

Lek behaviour in birds: do displaying males reduce nest predation?

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Abstract. Male lek display in birds may reduce nest-related predation by decoying predators away from nests and alerting incubating females when a predator is approaching. The sentinel/decoy model predicts a region of decreased predator density just inside the maximum range at which predators are attracted by displaying males. The expected ring of successful nests is evident in data from three species of North American prairie grouse. Well-documented features of female mate choice in lekking species, including repeated visits to male display sites prior to mating, mate fidelity and mate copying, are consistent with females maximizing the proposed antipredator benefit. The sentinel/decoy model makes a number of unique predictions that will facilitate critical tests of the model.

Lek mating systems have drawn the interest of evolutionary biologists because it is assumed that sexual selection and, in particular, female choice can be studied without the confounding influence of direct (or 'material') benefits that males provide to females (Borgia 1979; Bradbury & Gibson 1983). In lek mating systems, males display conspicuously from small display territories, but do not control resources that are necessary for reproduction or provide parental care, and do not control access to females (Bradbury 1981). This definition of lek behaviour includes both 'classical' leks in which male display sites are densely clustered and 'exploded' leks in which display sites are more dispersed.

Several recent models have attempted to explain various aspects of lek behaviour in birds such as dispersion of male display sites, variation in male mating success and location of nests relative to male display sites (see Bradbury & Gibson 1983 for a critique of older ideas).

The 'male-avoidance' model (Wrangham 1980) proposes that females select males that display away from nest sites to avoid costs associated with the presence of males (e.g. conspicuousness to predators, competition for food and wasted time and energy resulting from unsolicited courtship). The most important prediction derived from Wrangham's model is that nesting success should increase with distance from male display sites.

'Good genes' models (e.g. Bradbury 1981) propose that females select males with superior genotypes that increase the genetic quality of the females' offspring. According to the good genes models, preference for mating within a group of

males may arise because direct comparison of males enables females to assess male quality more efficiently or more accurately (Emlen & Oring 1977). Although there is no evidence to indicate whether mate choice in lekking species results in an increase in the overall fitness of offspring, good genes models remain popular because of the assumed absence of a direct benefit of mate choice in lekking species (e.g. Borgia 1979).

The 'hotspot' model (Bradbury & Gibson 1983; Bradbury et al. 1986) proposes that leks form at local regions of high female density ('hotspots'). According to the hotspot model, classical leks should occur in species where there is considerable variation in the density of females, while exploded leks should occur in species where the distribution of females is more uniform. Bradbury & Gibson provide data consistent with these predictions, which suggests that classical leks organization generally occurs in species with large, overlapping female home ranges and diets (e.g. frugivory) that promote female aggregation (see below).

The 'hotshot' model (Beehler & Foster 1988) proposes that initial differences in male attractiveness to females, coupled with 'conservative' female mating patterns (e.g. mate fidelity and copy of other females), produces male 'hotshots' that are highly successful in mating. Unsuccessful males associate with hotshots to gain access to females, but mating is restricted by dominance interactions within the group of males. The principal predictions of the hotshot model stem from the presumed influence of female mate fidelity and female copying on male mating success. These predictions will be discussed in a later section (below).

