A Technical Description Of Lekking Behavior in Avian Species

Annabelle Rankin

Writer's Comment: Enrolling in UWP 104E during my senior year was perhaps an ambitious decision, as I was simultaneously scrambling to finish my senior thesis. The workload for both was considerable, and the amount of writing daunting, that is until Dr. Herring made a suggestion: write about something you already know. Well, deep in my thesis work as I was, a study focused on the behaviors of greater sage-grouse, a bird which gathers on communal breeding grounds called leks to duke it out with other males and win over female mates, I certainly knew animal behavior. Recalling the many times I had explained my thesis to a family member or friend, to be met with general confusion—spare the outdoorsy few who themselves had seen a grouse lek in action—I was gripped with the urge to write about my research in a way that was approachable for those outside of my discipline. I discovered, in this, a passion for scientific writing I didn't realize I had, and this specific piece became the first step in what I hope will be a long career of writing in the sciences.

Instructor's Comment: Spend enough time in the outdoors, and you will eventually blunder into a lek. In the western United States, when it happens, you will likely find yourself surrounded by handsome mottled-brown sage grouse who will regard you with surprising nonchalance. When it happens to me, I have always felt embarrassed, but still read the first version of Annabelle's winning essay with the pleasure of recognition. This reaction alone is a testament to its extraordinary readability. The essay came from the final assignment in my Writing in the Professions: Science class (UWP 104E), in which the students were asked to explain some feature of a science they know, and to write the explanation as if for the education of fellow scientists. The students thus have to write at the level of working profession-

als. Anna knows leks well, having worked in them, and would never allow herself to be as flustered as I have been by the accusatory glances of the birds. She knows them well enough that the result is an essay of a clarity that makes it seem in places less like a piece of technical writing than an article in a popular magazine.

—Scott Herring, University Writing Program

Lek mating systems are some of the most prolific in nature, and appear across biomes and taxa with remarkable structural consistency. The ubiquity of such systems has made them the subject of widespread research and discussion spanning decades. A lekking system is generally defined as any mating system which utilizes a common area for male display, termed a lek. This lek involves display efforts by multiple males, aggregating in a common area to engage in direct and indirect competition for female attention. Though leks may vary in size, location, and proximity of attending individuals, males must be grouped such that female mate comparison and choice is facilitated. A primary assumption of all lek systems is that females choose male mates based solely on male phenotypic traits—frequently display quality—as opposed to associated benefits such as territory, access to food, etc. Although lekking systems are not confined solely to Aves, studies of avian lekking systems have provided a strong baseline for the studies of similar systems across diverse taxa.

Historical Context

Avian breeding systems have long provided models for theories on mating behavior across the animal kingdom. From long-term monogamy to extreme polygyny to brood parasitism, avian species display a remarkable diversity of mating strategies, aiding in research and classification of broader mating trends across other taxa. Classically, avian breeding systems were catalogued by the number of matings per individual male or female (Lack 1968). Traditionally, systems were defined as monogamous, with one mating per individual, polygynous, with multiple matings per one male, polygynandrous, with multiple matings per one female, and so on. However, these definitions have fallen out of use as modern studies utilizing genetic analysis have revealed more complex mating trends than previously estimated. Contemporary studies suggest that the incidence of multiple female matings, especially on lek systems initially thought to exclude polygynandry, is in fact much higher than previously estimated (Gowaty and Karlin 1984, Bird et al. 2013). Accordingly, modern definitions emphasize parental investment as a defining factor for avian mating systems, coupled with spatial analysis specific to the distribution of males and females in a given system (Ligon 1999). Under this updated definition, lekking species are defined as those having no male parental care, and involving geographically concentrated incidents of males performing display or aggression. Additionally, selective pressures on leks are generally understood to be imposed by female mate choice, essentially meaning males compete for female copulations, with females gaining no fitness other than matings from attendance (Jiguett 2000). The discussion of female fitness benefits has been disputed in recent years as predator evasion has been proposed as a possible mechanism for lek evolution, which would confer equal direct benefits to both attending males and females through a decrease in predation risk (Boyko et al. 2004).

Technical Qualities

Lek systems are broadly grouped into two categories: classic leks and exploded leks (Alonso et al. 2012). Classic leks involve single mating centers and high concentrations of competing males. Technically, classic leks require males to be within visual and auditory range of one another; more broadly, concentric rings of males may exist around a single center without direct visual or auditory communication between central and peripheral groups.

