

and the male was with the other female. It was thus used in two contexts: to attract a new mate (by #421) and to call back a straying mate (by #442).

We thank Carl Wilcox and Jack Fancher for their participation in the field work that led to this paper and Ned Johnson and Tom Webber for constructive reviews of the manuscript. Our studies were funded by Federal Aid for Endangered, Threatened, and Rare Wildlife through a California Department of Fish and Game contract with California State University, Long Beach.

Do Blue Grouse Form Leks?

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Mating patterns in grouse range from monogamy to extreme promiscuity (Wiley 1974, Wittenberger 1978), and as such they are a useful group for testing ideas on the evolution of mating systems. Blue Grouse (*Dendragapus obscurus*) have been studied extensively throughout their range in western North America and are considered promiscuous (Wiley 1974, Wittenberger 1978), with males generally displaying solitarily from dispersed territories (e.g. Hoffmann 1956; Blackford 1958, 1963; Bendell and Elliott 1967). Instances of apparent communal display have been observed, however (Schotellius 1951; Caswell 1954; Blackford 1958, 1963), and these have led some authors to conclude that Blue Grouse form leks, at least in certain habitats (Blackford 1963; Short 1967; Wittenberger 1979, 1981). The "communal displays" that have been documented occurred in relatively open habitats, whereas in denser habitats such behavior has not been observed. This apparent difference in breeding behavior by a single species occupying both open and dense habitats also was cited by Wittenberger (1979, 1981) as evidence for his hypothesis that lekking behavior evolved in open habitats as an adaptation to reduce predation.

I do not believe, however, that the evidence is adequate to suggest that male Blue Grouse form leks, even in open habitats. I base this argument on a critical examination of references cited by Wittenberger and others, and on personal experience working with this species in both types of habitat. The purpose of this report is to evaluate past references to leklike behavior in Blue Grouse and to provide information I have on their behavior in open and dense habitats. I then discuss the validity of considering Blue Grouse a lek species.

Definition of lekking behavior.—A lek may be defined simply as a group of breeding males that regularly congregate on a fixed area (commonly referred to as an arena) to perform courtship displays. Bradbury (1981) and Oring (1982), however, provide more

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Received 20 April 1984, accepted 7 July 1984.

elaborate definitions in which they present criteria that distinguish lek mating behavior from other types of mating patterns. Of particular importance here, however, are the following: (1) Males regularly congregate on a display area, which results in displaying males being clustered within the habitat used by the species. (2) Females visit the lek to copulate but do not feed or nest there to any significant degree. (3) Displaying males do not obtain all of their food within their display areas; males usually leave these areas to feed and rest.

Past references to lekking behavior in Blue Grouse.—Blackford (1958, 1963) studied the behavior of territorial male Blue Grouse in Montana in an area of mixed yellow pines (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) interspersed with frequent grassy openings. On 3 occasions over 3 yr, he saw 2 or more males displaying within a small area and from this concluded that Blue Grouse display on leks (Blackford 1963: 512). He noted, however, that the site used for communal display changed each year, which differs from other lek species, in which traditional display grounds often are used year after year (Robel 1972, Wiley 1973). Also, in most instances Blackford (1958, 1963) found males hooting (singing) or displaying from dispersed territories. The apparent communal display he observed, therefore, could have occurred when males followed females to areas where territories adjoined, onto territories of other males, or onto neutral ground between territories (see below).

Short (1967: 20) cited Wing (1946) and Hoffmann (1956) when suggesting that Blue Grouse (*D. o. obscurus*) show a "tendency toward lek behavior." I found no mention of such behavior in Wing (1946), and Hoffmann provided no evidence of communal display in Blue Grouse from his studies but referred to studies by Schotellius (1951) in Washington State and Caswell (1954) in Idaho.

