes' (*Parotia lawesi*)
 Prairie chicken, greater (*Tympanuchus cupido*)
 Ruff (*Philomachus pugnax*)
 Sandpiper, buff-breasted (*Tryngites subruficollis*)
 Seal, northern elephant (*Mirounga angustirostris*)
 Snipe, great (*Gallinago media*)

Toad, natterjack (*Bufo calamita*)
 Topi (*Damaliscus lunatus*)
 Widowbird, Jackson's (*Euplectes jacksoni*)

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