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DISPLAY BY APPARENT HYBRID PRAIRIE-CHICKENS IN A ZONE OF GEOGRAPHIC OVERLAP

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Abstract. Greater (*Tympanuchus cupido*) and Lesser (*T. pallidicinctus*) Prairie-Chicken are thought to be historically and presently allopatric. We documented an area of approximately 250 000 ha in western Kansas characterized by leks with displaying males of both species. Display booms unlike typical Greater or Lesser Prairie-Chickens were heard and recorded at nine mixed leks. Spectrograms of these vocalizations contained elements of Greater and Lesser Prairie-Chicken booms, and comparisons suggested intermediate similarity. Males giving these booms had additional novel characters as well as novel combinations of Greater and Lesser Prairie-Chicken characters, and might represent the first case of hybridization in the wild.

Key words: display, Greater Prairie-Chicken, hybridization, lek, Lesser Prairie-Chicken, sympatry.

Despliegues de Híbridos Aparentes de *Tympanuchus* en una Zona de Simpatría

Resumen. Aunque se ha pensado que *Tympanuchus cupido* y *T. pallidicinctus* son especies histórica y actualmente alopátricas, documentamos un área de aproximadamente 250 000 ha en el oeste de Kansas que está caracterizada por asambleas de cortejo integradas por machos de ambas especies. Escuchamos y grabamos vocalizaciones de despliegue diferentes de las típicas de *T. cupido* y *T. pallidicinctus* en nueve asambleas de cortejo mixtas. Los espectrogramas de dichas vocalizaciones contenían elementos de los cantos de *T. cupido* y *T. pallidicinctus* y presentaban similitud intermedia. Los machos que emitieron esas vocalizaciones presentaban caracteres adicionales novedosos, así como nuevas combinaciones de caracteres de *T. cupido* y *T. pallidicinctus.* Éste podría representar el primer caso de hibridación de estas dos especies en condiciones naturales.

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Differences between Greater (*Tympanuchus cupido*) and Lesser (*T. pallidicinctus*) Prairie-Chicken include feather coloration and pattern (Short 1967), inflated air-sac shape, size, and color (Jones 1964, Sharpe 1968), and stereotyped lek displays (Sharpe 1968, Giesen 1998). These displays are characterized by high-intensity booms, which are highly stereotyped and ritualized, and appear to have epigamic and agonistic functions (Sharpe 1968). Greater Prairie-Chicken booms consist of three low-frequency syllables (ca. 268 Hz) and ca. 2 sec in duration (Sharpe 1968, Schroeder and Robb 1993). Lesser Prairie-Chicken booms consist of three higher frequency syllables (ca. 750 Hz), are ca. 0.6 sec in duration, and are often antiphonal (Sharpe 1968, Giesen 1998). Lesser Prairie-Chicken display vocalizations have been termed ''gobbling,'' ''bubbling,'' and ''yodeling'' (Giesen 1998);

we use the term ''booming'' to encompass these three terms. Both species also exhibit low-intensity booming (Sharpe 1968); we refer to high-intensity booms unless otherwise specified.

Both species stamp their feet prior to booming (Sharpe 1968). Greater Prairie-Chicken snap and spread their rectrices at the onset and after booming, respectively, while Lesser Prairie-Chicken give an exaggerated tail spread at the peak of the boom (Sharpe 1968, MRB, pers. obs.).

Anecdotal accounts from Kansas (Horak 1985) and Oklahoma (Baker 1953, Jones 1964), and museum specimens from Kansas (Baker 1953) and Nebraska (Sharpe 1968) suggest that Greater and Lesser Prairie-Chickens were sympatric historically. Applegate and Horak (1999) imply a zone of sympatry in western Kansas based on recent road surveys. However, most literature suggests historic and current allopatry (Aldrich and Duvall 1955, Giesen 1998, Busby and Zimmerman 2001). The taxonomic status of the two species has undergone extensive debate: the forms have been considered separate subspecies (Aldrich and Duvall 1955, Short 1967, Johnsgard 1983), separate species (Jones 1964, Crawford 1978), and a single superspecies (AOU 1998). In a recent phylogenetic analysis of the 17 species of Tetraoninae, Lucchini et al. (2001) considered Greater and Lesser Prairie-Chicken ''nominal'' species.