Exploded leks may involve multiple mating centers, with looser overall organization (Merton et al. 1984). Exploded leks require only auditory communication between mating centers, thus allowing for a larger overall lek area. Additionally, exploded leks may exist in conjunction with resource-defense mate displays, wherein dominant males defend high quality, food-rich mating centers, and females choose mates through an analysis both of display and location quality (Alonso et al. 2012). Recent studies have attempted to parse the exact interplay between exploded leks and resource defense, however results are largely variable, and the importance of food and resource defense appears to vary across avian species. Lek organization, as well as many other avian mating systems, is thought to be primarily determined by a phenomenon colloquially termed "choosy females." In lek systems, females exhibit high specificity in their selection for certain traits, even if these traits confer only a very small or even indistinguishable fitness benefit to the female and her offspring. Female "choosiness" often and most notably manifests through sexual dimorphism, with many lekking species displaying significant size and plumage differences between sexes. Extreme examples of sexual dimorphism in accordance with strong female preference may result in Fisherian runaway selection, commonly exemplified by dimorphism in peacocks. However, despite this distinct possibility in systems with defined female preferences, leks rarely exhibit runaway selection in this manner, a discordance known as the Lek Paradox. Additionally, it is important to note that female preference may focus on behavioral traits, with several examples of monomorphic lekking systems involving complex male song displays rather than plumage or size displays. Lek systems may also display extreme differences in mating success across males. In the most extreme cases, leks with as many as a hundred birds may see only one or two high-quality males enacting 99% of copulations. In Greater Sage-grouse (*Centrocercus urophasianus*) a single high quality male may dominate the copulations on a lek, with mid- or low-quality males instead engaging in male-male aggression or display without female attention. Generally, high quality males are marked by the frequency of display behavior and by species-unique quality markers defined by the specific display model. High-quality males generally engage in more vigorous,

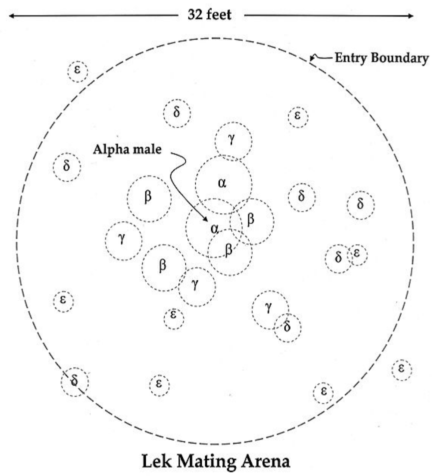


Figure 1. A simplified diagram of a classic lek. Note the central position of the dominant male and the peripheral arrangement of non-dominant males. Classic leks may be ordered into concentric "rings" of nondominant males surrounding the central most dominant male/males. https://commons.wikimedia.org/wiki/File:Lek-diagram.jpg

faster, or more frequent displays when females are present, creating a visual or audio quality gradient along which visiting females may judge male displays. Though the exact mechanism of female choice is not understood for all lekking species, it is generally accepted that females compare male phenotypes to choose their mate on any given lek. Additionally, while lek systems involve geographic concentration of displaying males, the specific number and pattern of lekking males may vary. In some leks, specifically those of prairie species like *Centrocercus urophasianus*, there does not appear to be a hard upper limit to lek attendance; rather, males socially enforce hierarchical spacing within the lek, concentrating low-quality males in the periphery. Black grouse (*Lyrurus tetrix*) may display in leks of between ten and twenty individuals, with significant variation, while the Kakapo (*Strigops habroptilus*), a critically endangered species which utilizes exploded leks, may congregate with only a few adult males (Merton et. al 1984). Lek fidelity may also vary, with some grouse species experiencing dispersal of sub-adult males to new leks, while many tropical bird species display lifetime male fidelity to single lek locales.

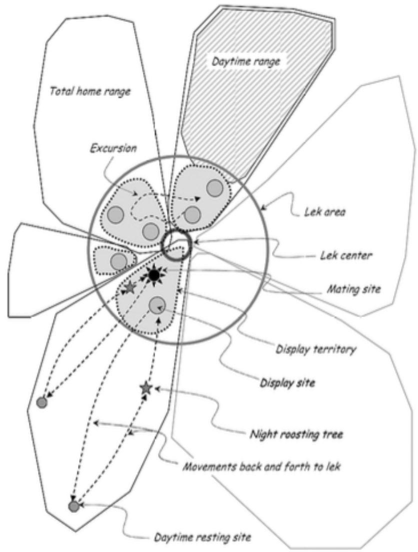


Figure 2. An example diagram of an exploded lek from a study of Capercaillie grouse (Tetrao urogallus)*. Note the distinct, non-overlapping individual display territories surrounding a lek center. Exploded leks overall exhibit larger distances between displaying males, and looser overall lek organization. Image provided by Wegge et al. 2013*