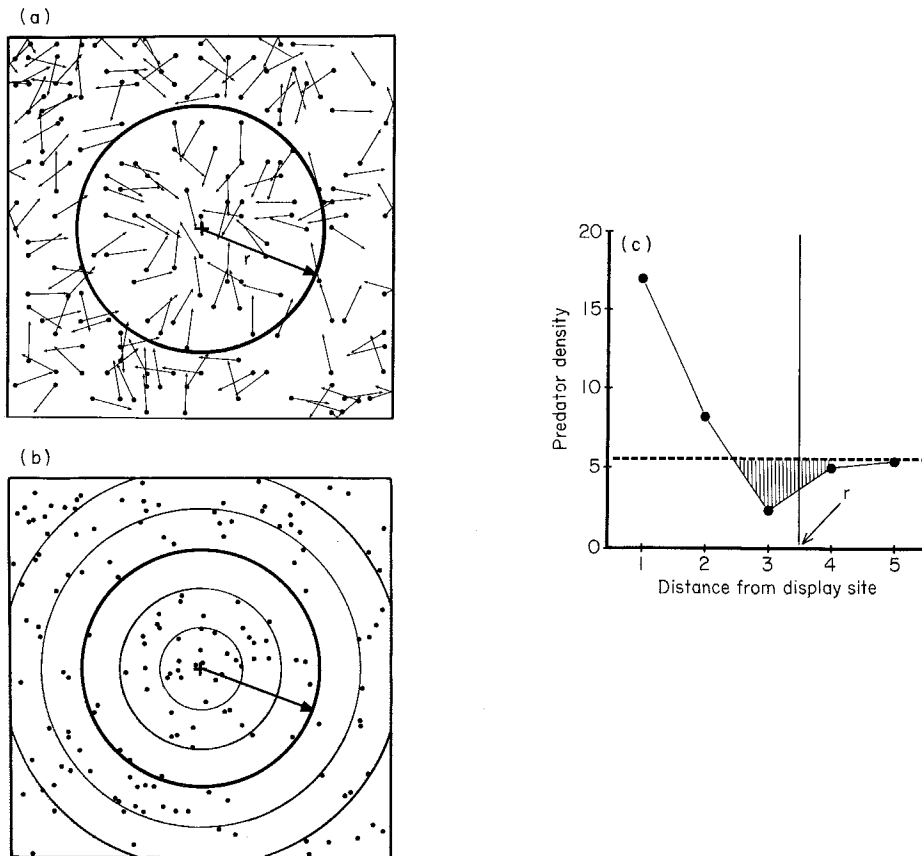


Figure 1. (a) Predators (solid dots) were assigned random locations and directions of movement. Outside the radius (' r ') at which predators are attracted to the male display site ('+'), the predators' movements (arrows) were assumed to be independent of the displaying males. For predators located within the radius of attraction, however, the arrows are the average of the 'spontaneous' (randomly assigned) directional preference and a 'male-directed' directional preference of twice its strength. (b) The location of each predator is shown after an arbitrary distance of movement (indicated by the length of arrows in a). The average density of predators at progressively greater distances from the male display site is plotted in (c). Just inside ' r ', the density of predators is lower than the average density in the habitat (---), creating an optimal zone (▨) where nests and incubating females will experience lower predation.

Common to all four models is the assumption that males in lekking species contribute only their gametes to the next generation. This assumption is virtually universal in the recent literature on lek behaviour (e.g. Emlen & Oring 1977; Wittenberger 1978; Bradbury & Gibson 1983; Beehler & Foster 1988). In this paper, I propose a direct benefit of lek display to nesting females: a reduction in nest predation due to the presence of conspicuously displaying males.

Lekking birds are subject to high levels of nest predation. Typically 40–60% of nests are depredated in temperate zone, ground-nesting species

and 80–90% in tropical species (Snow 1963; Lill 1974a; Pitelka et al. 1974; Wittenberger 1978). Although males do not directly defend nests or incubating females against predators, a majority of nests are located within the range of male displays (see below). Hence, the behaviour of displaying males may affect the likelihood of predation on nests and incubating females.

Males may benefit females by serving as decoys. If predators are drawn toward the males' display site, a region of decreased nest predation should occur just inside the maximum distance at which these predators are attracted (Fig. 1). Nests located

in this 'optimal' zone should be exposed to a lower density of predators because predators drawn away from nests by the displaying males will be replaced at a lower rate by predators entering the optimal zone by chance from the region beyond the range of male displays. Predators may also be less effective in searching the area within range of the displaying males, either because they focus their attention on the displaying males or alter their behaviour to stealthily approach male display sites.

Males may also serve as sentinels. If incubating females can detect male responses to a predator approaching the display site (e.g. an alarm signal, escape response, cessation of display or shift in the location of display), they can use displaying males as sentinels. A female that is forewarned to the approach of a predator can behave cryptically to decrease the likelihood of being located. In contrast to the decoy function of males, the value of males as sentinels will be greatest for females nesting close to the male display site and will decrease gradually with increasing distance until females are no longer able to detect the male response.

