

PREDATION AND THE DAILY TIMING OF SAGE GROUSE LEKS

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IN lek species males gather on communal, traditional display grounds called arenas. There they attract and copulate with females. The male's role in reproduction ends at this point and the females leave the arena for nesting and rearing of young. The evolution of lek systems implies that advantages must outweigh disadvantages. Many potential advantages have been suggested. Aggregations may aid in synchronization of breeding activities and thus reduce the length of time when young are most vulnerable to predation (Darling 1938). Lek breeding might allow population density assessment and subsequent adjustment of reproductive output (Wynne-Edwards 1962). Groups of animals are more likely to detect predators than solitary animals because of the increased sensory capacity of the group (Allee 1938). Larger groups of displaying males are more conspicuous and thus may attract females more efficiently than smaller groups or solitary males (Snow 1963, Braestrup 1966). Conspicuousness is potentially disadvantageous because of the increased danger of attracting predators. Predation has probably influenced the sites chosen for leks and the timing of leks. Most arenas are located on sites where the view of horizons is good. Sage Grouse (*Centrocercus urophasianus*) arenas are located in treeless terrain on sites with hills sloping upward on most sides (Patterson 1952, Wiley 1973). Here predators could not be easily hidden while they approached the lek. The restriction of lek behavior in Black Grouse (*Lyrurus tetrrix*) to dawn and dusk may minimize disturbance from aerial predators (Hjorth 1969). This interpretation might also help explain crepuscular lek activity among other grouse.

Although there are no eyewitness accounts, most researchers are convinced on the basis of carcasses found near lek sites that raptors do take Sage Grouse (Patterson 1952, Lumsden 1968, Wiley 1973). The Golden Eagle (*Aquila chrysaetos*) was the only common raptor large enough to pose a threat to adult cock Sage Grouse, which may weigh 7 pounds during the lek season. Eagles flew over the Ford's Creek lek five times in April 1965 without making a kill (Lumsden 1968). Wiley (1973) reported Golden Eagles attacking Sage Grouse leks on eight occasions during three springs. Although never seeing a kill, he found two dead grouse on display sites, one of which he thought was an eagle kill. Prairie Falcons (*Falco mexicanus*) are common in Sage Grouse country and might be able to take the smaller hens, which weigh about 3 pounds.

During the breeding seasons 1969–71 I watched Sage Grouse 172 mornings and 95 evenings from a blind at the Ford's Creek lek in central Montana (Hartzler 1972). During these observations I noted the responses of Sage Grouse to potential predators.

When an object appeared in the sky, Sage Grouse sleeked their feathers, elevated their heads, and turned their necks and heads to watch it. By the time the object became identifiable to me as an eagle, the grouse had turned to face away from it and had crouched low to the ground. Many grouse walked or ran to sage brush clumps before crouching. If the eagle approached within 200 m, all the grouse flew in the opposite direction. Such flights were straight, fast, and long, usually out of sight (at least 1 mile). Although Golden Eagles appeared 5–10 times each spring, only once during the study did an eagle approach to within 20 m of a grouse. In that instance, the eagle approached from a ravine below the horizon and out of sight until within 60 m of the lek. All the grouse escaped by outspeeding the eagle. Occasionally eagles must succeed in catching Sage Grouse. I found one dead cock on the arena with deep puncture wounds in the neck. I suspect that he was hit by an eagle, escaped, and later bled to death on the arena. It seems unlikely that he was killed outright because he was not eaten.

Prairie Falcons flew over the lek four times during my study and on one of these occasions attacked. On 17 April 1970 a Prairie Falcon stooped six times at a cock that was crouched 30 m from my blind. Each time the falcon swerved at the last moment and avoided the grouse. About half the other cocks and most of the hens flew during this attack. One grouse ran and crouched within 1 m of my blind, apparently using it as cover. During the other three encounters the grouse stretched, or crouched, or both, but did not fly. Other large birds in the sky such as Short-eared Owls (*Asio flammeus*), Red-tailed Hawks (*Buteo jamaicensis*), Marsh Hawks (*Circus cyaneus*), and Common Crows (*Corvus brachyrhynchos*), elicited stretches and glances when they first appeared, but the grouse quickly returned to lek activity.

One fact is prominent among these observations. Sage Grouse responded selectively to eagles. They not only stopped lek activity at first sight of an eagle, but they also flew long before the eagle came close. Other raptors rarely interrupted lek activity for more than a few seconds and the grouse flushed only in response to attack. This supports the contention that Golden Eagles are the most important aerial predators of Sage Grouse.

