DISSERTATION

SHARP-TAILED GROUSE RESPONSE TO LEK DISTURBANCE IN THE CARBERRY SAND HILLS OF MANITOBA

Submitted by

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In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

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COLORADO STATE UNIVERSITY

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY RICHARD KENITH BAYDACK ENTITLED SHARP-TAILED GROUSE RESPONSE TO LEK DISTURBANCE IN THE CARBERRY SAND HILLS OF MANITOBA BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

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ABSTRACT OF DISSERTATION

SHARP-TAILED GROUSE RESPONSE TO LEK DISTURBANCE IN THE CARBERRY SAND HILLS OF MANITOBA

Characteristics of sharp-tailed grouse (Tympanuchus phasianellus) leks, response of grouse to experimental disturbances of leks, and use of replacement leks were studied in the Carberry Sand Hills, southwestern Manitoba, from May 1983 through June 1985.

Ten active leks were located an average of 2.2 km apart and were generally oval-shaped, with a NW to SE orientation. Leks averaged 450 m^2. Leks were higher than most surrounding terrain, and sloped ≤1% over display areas. Vegetation height was less on display than on perimeter areas. Cover consisted of grass (68%), forbs (15%), bare ground (15%), and shrubs (1%). Visibility on display areas increased progressively from summer to fall to spring. Each lek had escape cover ≤500 m and trees used for perching ≤400 m from lek center.

Response of sharp-tailed grouse to lek disturbance varied between sexes. Male sharptails were tolerant of all experimental lek disturbances except visible human presence. They continued to display in spite of parked vehicles, snow fencing, propane 'bangers', scarecrows, radio sounds, and leashed dogs. Males displaced due to human presence generally remained in prairie habitat within 400 m of the traditional lek. They often returned to the lek within 5 minutes of cessation of disturbance. Displaced male grouse spent most of their time (70%) 'sitting motionless' during disturbance. Female sharptails were displaced from leks by all tested disturbances but were not monitored.

Replacement leks attracted some displaced male sharp-tailed grouse. Successful replacement leks resembled traditional leks at test distances of 200 or 400 m. Male decoys, female decoys in precopulatory position, and tape-recorded grouse vocalizations were necessary to induce males to attend replacement leks. Some replacement leks were used daily by males during disturbance, but use was limited to <40% of total disturbance time. Males attended replacement leks more often during morning than evening display periods. Activity of males on replacement leks was dominated by 'sitting motionless', although some displaying occurred. Female sharptails were rarely observed at replacement leks, but when present their attendance incited male display activity.

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Above all, I acknowledge the support and understanding shown by my wife Lorraine, especially given our first child, Angela, was born in the midst of the 1984 field season. This dissertation is dedicated to these two very special people.

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INTRODUCTION

JUSTIFICATION

Impacts of human activities on prairie grouse vary by species or subspecies, geographical location, habitat condition, and other factors (Hamerstrom et al. 1952, Arthaud 1970, Brown 1978, Miller and Graul 1980, Robel 1980, Kessler and Bosch 1982). Although reduced populations and distribution generally result (Hamerstrom and Hamerstrom 1961, Crawford and Bolen 1976a, Johnston and Smoliak 1976, Vance 1976, Drobney and Sparrowe 1977), benefits to species sometimes occur (Taylor 1979, Horkel and Silvy 1980, Connelly et al. 1981).

Although sharp-tailed grouse (*Tympanuchus phasianellus*) have not been affected as drastically as other species of prairie grouse (Hamerstrom and Hamerstrom 1961, Aldrich 1966), distributions and population levels have been altered (Miller and Graul 1980). This is especially true for the more southern ranges of Columbian (*T.p.columbianus*), plains (*T.p. jamesi*), and prairie (*T.p. campestris*) sharptails, which are particularly vulnerable to land use impacts (Kessler and Bosch 1982).

In southern Manitoba, populations of prairie and plains sharp-tailed grouse have remained relatively secure and stable (Johnsgard 1973, Hatch 1975, Rusch 1976, Man. Dep. Nat. Resour. 1983). Robel

(1980) expressed a need for increased research on prairie grouse in areas where populations are relatively high.

Miller and Graul (1980) suggested that habitat reduction will significantly deplete sharptail range in all parts of southern Canada over the next ten years. In Manitoba, continued habitat loss was cited as the major negative factor affecting many wildlife species, resulting in long-term demands not being met for waterfowl, deer, some furbearers, and grouse (Man. Dep. Nat. Resour. 1983). Therefore, Manitoba's sharptail populations may not "provide use opportunities for recreational benefit and enjoyment, and may not be passed on to future generations in at least as vigorous a state as received" -- management goals of the provincial Wildlife Branch.