The maximum benefit to incubating females should be derived from males that serve as both decoys and sentinels. Predators attracted by displaying males will be drawn away from nests located at an optimal distance from the male display site (Fig. 1), but will again pose a threat as they leave the vicinity of the displaying male(s). However, if male behaviour alerts incubating females to nearby predators, females will be able to minimize the danger from departing predators by behaving cryptically. The sentinel function of males may cause the optimal distance for nests to be closer to male display sites than would occur if only the decoy benefit was operating (and may moderate to some degree the impact of high predator densities near the male display site). However, the qualitative predictions of the model remain the same (see below).

After examining the proposed antipredator benefit to females, the remainder of this paper discusses: (1) evidence that displaying males are effective as sentinels and decoys, (2) patterns of mate choice that should arise if the proposed antipredator benefit exists, and (3) the possibility that selection on females to maximize the hypothesized antipredator benefit has been an important factor in the evolution of lek behaviour in birds. Examples are drawn primarily from lekking species of grouse (Tetraonidae), although other species will be discussed where relevant data are available.

NESTING SUCCESS

The male sentinel/decoy model makes several testable predictions about the influence of displaying males on the relative spatial and temporal distribution of successful and unsuccessful nests.

(1) Nests located in the hypothesized region of reduced predator density (Fig. 1) should experience lower levels of predation relative to nests located both closer to and farther from display sites than this optimal distance. Therefore, successful nests should occur at approximately the same mean distance from the nearest display site, but exhibit less variance in that distance, than do nests and incubating females that are preyed upon.

This prediction contrasts with the male-avoidance model (Wrangham 1980), which predicts that successful nests will on average occur at greater distances from male display sites, because at greater distances, there will be fewer of the costs associated with the presence of the conspicuously displaying males.

(2) Nest sites at the optimal distance from male display sites should be occupied preferentially. If there is competition for nest sites, subordinate females should be displaced closer to, or farther from, the display sites than the optimal distance.

This expectation of the male sentinel/decoy model also differs from Wrangham's model, which predicts that nests located beyond the influence of displaying males should be occupied preferentially.

(3) If displaying males are removed or cease displaying while females are incubating, nest success should decrease and the predicted clustering of successful nests should be eliminated.

In Wrangham's model the absence of displaying males should (if anything) increase nesting success, because the proposed costs associated with the presence of displaying males would be eliminated.

Suitable data on the spatial distribution of successful and unsuccessful nests (Fig. 2) are available from studies of the greater prairie chicken, *Tympanuchus cupido* (Bowen 1971; Svedarsky 1979), the sharp-tailed grouse, *Pediacetes phasianellus* (Christensen 1970), and the lesser prairie chicken, *Tympanuchus pallidicinctus* (Davis et al. 1981). Data from the first 2 years of the study by Svedarsky were excluded because of the use of cannon nets on the display grounds, which were