Evidence of species distinction of Greater and Lesser Prairie-Chicken might be provided in a zone of sympatry where reproductive isolation could be tested (Jones 1964, Crawford 1978). We begin to address the degree of reproductive isolation in the only known area of sympatry of these species.

METHODS

DATA COLLECTION

As part of a larger study of spatial and behavioral interactions of Greater and Lesser Prairie-Chicken, we surveyed remnant mixedgrass prairie in seven western Kansas counties (Ellis, Gove, Lane, Ness, Rooks, Russell, and Trego; Fig. 1A) by road, ATV, and foot from 17 March to 18 May 2001. During this sampling interval we observed leks for 21 hr. A global positioning system was used to mark locations of leks, and a geographic information system was used to determine the area of the polygon where both species were found. Apparent hybrids were defined as displaying male prairie-chickens that gave high-intensity ritualized booms unlike equivalent Greater and Lesser Prairie-Chicken booms. For brevity, we refer to these birds as hybrids, but this designation remains to be confirmed. At one mixed Greater and Lesser Prairie-Chicken lek and one display site repeatedly occupied by a single hybrid, we made audio and video recordings using a Marantz PMD-222 field recorder, Sennheiser directional microphone, and a digital camcorder. Eighty minutes of audio recordings of booming males from four allopatric Greater and four allopatric Lesser Prairie-Chicken leks were obtained from Macaulay Library of Natural Sounds (MLNS), Cornell Laboratory of Ornithology (MLNS Catalog # and recordist: 2532, C. P. Grant; 2533, 2534, 2536, 2537, 2538, H. G. Lumsden; 2535, V. W. Maupin; 50136, G. Keller). MLNS recordings were from 1961 to 1990.

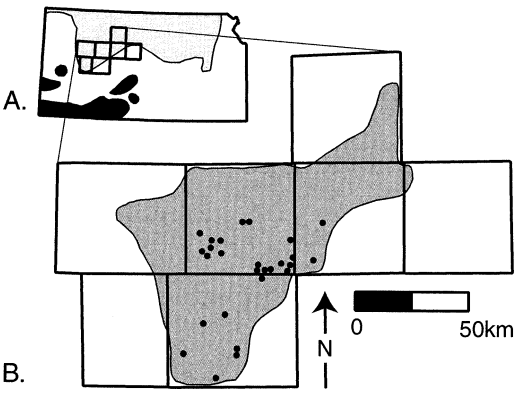

FIGURE 1. (A) Distribution of Greater Prairie-Chicken (light gray) and Lesser Prairie-Chicken (black) in Kansas (adapted from Schroeder and Robb 1993 and Giesen 1998). Rectangles indicate Ellis, Gove, Lane, Ness, Rooks, Russell, and Trego Counties. (B) Extent of 2001 lek surveys (dark gray), with locations of 27 mixed leks (filled circles).

ANALYSES

We analyzed 12 booms, four Greater and four Lesser Prairie-Chicken (MLNS recordings), two hybrids, and one Greater and one Lesser Prairie-Chicken from the same lek where one of the hybrids was recorded. Visual identification (Nowicki and Nelson 1990) was used to compare syllable arrangement, duration, and pitch, and Canary 1.2.4 (Charif et al. 1995) was used to construct spectrograms and conduct spectrogram cross-correlations. Spectrogram cross-correlations were normalized to prevent differences in amplitude from affecting similarity values, and bandpass filtered to reduce noise (Charif et al. 1995).

Cross-correlations produce a similarity value that represents the degree of fit between two spectrograms if they are overlain (Clark et al. 1987). Pairwise correlations of spectrograms of the 12 booms resulted in an array of similarity values with values of zero being completely dissimilar and one being identical (Charif et al. 1995). The technique of multidimensional scaling provided a visual representation of these values by positioning individual points according to their acoustic similarity (Nowicki and Nelson 1990).