Schotellius and Caswell worked in a variety of

habitat types ranging from closed coniferous forests and forest-grassland edge to nonforested areas of mixed sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), and native bunch grasses (primarily *Agropyron spicatum*, *Poa secunda*, and *Festuca idahoensis*). Both examined the life-history and general breeding behavior of Blue Grouse, and most observations of males were made while traversing transects. Each of their descriptions of territorial behavior and apparent communal display is restricted to one, short paragraph in which they state:

In May, a two acre area was located which came to be called 'hooter hill' because of the number of males congregating there. As many as seven males in simultaneous display were to be found at various times of the day on this area. The displaying birds were watched in the morning and evening. Intraspecific aggression was not observed. (Schotellius 1951: 28)

If males have a territory, which they defend during the courtship season, it is not apparent. A territory would have to be rather large, for in chasing hens they commonly travel 200 to 300 feet. An estimated six to eight males were found on each of two nine to twelve acre hooting sites. However, only one or two were seen in full display at any one time. (Caswell 1954: 51)

These methods and observations are not sufficient to make definitive statements on male behavior. We now know that territories can exceed 200-300 feet (61.0-91.4 m) in length (Blackford 1958, 1963; Bendell and Elliott 1967), and the possible communal displays that Schotellius and Caswell observed could have involved males displaying near territorial boundaries (see below).

Wittenberger (1979, 1981) cited Hoffmann (1956) and Blackford (1958, 1963) in stating that male Blue Grouse display communally in open habitats, and these references have been discussed above. Thus, I submit that in no past reference is there sufficient evidence for concluding that Blue Grouse display on leks.

Personal observations.—I studied aspects of territoriality in male Blue Grouse on a 485-ha area, Comox Burn, on Vancouver Island, British Columbia from 1977 to 1979 (Lewis and Zwickel 1980, 1981). Activity centers (Lewis and Zwickel 1981) of territories there were distributed uniformly ($P < 0.01$, Lewis and Zwickel 1981). Other studies on Vancouver Island produced similar results (Bendell and Elliott 1967). Habitats on Vancouver Island where Blue Grouse were studied were clearcut and replanted with Douglas fir (Zwickel and Bendell 1972, Zwickel 1977) and have relatively dense understories.

I studied the dispersion of territorial male Blue Grouse in north-central Washington from 3 to 22 May 1983 in the same general area where Schotellius

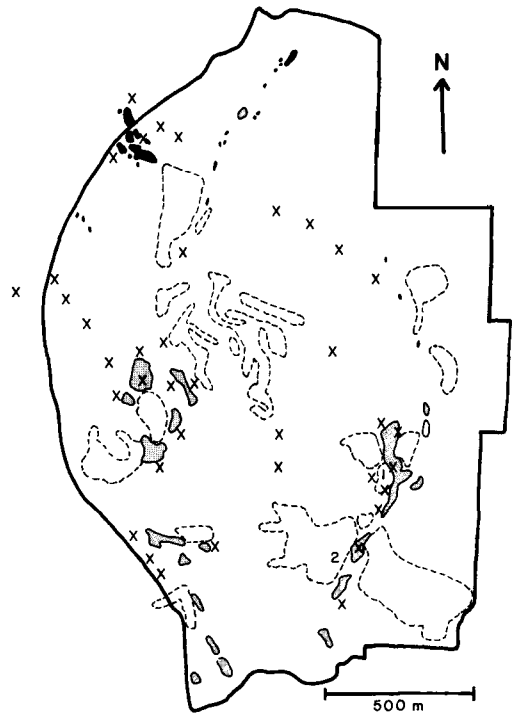


Fig. 1. Locations (X) and vegetation types of areas where individual males usually were hooting on Frazer Creek, Washington in 1983. Darkly and lightly shaded areas are conifers and aspen, respectively. Agricultural fields are outlined with dashed lines. Unmarked areas are open shrub-grassland, primarily sagebrush, bitterbrush, and bunch grasses. Numbers designate the two agricultural fields where I saw 2-4 males displaying at the same time.

worked. My work was concentrated on the 256-ha Frazer Creek study area of Zwickel (1972, 1973). Vegetation there consisted of open shrub-grasslands with scattered groves of aspen (*Populus tremuloides*) and very small, widely scattered patches of coniferous trees. Fields of cultivated rye and alfalfa were interspersed among native vegetation and provided areas that were very open. This habitat type was similar to those described by Schotellius (1951) and Caswell (1954) and probably would have been considered open by Wittenberger (1979, 1981).

I searched for birds daily, primarily between 0700 and 1100 and 1600 and 2130, when activity was greatest. I located most territorial males by listening for hooting, but also used a trained pointing dog to find silent males and females. By concentrating my search on a limited area, I was able to obtain information on both density and dispersion of territorial males and to obtain repeated sightings of individuals.