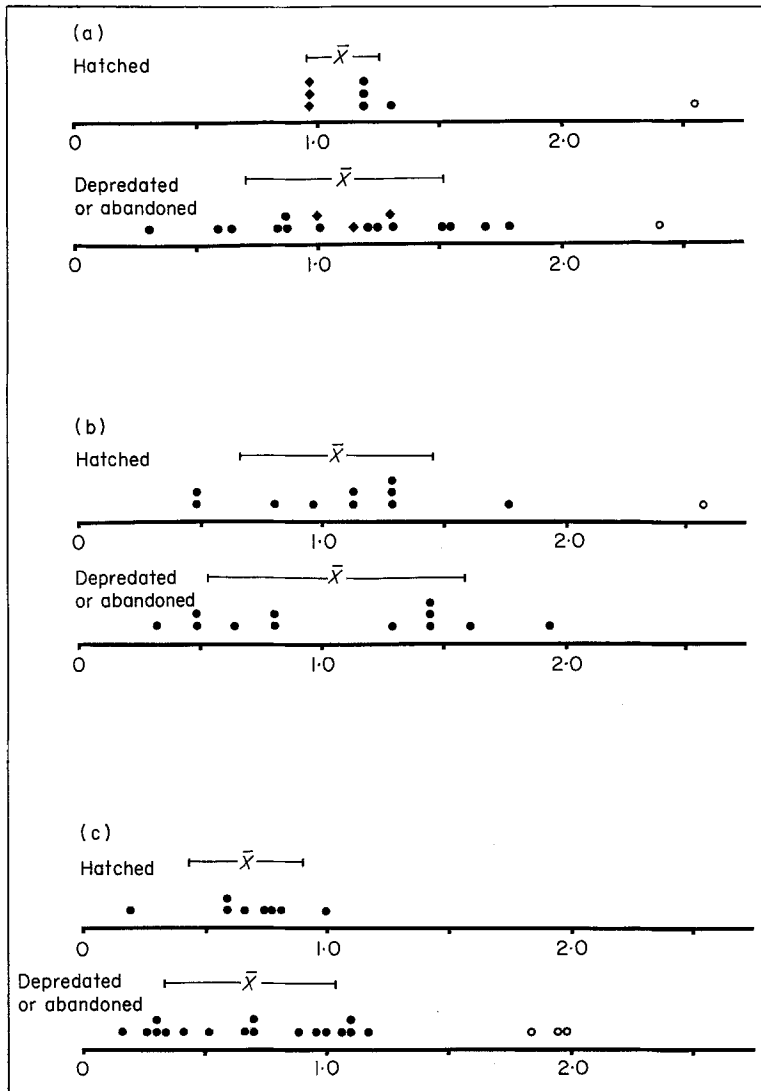


Figure 2. (a) The distance (km) of successful (upper graph) and unsuccessful (lower graph) nests of the greater prairie chicken from the nearest display ground (dots from Bowen 1971, diamonds from Svedarsky 1979, and unpublished data): successful nests averaged (\pm SD) 1108 ± 143 m, unsuccessful nests averaged 1109 ± 404 m ($F_{16,6} = 7.98$, $P < 0.01$). (b) Sharp-tailed grouse (data from Christensen 1970): successful nests averaged 1063 ± 396 m, unsuccessful nests averaged 1060 ± 530 m ($F_{11,9} = 1.79$, $P > 0.10$). (c) Lesser prairie chicken (Davis et al. 1981): successful nests averaged 664 ± 234 m, unsuccessful nests averaged 678 ± 348 m ($F_{16,7} = 2.21$, $P < 0.10$). Outliers (nests greater than 3 SD from the mean nest distance of each species; open symbols) are excluded from this analysis. If outliers are included, the probability levels for the greater prairie chicken becomes $P < 0.10$, and for the lesser prairie chicken, $P < 0.01$. The data for the sharp-tailed grouse are not significant in either case.

reported by the author to have disrupted male display and delayed mating (Svedarsky 1979, page 24). Nests in all three studies that were lost because of agriculture or fire and nests abandoned because of disturbance by observers were also excluded.

In all three species the mean distances of successful and unsuccessful nests from the males' display sites are similar, but successful nests exhibit less variance in distance from the nearest active display site than do unsuccessful nests. In one case the