RESULTS

Of 96 leks located, 52 contained only Greater Prairie-Chickens, 17 contained only Lesser Prairie-Chickens, and 27 were mixed (Fig. 1B), forming an approximately 250 000-ha area of overlap. A total of 12 hybrids was located on nine mixed leks. Two hybrids were included in the acoustic analysis; one had intermediate feather coloration and patterning and intermediate inflated air-sac shape, size, and color. The second had Greater Prairie-Chicken feather coloration and patterning, Greater Prairie-Chicken inflated air-sac

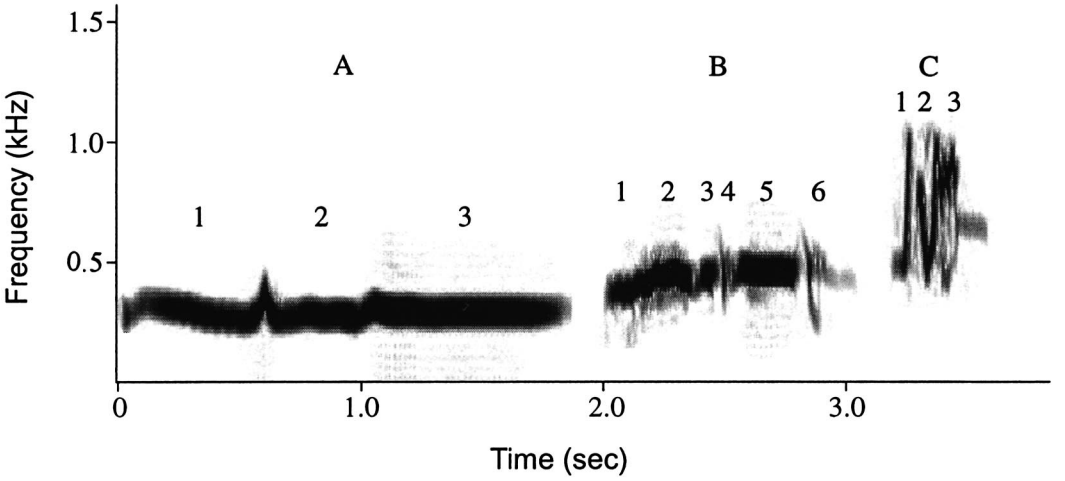

FIGURE 2. Representative spectrograms of high-intensity booms with numbered syllables. (A) Greater Prairie-Chicken, MLNS #50136, Nebraska, 1990. (B) Hybrid, Kansas, 2001. (C) Lesser Prairie-Chicken, MLNS #2537, Oklahoma, 1962.

shape and color, and intermediate Greater Prairie-Chicken/Lesser Prairie-Chicken air-sac size.

All hybrids exhibited foot stamping, low-intensity booming, and a series of two or three tail movements. The first was intermediate between a Greater Prairie-Chicken snap and a Lesser Prairie-Chicken exaggerated tail spread, followed by one or two more typical Greater Prairie-Chicken tail spreads. We did not observe antiphonal booming by hybrids.

Hybrid boom syllables 1, 2, 3 and 5 (Fig. 2B) were similar to the three Greater Prairie-Chicken syllables (Fig. 2A). These were interrupted by two frequency modulations similar to Lesser Prairie-Chicken syllables 2 and 3 (Fig. 2C), producing hybrid syllables 4 and 6. Hybrid booms contained elements of both species and were intermediate in duration and pitch (~1 sec, ~440 Hz; Fig. 2). Hybrid booms appeared to be intermediate between Greater and Lesser Prairie-Chicken booms (Fig. 3): in similarity analysis, the distances between the hybrid cluster, the Greater Prairie-Chicken cluster, and Lesser Prairie-Chicken cluster, were nearly equal.

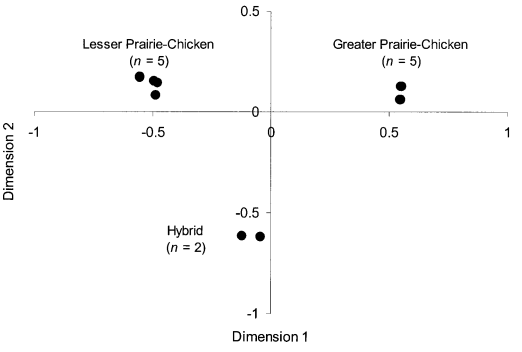

FIGURE 3. Multidimensional scaling of similarity values among prairie-chicken booms. Each filled circle represents an individual's boom. In the Greater Prairie-Chicken cluster, three points completely overlap other points; in the Lesser Prairie-Chicken cluster, two points completely overlap.