I did not mark grouse, but based on previous studies with banded birds, I assumed that repeated sightings of a hooting male within a small area represented one individual. Several males usually were hooting at the same time, which aided in determining their identities and spatial relationships. I believe that I found most territorial males on Frazer Creek, and although their distribution tended toward clumping ($R = 0.867$; Clark and Evans 1954), it was not significantly so ($c = 1.57$, $P > 0.05$; Fig. 1). Martinka (1972), working in Montana in open habitats similar to those of Schotellius (1951) and Caswell (1954), found territorial male Blue Grouse to be uniformly distributed.

On four occasions I observed 2-4 males displaying to females in close proximity to each other. This occurred in the evening in two open fields bordered by aspen where females came to feed (Fig. 1). However, during the day, when females were absent, these males were not found in the field; instead they usually were hooting at other locations in their territories. In other areas where territorial males tended to be clumped I observed no instances of 2 or more males displaying together. In addition, many males occupied dispersed territories, even in the most open areas (Fig. 1), and on most occasions when I saw males displaying to females they were doing so solitarily ($n = 12$). Thus, my observations of "communal display," and probably those of Schotellius (1951), Caswell (1954), and Blackford (1958, 1963), likely resulted from males being attracted by females to areas where territories adjoined or to areas between territories.

Discussion.—Although male Blue Grouse sometimes display near each other, such behavior does not appear to be a general feature of their breeding behavior. In no case has it been demonstrated that males regularly congregate on an arena for the purpose of attracting and displaying to females; in most, if not all, instances where "communal display" has been observed, males may have been attracted to areas where females were located. In areas where males sometimes have been seen displaying "communally," solitary display from dispersed territories was still the normal behavior pattern, even for the males that occasionally were seen displaying together (Blackford 1958, 1963; this study). Thus, I conclude that there is no evidence to suggest that male Blue Grouse adopt a mating pattern consisting of communal display on an arena, and I consider it inappropriate to classify them as a lek species. Additionally, male Blue Grouse, in both open and dense habitats, feed and rest on the areas where they display (Blackford 1958, 1963; Bendell and Elliott 1967), and instances I observed of males displaying close together occurred in areas where females were feeding. These behaviors also are inconsistent with those associated with lekking behavior (Bradbury 1981, Oring 1982).

Why did males on Frazer Creek tend to be clumped rather than uniformly spaced? Clumping occurred more in areas where territories were associated with aspen thickets than in areas of shrub-grassland where trees were absent (Fig. 1). Aspen thickets may provide preferred habitat for territorial male Blue Grouse here; if so, the apparent clumping probably was a consequence of the patchy distribution of the thickets.

Gullion (1967) also noted that Ruffed Grouse (*Bonasa umbellus*) territories tended to be clustered, and originally he interpreted this as indicating that Ruffed Grouse used communal display grounds that he called "expanded" leks. Later, however, he concluded that "activity clustering" was a consequence of the distribution of preferred habitat and that effects of social interactions on spacing were secondary (Gullion 1976).

McNicholl (1978) studied social behavior of male Blue Grouse on Vancouver Island and reported that males sang in social groups. He concluded that this behavior was similar to that of lek species and referred to the dispersion of territorial males as an "exploded lek." Could the singing behavior of males be considered functionally similar to lek behavior? That is, do males sing together because of reproductive benefits that could result from doing so, such as attracting proportionately more females than solitarily singing males? Singing together is not a behavior exclusive to lek species. Territorial males of many birds with other mating systems sing together (countersinging), and individuals are stimulated to sing by the songs of others (e.g. see Kroodsma 1971, 1979; Verner 1975; Falls 1978). Group singing by male Blue Grouse may be equivalent to countersinging, and hence I suggest that it is not a sufficient criterion by which to consider Blue Grouse as a leklike species.

If Blue Grouse do not form leks, how do my results on dispersion of breeding males affect Wittenberger's (1979, 1981) claim that lekking behavior evolved in open habitats as a means of reducing predation? Breeding males in the open habitat in Washington where I worked showed a tendency towards clumping, whereas in denser habitats on Vancouver Island they were uniformly spaced. However, clumping in Washington was more evident in areas where thickets of trees were present than in the more open sagebrush-bitterbrush areas (Fig. 1). This is not consistent with what would be predicted from Wittenberger's hypothesis.