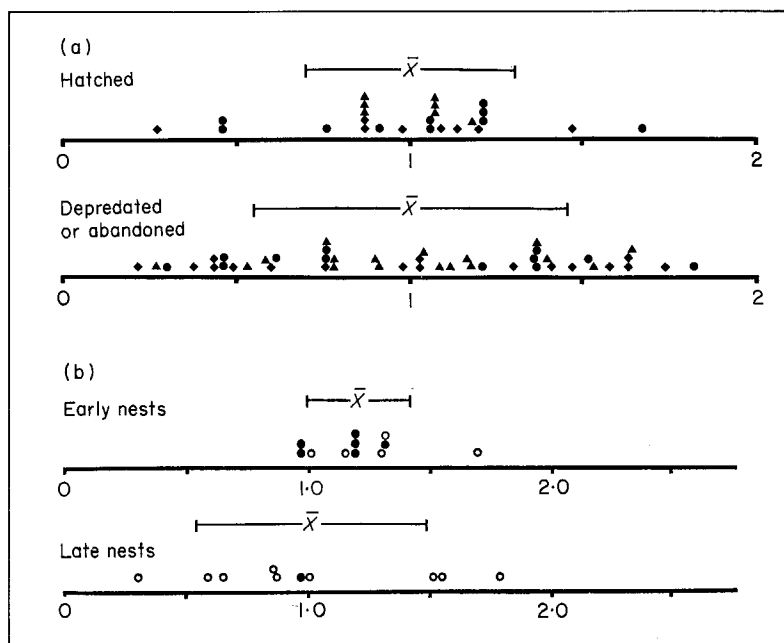


Figure 3. (a) Nest-location data from Fig. 2 were pooled after normalizing the distributions with respect to the mean distance of nests for each species (greater prairie chicken: triangles; sharp-tailed grouse: dots; lesser prairie chicken: diamonds). The average distance of successful and unsuccessful nests are identical. However, successful nests exhibit less variance in distance from the nearest active display site than do unsuccessful nests ($F_{45,24} = 2.25$, $P = 0.01$). (b) Early nests of the greater prairie chicken incubated during the period of male display exhibited significantly lower variance in distance from the nearest display site than did late nests ($F_{10,9} = 5.25$, $P < 0.01$). Furthermore, six of 11 early nests escaped predation (solid symbols are successful nests, open symbols are unsuccessful nests), while all 10 of the late nests had some or all of their eggs taken by predators (one-tailed $\chi^2 = 5.20$, $df = 1$, $P < 0.05$). The one late nest indicated by a solid symbol was partially depredated.

difference in variance was highly significant ($P < 0.01$, Fig. 2a) and in another the difference approached significance $P < 0.10$, Fig. 2c). A pool of the normalized data from all three species clearly shows the clustering of successful nests (Fig. 3a). Fifty-three per cent of nests (20/38) in the central third of the range of distances from the nearest lek were successful, as compared to only 15% of nests (5/33) located either closer to, or farther from, display grounds (one-tailed $\chi^2 = 9.29$, $df = 1$, $P < 0.001$). Thus, the gain to females nesting at the optimal distance from a lek could be as great as a three- to four-fold increase in nesting success. It should be noted that the data for each species in Figs 2 and 3a are pooled from several different display grounds, and data for the greater prairie chicken are from two independent studies carried out in different locales, so the observed pattern is not an artefact of a few locations.

The sentinel/decoy model also predicts that the clustering of successful nests should depend on

the presence of displaying males. In the North American prairie grouse, male display does not continue for the entire incubation period. Mating is concentrated in two peaks, a distinct primary peak early in the season and a secondary, less-well-defined peak approximately 4 weeks later, consisting of reneeding females that lost their first clutch (e.g. Robel 1970; Hamerstrom & Hamerstrom 1973; Jenni & Hartzler 1978). Male attendance at display sites ceases shortly after the secondary peak of mating. As a consequence, early nests from the primary mating peak are incubated while males are present at the display grounds, whereas nests from the secondary mating peak are incubated after the cessation of male display.

In the greater prairie chicken, data on both nest success and date of nest initiation are available for a majority of nests from the studies of Bowen (1971) and Svedarsky (1979). When the locations (relative to the display grounds) of early and late greater prairie chicken nests are plotted separately

Table I. Male size, mean nest distance and range of male displays in North American prairie grouse

	Male size* (cm)	Mean nest distance (m; \pm SE) [†]	Auditory range (km) [‡]	Visual range (km) [§]
<i>Tympanuchus pallidicinctus</i>	24	673 \pm 62 (N=25)	1.5	1.6–2.2
<i>Pedioecetes phasianellus</i>	35	1060 \pm 99 (N=22)	2–3	2.4–3.2
<i>Tympanuchus cupido</i>	36	1110 \pm 70 (N=24)	3–4	2.5–3.3

*Length excluding tail; from Hjorth 1970.

[†]Data from Fig. 2.

[‡]Maximum range audible to human observer under calm conditions; references in Hjorth 1970.

[§]Maximum visual detection range based on size of displaying males and estimated predator visual acuity of 60–80 cycles degree⁻¹.

(Fig. 3b), early nests show a significantly tighter clustering, as well as greater hatching success, than do later nests. These findings are consistent with the predictions of the sentinel/decoy model and suggest, moreover, that the summary of data for the three species shown in Fig. 3a (which includes nests incubated after the cessation of male display) may underestimate the magnitude of the benefit to females when males are present at the display site.

Other studies of the North American prairie grouse in which males at display grounds and incubating females were not subjected to excessive disturbance, also suggest that early nests are more successful than later nests (Lehman 1941; Baker 1953; Eng 1963). In contrast, the expected seasonal pattern of nesting success is not evident in studies where the observers disrupted male display (Schiller 1973; Svedarsky 1979).