Figures 3 and 4. Comparison of the monomorphic and dimorphic lekking species. At left is the Great Snipe (Gallinago media)*, a nearly completely monomorphic lekking species. The male pictured is engaging in a song display to attract females; females are nearly morphologically indistinguishable from males. Female preference is thought to center on the quality of vocal display rather than visual markers. At right is the Greater Sage-grouse* (Centrocercus urophasianus)*, a dimorphic lekking species (note the differences in plumage between the [far] male and [near] three females).* *https://commons.wikimedia.org/*

Selective Pressures / Evolutionary Mechanisms

Two main mechanisms have traditionally been proposed to explain the structures of lek systems: female preference and hotspot models. The female preference model posits that males congregate on leks for display because females prefer to mate with aggregated males (Queller 1987, Bradbury 1981). Females may show this preference for a number of reasons, the most prominent of which is the lower cost of mate searching when males are aggregated, reducing the time and resources required for females to compare potential mates. Conversely, the hotspot model posits that males form leks in areas of high female concentration, so-called “hotspots.” In this model, female preferences either for aggregated males or male quality is generally disregarded as a factor in the formation of lekking systems, instead crediting female population centers as the impetus for male aggregations.

In the past few decades, these two models have been synthesized into what is termed the “hotshot” model (Beehler and Foster 1988). Leks often form in concentric patterns, with more experienced, higher performing, and more successful males occupying the lek center, and lower quality males occupying the lek periphery. The hotshot model posits that leks form because high quality males gain more copulations from displaying together, while low-quality males increase their probability of mating by displaying as near as possible to high-quality males. This model synthesizes both male and female preferences, inferring that leks are a product of behavioral selection on both sexes. Notably, the hotshot model does not imply female preference for clustered males in general, but specifically for aggregates of high-quality males, termed an “indirect” preference for aggregation.

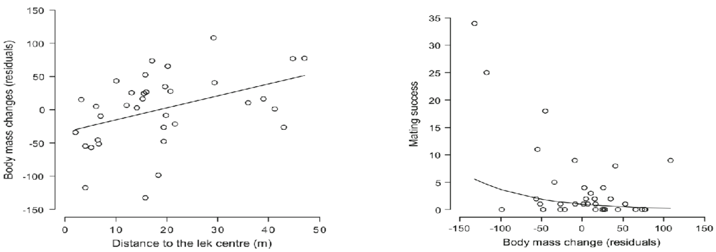
Modern discussions of leks hybridize these theories, and investigate the more complex male-male interactions which drive the formation and overall structure of any given lek. Territoriality, male-male as well as female-female aggression, and the differential benefits between long and short term mating strategies for males of differing quality, all interact with female population size and preference to explain the size, structure, and operation of lekking systems. Direct benefits of lekking systems have also been proposed as evolutionary drivers, for example, protection from predators conferred by large group aggregations (Boyko et al. 2004). This theory notably ascribes benefits other than mate choice to female lek attendance, challenging some classic definitions of lekking. Some species of lekking birds may also benefit from kin selection due to high levels of interrelatedness among males on a given lek (Concannon et al. 2012). Current research attempts to parse out specific fitness benefits for males and females on leks, and points to a high degree of variability among lekking species, moving towards species-specific investigations of lek evolution.

The Lek Paradox

Much of the research into lekking species centers around what has been termed the Lek Paradox. Because of the unilateral selective pressure on displaying males imposed by females with distinct preferences for certain traits, Darwinian evolution would predict a reduction in overall genetic diversity. Essentially, if females select for a single trait, they should enforce a selective pressure towards homogeneity of males in this trait, effectively eliminating choice, and yet in lek systems this choice persists. Hypothetically, specific female preferences should lead to runaway selection for these traits, while in reality genetic diversity is preserved on leks.

Proposed explanations for this maintenance of diversity focus mainly on the idea of imposed handicaps on male display quality (Kotiaho et al. 2001, Lebigre et al. 2013). Essentially, female preference is centered on traits which are mediated by male body condition, health, fitness, etc. This prevents cheating as well as runaway selection, as low-quality males are unable, due to either external or internal handicaps, to produce high quality displays.

Another explanation for the Lek Paradox focuses on gene flow, or the movement of genetic traits between populations. As long as populations are large, gene flow is maintained between leks, allowing for genic capture (selection for high genetic variance to improve overall condition). Research has been done to explore both of these hypotheses, with studies showing strong correlations between mating success and body quality in many lekking species, indicating that displays are indeed condition-dependent.



Figures 5 and 6. Graphs showing the relationship between body mass changes and male dominance from a study of Black grouse (Tetrao tetrix). *According to the handicap theory, display traits must be energetically costly, and in many grouse species male body mass significantly decreases over the mating season as fat reserves are utilized to meet the metabolic cost of display. These graphs indicate that centrality of a male (left) and mating success (right) are correlated with smaller decreases in body mass, suggesting that dominant males are better able to mediate the costs of display and maintain energy stores over time.*

Images provided by Lebrige et al. 2013.

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