Ground predators were seen much less frequently than aerial predators but killed more grouse. On 2 May 1969 I found blood, feathers, and bobcat (*Lynx rufus*) tracks close to my blind. One of my permanently marked cocks was missing thereafter. At 0515 the next morning, the

first cocks landed on the arena. It was so dark that I could barely see their white esophageal pouches at 20 m. A "thump" followed by other sounds of a struggle and wildly flushing grouse attracted my attention. With the aid of binoculars I recognized a bobcat with an adult cock in his mouth walking approximately 20 m from the blind. The grouse was either unconscious or feigning death because he was not struggling. Two days later I found another bobcat kill on the edge of the arena. In 1970 an adult cock was found dead near one of my blinds. Tracks in the snow and damage to the bird indicated a mink (*Mustella vison*) had killed and partially eaten it. Although the general area appeared to be excellent habitat for coyotes, none were seen near the arena. The response of Sage Grouse to a potential ground predator during daylight was noted when my German shepherd dog approached the arena late one morning after being released 400 m from the arena. The few grouse remaining on the arena were resting when the dog appeared. As the dog approached, the grouse stretched and walked slowly away; they flew only when the dog was within 10 m.

Twenty to sixty cocks attended the Ford's Creek lek regularly. An average of 3.5% were killed on the arena each spring. Mammalian predators accounted for all known losses except the male with deep puncture wounds. Other researchers have reported few grouse kills during lek activity. During 4745 mornings only three Greater Prairie Chickens (*Tympanuchus cupido*) were known to have been killed by raptors, even though raptors were observed 1379 times (Berger et al. 1963). Although highly exposed during lek activities few grouse are killed. Modern ranching and associated predator control have probably greatly reduced the importance of predation and the "many eye" effect at leks is an efficient mechanism for detecting predators.

Cock Sage Grouse arrived in the predawn twilight, often when available light was very low (Hartzler 1972). The onset of lek activity in Black Grouse was also correlated with available light intensities (Hjorth 1969). At Ford's Creek I saw eagles only after light intensities were high enough for me to distinguish objects all the way to the horizon. The occurrence of the first part of Sage Grouse lek activity before eagles started hunting may be an adaptation to reduce exposure to eagles. Most hens arrived while light intensities were rapidly increasing, and only 3 of 420 copulations occurred earlier than 30 min before sunrise. Most hens were present and most copulations occurred while light intensities were high enough for aerial predation. The majority of lek activity occurred after eagles began hunting, and a few grouse usually remained for several hours after sunrise. During early morning when the sun is near the horizon, aerial predators probably cannot see well in the direction of the rising sun. Thus, raptors would be

about 75% as efficient in hunting during this time as they would be when the sun is higher in the sky. More copulations occurred during the first 40 min after sunrise at the Ford's Creek lek than during any other 40-min period (81 of 420 copulations occurred during the 40 min before sunrise, 215 of 420 during the 40 min after sunrise, and 101 of 420 during the next 40 min in the combined data from 1970 and 1971). All prairie raptors capable of taking adult grouse are diurnal, and antiraptor defense would be enhanced by limiting activity to hours of darkness or at least, reduced visibility. Mammalian predators are primarily nocturnal and their activity would tend to favor daytime lek activities. Dawn and dusk lek activity in Sage Grouse and perhaps in other lek grouse may be a compromise between these two opposing selective pressures.

Wiley (1973) has suggested that cocks around the edges of leks should be more vulnerable to predation. Adult cocks tend to occupy the center of the lek, younger cocks the periphery. The two dead cocks found on the arena by Wiley (1973) were both adults. One of the three cocks a bobcat took during my study was a peripheral cock of unknown age; the other two cocks and the one taken by a mink were individually marked central adult cocks. The cock with deep puncture wounds was found near the center of the arena but he was not individually marked and thus was not a regular attender at that site. The available evidence suggests that instead of enjoying an advantage in regard to predation central cocks may be killed more often than peripheral cocks. Central cocks may become more fatigued because of their higher activity levels (Wiley 1973), but all the kills I witnessed occurred at night or early in the morning, before the central cocks appeared tired. The central cocks are usually the first to arrive and the last to leave each morning. They are also more faithful lek attenders than peripheral cocks (six of my central cocks attended every morning and evening that lek activity occurred and most central cocks rarely missed). Their increased time at the lek may be adequate to explain why they are more often killed by predators.

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