Other seasonally varying factors (e.g. number and type of predators, availability of alternative prey items, habitat quality, etc.) may also influence nesting success. To test directly the proposed antipredator benefit to females, males could be removed after the primary peak of mating to determine the effect on female behaviour and nesting success. Alternatively, male display could be prolonged after the normal cessation of display through the use of hormonal implants (Trobec & Oring 1972), so that females nesting after the secondary peak of mating could benefit from the displaying males' presence.

MALE SENTINEL/DECOY FUNCTION

Males as Decoys

A predator is most likely to locate a nest when the incubating female is coming or going from the nest (Storass 1988). In lekking species, bouts of foraging by incubating females generally coincide with periods of male display (e.g. Lumsden 1961; Dalke et al. 1963; Gullion 1967; Silvy 1968; Lill 1974b). Although the timing of both male display periods and female foraging bouts are subject to a variety of factors unrelated to the proposed sentinel/decoy function of males, the temporal synchrony of these behaviours increases the likelihood of a significant antipredator benefit to females.

A majority of nests in lekking species are located within the range at which predators can detect male displays. In the prairie grouse, the average distance of nests from the nearest displaying males is approximately one-third of the maximum range at which species of raptors commonly observed at the display grounds can detect an object the size of a displaying male and about one half of the maximum range at which a human observer can hear the displaying males of each species under calm conditions (Table I). These values undoubtedly overestimate the maximum visual and auditory ranges at which predators can recognize displaying males as potential prey items, especially late in the breeding season when the intensity of display is reduced. Nevertheless, a majority of nests are close enough

to the males' display site that they are likely to be within the range at which both avian and mammalian predators can detect, and may be attracted by, the displaying males.

In dispersed or exploded lekking species, nests are generally interspersed among the display sites of males and located closer to the male display sites than the distance at which adjacent males respond to each other's displays (e.g. Bendell & Elliot 1967; Brander 1967; Pruett-Jones & Pruett-Jones 1982). Therefore, most nests are likely to be within the range where both females and predators can detect the male displays.

Evidence from studies carried out in areas with natural numbers and diversity of predators indicate that lekking males attract at least some types of predators. For example, many species of raptors are attracted to male display sites (Lehman 1941; Scott 1942; Eng & Gullion 1962; Berger et al. 1963; Koivisto 1965; Wiley 1973; Hartzler 1974; Beehler 1983; Beehler & Pruett-Jones 1983; Trail 1987). Raptors rarely prey on nests, but may contribute indirectly to nest failure, because an attack by a raptor on a nesting female can give away the location of the nest to a nest predator, delay the female's return to the nest (leaving the highly conspicuous eggs exposed) or cause the female to abandon her nest.

Avian nest predators can be an important source of nest failure. However, little attention has been paid to the response of these predators to lekking males. More systematic study is warranted in light of reports of crows diving on displaying male prairie chickens (Sparling & Svedarsky 1978) and landing on the display grounds of the black grouse, *Lyrurus tetrix* (Koivisto 1965).

Mammalian predators account for a large proportion of nest failures in many lekking species (e.g. Bowen 1971; Hamerstrom & Hamerstrom 1973; Davis et al. 1981), but relatively little is known about the extent to which their behaviour is influenced by displaying males. Anecdotal observations suggest that mammalian predators are at times decoyed by displaying male grouse (Koivisto 1965; Gullion 1967; Hartzler 1974). However, the only systematic observations of mammalian predators at the display sites of lekking birds are from studies where observers were present (Hamerstrom et al. 1965; Sparling & Svedarsky 1978). Because mammalian predators are unlikely to visit a male display site when an observer is present, or to behave normally if they do visit, remote-tracking

techniques are needed to obtain meaningful data on the response of these predators to displaying males.

Male displays appear to be well-suited to decoying predators. Advertisement displays in most lekking birds involve slow, laboured flight, rapid, fluttering flight, or frenzied, often asymmetrical, wing flapping (e.g. Lumsden 1961; Hogan-Warburg 1966; Hjorth 1970; Lill 1976). These behaviour patterns are common in distraction displays of both lekking and non-lekking species (Armstrong 1947). A resemblance between lek displays of males and distraction displays used by females to defend eggs and young has been noted by several authors (e.g. Armstrong 1947; Skutch 1949; Bendell & Elliot 1967). In addition, in a number of lekking species males construct bowers or clear courts which are reported to attract predators (Gilliard 1959). Thus, many features of lek display increase the attraction of predators by males.