In conclusion, I would note that lek behavior is a mating pattern adopted by many species in diverse taxonomic groups (Emlen and Oring 1977), yet the behaviors associated with it are such that "true" lekking behavior usually can be distinguished readily from other mating patterns (Bradbury 1981, Oring 1982). This is not to say, however, that other mating patterns do not have certain features in common with lek behavior. Rather, even among species with pro-

miscuous mating systems a continuum of behaviors is exhibited, such as a continuum of dispersion ranging from solitary, dispersed display to clumped, communal display; lek behavior represents one extreme. My purpose here was to demonstrate that there is not sufficient evidence to suggest that Blue Grouse form leks. Determining the consequences, in terms of individual reproductive success, of the possible difference in dispersion of territorial males in different habitats, or explaining the evolution of leks in general, would require more intensive studies.

I thank J. O. Murie and F. C. Zwickel, Department of Zoology, University of Alberta; S. J. Hannon, Museum of Vertebrate Zoology, University of California at Berkeley; K. Martin, Department of Biology, Queen's University; and three anonymous reviewers for helpful comments on the manuscript. Permission to work on Comox Burn was granted by Crown Zellerbach of Canada Limited, and field work in Washington State was conducted on the Methow Habitat Management Area; the cooperation of Crown Zellerbach and Washington State Department of Game personnel is greatly appreciated. My studies were supported by the Natural Sciences and Engineering Research Council of Canada, the University of Alberta, and the British Columbia Fish and Wildlife Branch.

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Received 12 December 1983, accepted 8 July 1984.

Selective Alarm Calling by Downy Woodpeckers in Mixed-species Flocks

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Many species of birds and mammals give alarm signals when disturbed by predators. Although these alarm signals may appear altruistic, the alarm calls could benefit the caller. Individual fitness might be promoted by decreasing the probability of an attack, if the alarm call serves as a pursuit deterrent signal or discourages the predator from hunting in the immediate area (Smythe 1970, Trivers 1971, Woodland et al. 1980); by misdirecting the predator and increasing the probability that another individual is attacked (Perrins 1968, Charnov and Krebs 1977, Owens and Goss-Custard 1976); and by warning kin or a mate (Maynard Smith 1965, Williams 1966, Sherman 1977).

The balance between the risks and benefits associated with alarm calls presumably influences the conditions under which alarm calls are given. For example, the net benefit of alarm calling and the probability of giving an alarm call vary with age, sex, and reproductive status (Sherman 1977). The economics of alarm calling also may differ between species in mixed-species groups, so that one species is more likely to call than another in a given situation. Mixed-species winter flocks provide an opportunity to examine the situations in which several different species give alarm calls. During the winter, mixed-species flocks composed of Black-capped Chickadees (*Parus atricapillus*), Tufted Titmice (*Parus bicolor*), and several follower species [Downy Woodpeckers (*Picoides pubescens*), Hairy Woodpeckers (*Picoides villosus*), and White-breasted Nuthatches (*Sitta carolinensis*)] are common in eastern North America

(Morse 1970). All 5 species are vulnerable to predation by raptors and respond to each others' alarm calls (Bent 1937, 1938; Gaddis 1980). Yet within these flocks 2 of the species, chickadees and titmice, give almost all of the alarm calls (Gaddis 1980).

I examined the conditions eliciting alarm calls for 3 of these species (Black-capped Chickadees, Tufted Titmice, and Downy Woodpeckers) in winter flocks during encounters with naturally occurring predators (raptors) and predator models. Results indicate interspecific differences that can be interpreted in the context of benefit/cost logic.

Observations were made on alarm calling in mixed-species flocks during 3 winters from November 1979 to March 1982 at the Great Swamp National Wildlife Refuge in New Jersey. I recorded the flock composition and alarm calls during encounters with naturally occurring predators [Sharp-shinned Hawks (*Accipiter striatus*), Cooper's Hawks (*Accipiter cooperii*), and American Kestrels (*Falco sparverius*)] and predator models.

In the first predator-model tests, a stuffed Red-tailed Hawk (*Buteo jamaicensis*) was mounted on a pole and presented from a blind for 10 s to woodpeckers foraging 3-15 m away. I collected data only on woodpeckers with this model. I later replaced this model with a stuffed Sharp-shinned Hawk mounted on a pulley that ran down a wire between two trees. The model was released from a blind and immediately pulled back into the branches of the tree. In tests with this model, I collected data on woodpeckers, titmice, and chickadees foraging 2-15 m from the blind.

I presented predator models from blinds to 20 individually marked Downy Woodpeckers that were foraging with a mixed-species flock, with a conspecific, or alone. Two days generally were allowed be-

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