DISCUSSION

In this study area, ecological isolation between the two prairie-chicken species appears to be weak. Museum specimens collected in the late 1800s in Kansas (Baker 1953) and in the early 1900s in Nebraska (Sharpe 1968) indicate that both species might have inhabited this region. These specimens appear to represent range expansions (Sharpe 1968), which might have resulted from a limited amount of cropland being introduced into the landscape (Schroeder and Robb 1993). The distributions and population sizes of prairie chickens in Kansas likely have been as dynamic as land use; because our study area is on the periphery of both species' ranges, these populations might have been especially susceptible to these fluctuations.

We speculate that prairie-chickens have inhabited our study area since at least the late 1800s, with little interspecific contact until recent improvements in range management and land use. Furthermore, remnant mixedgrass prairie might provide a unique ecological opportunity for sympatry, because distinct habitat preferences might be met in the same location. We suggest that genetic interactions between these two species might have occurred historically if similar landscape-level conditions existed.

Booms used to identify hybrids were associated with their ritualized display sequence. These booms were neither low intensity (Sharpe 1968), nor atypical for the individual (Schwartz 1945, Hamerstrom and Hamerstrom 1960). Furthermore, geographic and temporal variation in the 10 Greater and Lesser Prairie-Chicken booms we examined was small. Individual

variation in this highly stereotyped vocalization is likely not responsible for the intermediate booms.

Sparling (1979) suggested vocal learning in grouse by examining Greater Prairie-Chicken and Greater Prairie-Chicken × Sharp-tailed Grouse (*Tympanuchus phasianellus*) hybrid whines, and internote interval and duration of Sharp-tailed Grouse coos. However, these vocalizations are not closely associated with stereotyped epigamic display (Sparling 1981, 1983). Greater and Lesser Prairie-Chicken booms are the most prominent feature of their stereotyped epigamic display (Sharpe 1968, Sparling 1981, 1983) and are therefore more likely subject to intense sexual selection and subsequent genetic rigidity. For example, Greater Prairie-Chicken × Sharp-tailed Grouse hybrid booms are thought to be a result of hybridization in contrast to vocal learning (Sparling 1983). Furthermore, we have observed a lek consisting of a single court-defending Greater Prairie-Chicken and 23–64 Lesser Prairie-Chicken six times throughout this study; individuals of both species gave only their respective stereotyped display. We hypothesize that intermediate booms are more likely the result of hybridization than vocal learning.

No documentation of wild Greater × Lesser Prairie-Chicken hybrids exists, but Crawford (1978) reported intermediate morphology and intermediate and novel booming display in a captive hybrid. This individual's booming vocalization also consisted of six syllables and was intermediate in duration. Calls of Greater Prairie-Chicken × Sharp-tailed Grouse hybrids were also intermediate or varied in complex ways from those of either parental species (Sparling 1983). Greater × Lesser Prairie-Chicken and Greater Prairie-Chicken × Sharp-tailed Grouse hybrids and offspring might be fertile (Crawford 1978, Sparling 1980). We suspect that the intermediate individuals we studied were Greater × Lesser Prairie-Chicken hybrids; however, additional behavioral observations and genetic analyses need to be conducted to test this hypothesis.

Given the extent to which congeneric *Tympanuchus* hybridize in the wild (Schroeder and Robb 1993) genetic introgression between *T. cupido* and *T. pallidicinctus* is a possibility. In addition, the highly skewed male mating success typical of lekking species (Höglund and Alatalo 1995), the possibility of epigamic sexual selection for distinctive vocalizations (Sparling 1983) and novel and larger phenotypes (Pierotti and Annett 1993), and tendency for females of lekking species to copy (Gibson et al. 1991, Clutton-Brock and McComb 1992), support a hypothesis of hybridization in this system. Upon further study of the spatial extent of this zone of sympatry, as well as the degree of reproductive isolation within this same area, conclusions affecting systematic and management questions might be possible.

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