Males as Sentinels

In order for incubating females to exploit displaying males as sentinels, they must be able to detect the males' response to predators (e.g. an alarm call, escape response, cessation of display or shift in the location of display). In the blue and ruffed grouse where a majority of nests are located 50–150 m from male display sites (e.g. Bendell & Elliot 1967; Brander 1967), males investigate disturbances in the vicinity of their display site, give alarm calls when potential predators are sighted, lead mammalian predators away from display sites while signalling their position with periodic displays, and flush noisily when attacked (Bendell & Elliot 1967; Gullion 1967; Hjorth 1970). These behaviours are likely to alert females when predators are present.

In the prairie grouse, nests are located at much greater distances from male display sites (Fig. 2) than in the woodland grouse. Nevertheless, a majority of nests are likely to be within auditory range of the displaying males (see earlier discussion). Furthermore, male prairie grouse may function as sentinels even when display is sporadic, as often occurs after the primary peak of mating when a majority of females are incubating. This is because males flush more readily when females are not present at the display grounds in large numbers (Berger et al. 1963; Sparling & Svedarsky 1978). Alarm calls and wing noise produced by flushing males, as well as the sight of a group of males fleeing

ahead of a predator, may provide advanced warning to females whose nests are located in the predator's path. Displaying male prairie grouse also flush in response to avian nest predators (e.g. crows, *Corvus* spp., gulls, *Larus* spp.), probably mistaking them for more lethal aerial predators (Koivisto 1965; Sparling & Svedarsky 1978). Displaying males do not, however, respond to other large non-predatory birds with distinctive silhouettes and wingbeats, e.g. ducks. Thus, male behaviour may also help to alert incubating females to the approach of avian nest predators.

FEMALE CHOICE

If the presence of displaying males can cause a significant reduction in nest predation, selection will favour females that maximize this benefit. If so, female mate choice should be influenced by (1) a male's ability to decoy predators (i.e. traits that increase the conspicuousness of displays and give the appearance of vulnerability to attack) and (2) a male's reliability in attending and displaying at a particular site. Mate choice is an important determinant of the benefit a female receives because a male's mating success influences its display site fidelity and persistence of display (DeVos 1983; Trail 1984, 1985). Thus, a female that mates with a male exhibiting the attributes of an effective and reliable sentinel/decoy will increase the length of time during which she benefits from that male's presence.

In exploded lekking species, a female mating with a male whose display site is located adjacent to her nesting territory would clearly benefit from the prolongation of that male's display. The significance of female mate choice is less obvious in classical lekking species where a female nesting at the optimal distance from a lek benefits from the entire group of displaying males. Even in these species, however, a female may benefit from prolonging the display of an individual male because, in many classical lekking species, only a small number of males actively display late in the season (e.g. Hamerstrom & Hamerstrom 1973; Payne & Payne 1977; Lank & Smith 1987).

A large number of studies have been carried out to determine the basis of female choice in lekking birds. Male display site attendance and intensity or persistence of display have been found to correlate with male mating success in a wide variety of

lekking species (Skutch 1949; Snow 1972; Payne & Payne 1977; Foster 1981; Pruett-Jones & Pruett-Jones 1982; Trail 1984; Gibson & Bradbury 1985; Pruett-Jones 1985; Robbins 1985, but see Hoglund & Lundberg 1987). If females are actively selecting mates that display conspicuously and reliably, however, they must be able to assess these components of male behaviour.

In lekking species, females typically visit display sites over an extended period of time prior to mating (Gilliard 1959; Kruijt et al. 1972; Lill 1974b, c, 1976; Payne & Payne 1977; Foster 1981; Pruett-Jones & Pruett-Jones 1982) and, thus, are potentially able to compare the display site attendance of individual males. In bowerbirds, female preference for males with elaborate bowers (e.g. Borgia 1985a, b) selects for males that attend display sites reliably, because bower quality is strongly influenced by the amount of time that a male has spent guarding his bower against destruction by other marauding males (Borgia 1985a). Female choice based on male dominance (Beehler & Foster 1988) is also compatible with the sentinel/decoy model as long as dominance status correlates with display site attendance and persistence of display (e.g. Foster 1981).

