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Function of a Rail "Mystery" Call

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Vocalizations of rails are a great challenge to the field ornithologist, and establishing the behavioral context of infrequently heard calls is especially difficult. One such call has been referred to as the "ornithological mystery" or "kicker" song, and its function has been the subject of much speculation (Manolis 1981). Several species of rails give this type of call, although there are certain to be some differences among species in the details. The call has been phoneticized as "kek(-kek-kek-kek)-burr" for the Yuma Clapper Rail (*Rallus longirostris yumanensis*; Tomlinson and Todd 1973) and "kik-kik(-kik)-kurr" for the King Rail (*R. elegans*; Meanley 1969). We refer to it as the kek-burr call.

Since 1979 we have studied the Light-footed Clapper Rail (*R. l. levipes*) in southern California and have accumulated many hours of observations on radio-collared and individually color-banded birds of known sex. In 1983 we were extremely lucky in observing a behavioral sequence that clearly established a function of the kek-burr, as the primary advertising call of the female.

The kek-burr is heard only in the spring and summer (Manolis 1981, Zembal and Massey pers. obs.). It begins with 1 or more evenly spaced keks followed by a trilled "burr." The burr sometimes is given without the keks. Figure 1 shows a call comprised of 4 keks followed by the burr. Overall, the burr phrase occurs somewhat less frequently than the kek phrase. We taped the call in the spring of 1983 in Upper Newport Bay, Orange County, California in the following circumstances (duplicates of the taped call have been deposited at the Bioacoustic Archive and Laboratory, Florida State Museum, Gainesville).

We were monitoring a radio-collared male (USFWS band #825-39443). His mate (#825-39442) and the pair in the adjacent territory were all color-banded. The parcel of marsh contained only these two pairs of rails and was isolated from the next nearest marsh by a 50-m wide mudflat. At the time of our observations the female in the adjacent territory (#825-39421) and her mate had a nest containing 5 eggs. The mate was killed by a Red-tailed Hawk (*Buteo jamaicensis*) at 0748 on 18 April, and by 20 April at 0615 #421 had begun to kek-burr. She called intermittently that morning and evening (there was no observer during midday) until 1723, when she broke in the middle of burring into a duet clapping call with #443. From 1723 to 1843 that first evening they clapped in duet 12 times and were seen copulating twice. The newly abandoned female, #442, began to kek-burr on the following morning. During that day and the following one, #443 divided his time between the two females. Without the aid of a full-time mate, #421 abandoned her nest. Each of the females, once alone, eventually kek-burred when #443 was with the other one, and #443 responded every time by returning to the calling female, often quickly. We witnessed #443 respond to kek-burring 11 times in 36.1 h of observations over 4 days. During one exchange he traveled the 190 m to the calling female within 18 min of the onset of kek-burring. When another male appeared on the fourth day, #443 returned to #442, #421 settled in with the new arrival (making use of the same nest), and kek-burring ceased.

Throughout this period the kek-burr was voiced only by the females, and only when they were alone

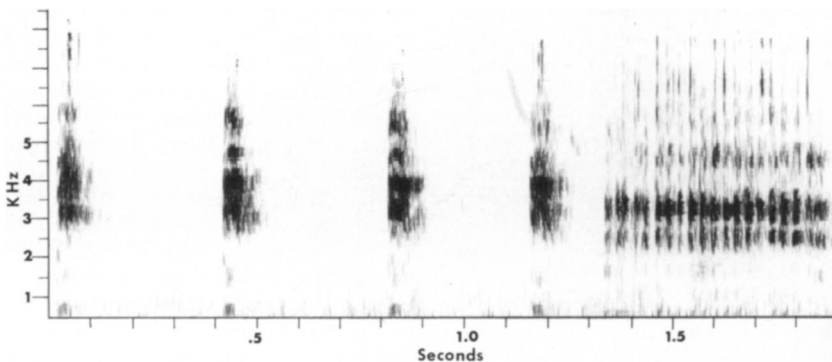


Fig. 1. Sound spectrogram of the kek-burr call of the Light-footed Clapper Rail (made on a Kay Elemetrics Co. Sona-Graph, Model #6061B, with wide-band setting).

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).

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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

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