A correlation between male mating success and display site fidelity is a necessary, but by no means a unique, prediction of the sentinel/decoy model. Furthermore, direct assessment by females of male display site attendance and conspicuousness of display is unlikely to account fully for the strong skew in male mating success observed in lekking species (Bradbury & Gibson 1983; Trail 1984; Gibson & Bradbury 1985). These characteristics of male display appear only to be 'permissive' variables (Gibson & Bradbury 1985). Clearly, some additional factors must account for the high degree of unanimity in female mate preference. One probable factor may be the copying of mate choice by other females (Van Rhijn 1973; Wiley 1973; Lill 1976; Trail 1984, 1985; see also Beehler & Foster 1988).

By copying the mate preference of an experienced female, an inexperienced female will increase the likelihood of mating with a male that attends the display site reliably. This is because experienced females exhibit strong mate fidelity both within and between seasons (Lill 1976; Payne & Payne 1977; Foster 1981; Trail 1984; Pruett-Jones 1985). As a consequence, the mate of an experienced female is likely to have been present at the display site over

an extended period of time and to have a strong attachment to that site. Under the sentinel/decoy model, mate fidelity is expected to be widespread in lekking species because a female encountering a male with which she has mated previously at the same site has direct evidence of his display site fidelity.

Beehler and Foster's hotshot model also identifies female mate fidelity and mate copying as important components of female choice in lekking species, but does not explain why these 'conservative' mating patterns are adaptive for females. The principal predictions of the hotshot model stem directly from the presumed importance of mate fidelity and mate copying and, thus, do not distinguish between the hotshot and sentinel/decoy models. For example, both models predict that removal of primary breeders from a lek (the most reliable sentinel/decoys?) should reduce female visitation rates and decrease the skew in male mating success (as reported by Robel et al. 1970).

A prediction of the male sentinel/decoy model that distinguishes it from the hotshot model is that female mate preference should be strongly influenced by male display-site fidelity. This is because the proposed antipredator benefit to females depends on males displaying from a fixed location during the incubation period. According to the sentinel/decoy model, a female should not exhibit mate fidelity if she encounters a former mate at a different lek from the one where an earlier mating(s) occurred. Likewise, a male's mating success is expected to decrease if he moves to a new lek, even if he occupies a 'preferred' (central?) display site.

LEK EVOLUTION

Lek behaviour occurs in species where males are unable to monopolize essential resources required by females and do not provide parental care (Wittenberger 1978). The sentinel-decoy model predicts that when females are not constrained by having to gain access to resources controlled or provided by males, they should reduce their risk of nest predation by mating with males exhibiting strong display site fidelity and conspicuous, persistent display (i.e. the principal attributes of lek display) and by locating their nests at an optimal distance from the male display site.

Mechanisms of female choice that select for reliable sentinel/decoys will also influence the

dispersion of male display sites. In particular, female mate fidelity and female copying will favour the aggregation of male display sites (Beehler & Foster 1988). Interestingly, two of the ecological factors that Bradbury & Gibson (1983) found to be associated with classical lek organization (overlapping female home ranges and diets that promote aggregation of females) are likely to facilitate female copying. In contrast, Bradbury & Gibson found exploded lek organization to be associated with exclusive space use by females, which should preclude, or at least sharply curtail, the extent to which female copying occurs.

Although the sentinel/decoy model predicts much the same relationship between female dispersion patterns and degree of clustering of male display sites as Bradbury & Gibson's hotspot model, the models differ in two important respects. If female copying is the principal factor leading to the aggregation of male display sites as suggested by the sentinel/decoy model, then classical leks need not occur in the regions of highest female density as the hotspot model predicts, i.e. females may leave nesting territories or communal foraging areas to visit displaying males (Beehler & Foster 1988). In addition, when nesting habitat is not limiting, the sentinel/decoy model predicts that females will be recruited into the local breeding population by the presence of displaying males. In contrast, the hotspot model assumes that female dispersion patterns occur independently of the location of male display sites.

CONCLUSIONS

The sentinel/decoy model is consistent with the principal features of lek behaviour in birds and makes specific predictions that will facilitate critical tests. Confirmation of the sentinel/decoy model's predictions would challenge the widely held belief that males in lekking species contribute only their gametes to the next generation.

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