Loss of habitat to agriculture was identified as the central cause of population reductions of sharp-tailed grouse in many parts of North America (Buss and Dziedzic 1955, Ammann 1963, Aldrich 1966, Evans 1968, Kobriger 1975, Sisson 1976, Brown 1978, Kirsch et al. 1978, Kantrud 1981, Mattise et al. 1982, Nielsen and Yde 1982). Optimal sharptail habitat consists of interspersed cover types (Hamerstrom and Hamerstrom 1961, Henderson 1964, Evans 1968, Kobriger 1968, Moyles 1981). Ammann (1957) and Sisson (1976) found that specific habitat preferences of sharp-tailed grouse corresponded with seasonal activities, and Ammann (1957) suggested that meeting seasonal habitat preferences was essential to a successful sharptail population or transplant.

A critical component of sharptail habitat in spring is the traditional dancing ground or lek[1] (East 1952, Ammann 1963, Lumsden 1965, Evans 1968, Hjorth 1970, Robel 1972, Rippin and Boag 1974, Evans 1976, Kermott 1977, Moyles and Boag 1981). Although limiting factors for sharp-tailed grouse are not as well-defined as for other tetraonines (Jones 1963, Zwickel and Bendell 1967, Gullion and Marshall 1968, Bendell 1972, Kirsch 1974, Herzog 1979), elimination of or changes in lek microhabitat may exacerbate a limiting factor for this species.

Characteristics of sharp-tailed grouse leks have been noted for a variety of habitat types (Baumgartner 1939, Grange 1948, Hart et al. 1950, Hanson 1953, Ammann 1957, Kobriger 1965, Pepper 1972, Twedt 1974; Sisson 1976, Ward 1984), but no attempts have been made as yet to mitigate loss of sharptail dancing grounds.

OBJECTIVES

I studied the feasibility of mitigating lek disturbance for sharp-tailed grouse by providing an optimal replacement alternative. Specific objectives were to:

1. Identify and describe environmental/ecological characteristics of sharp-tailed grouse leks.

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[1] Although the word lek is derived from Swedish terminology which means 'activity' or 'play' most authors now use it to refer to both activity and location, as in this study. Note: lek = dancing ground = arena.

2. Measure sharp-tailed grouse response to disturbance of lek sites.
3. Test the feasibility of attracting displaced sharp-tailed grouse to replacement leks.

STUDY AREA

The study was conducted in the Carberry Sand Hills of southern Manitoba, Canada. The Sand Hills, approximately 160 km west of Winnipeg, contain two large parcels of public land represented by Spruce Woods Provincial Park and Canadian Forces Base (CFB) Shilo Military Reserve (Fig. 1.1).

CFB Shilo provided a natural study area for investigating wildlife reaction to human influence over the time of research (Fig. 1.2). Observation of animal response to habitat alteration and testing of alternative strategies for mitigation were also accomplished without confounding effects from other external sources.

The Federal government classified the Sand Hills as a timber reserve in 1895 and closed it to further settlement (Stevenson 1938). Military activity commenced near Sewell Lake just prior to World War I (Stevens and Carreiro 1973). The first permanent military quarters were developed in 1932 at what is now known as CFB Shilo. During World War II, the Military Reserve became an important center for air force training. Since a 1974 NATO agreement, CFB Shilo has been used as an artillery and tank training area for troops from the Federal Republic of (West) Germany.

The Carberry Sand Hills derive their name from a Wisconsin glacial period deltaic deposit of sand formed as the ancient Assiniboine River system flowed into glacial Lake Agassiz (Nero 1976). The area is underlain by Cretaceous shales, and surficial deposits range from 3.5 to 122 m (Man. Dep. Mines, Resour., and Environ. Manage. 1977). Topography varies from nearly level to gently undulating, except in areas of sand dunes (Dixon 1979).

The study area is characterized by long, cold winters and short, cool summers (Energy, Mines, and Resour. Can. 1971). Average annual precipitation is 48 ± 3 cm, with ≥80% occurring as rain from April to October (Man. Dep. Mines, Resour., and Environ. Manage. 1977). Temperatures range from approximately -40 to 40 C, with January and July being the coldest and warmest months, respectively (Energy, Mines, and Resour. Can. 1971).

The Carberry Sand Hills are in the Boreal Forest and Grass Region of Canada (Rowe 1972). Principal tree species are trembling aspen (Populus tremuloides) and willow (Salix spp.). Bird (1961) described the area as part of the aspen parkland of central Canada, composed predominantly of aspen, with trees of lesser importance being bur oak (Quercus macrocarpa), willow, and the tamarack (Larix laricina) - black spruce (Picea mariana) swamp community. Dixon (1979) indicated that the southern portion of the Sand Hills has a predominant prairie community structure, comprised of porcupine needlegrass (Stipa spartea), blue grama (Bouteloua gracilis), and prairie junegrass (Koeleria cristata). Major forbs included sages (Artemisia spp.) and leafy spurge (Euphorbia esula) (Dixon 1979).

DISSERTATION FORMAT

The format of this dissertation is a series of three papers (= chapters) to be submitted for publication. Although written in Journal of Wildlife Management style, two papers may be modified for submission to other journals. Pages were numbered consecutively throughout and there is a cumulative abstract and literature cited to satisfy university dissertation standards. This format is a step toward ensuring that graduate student research is expeditiously submitted for publication.

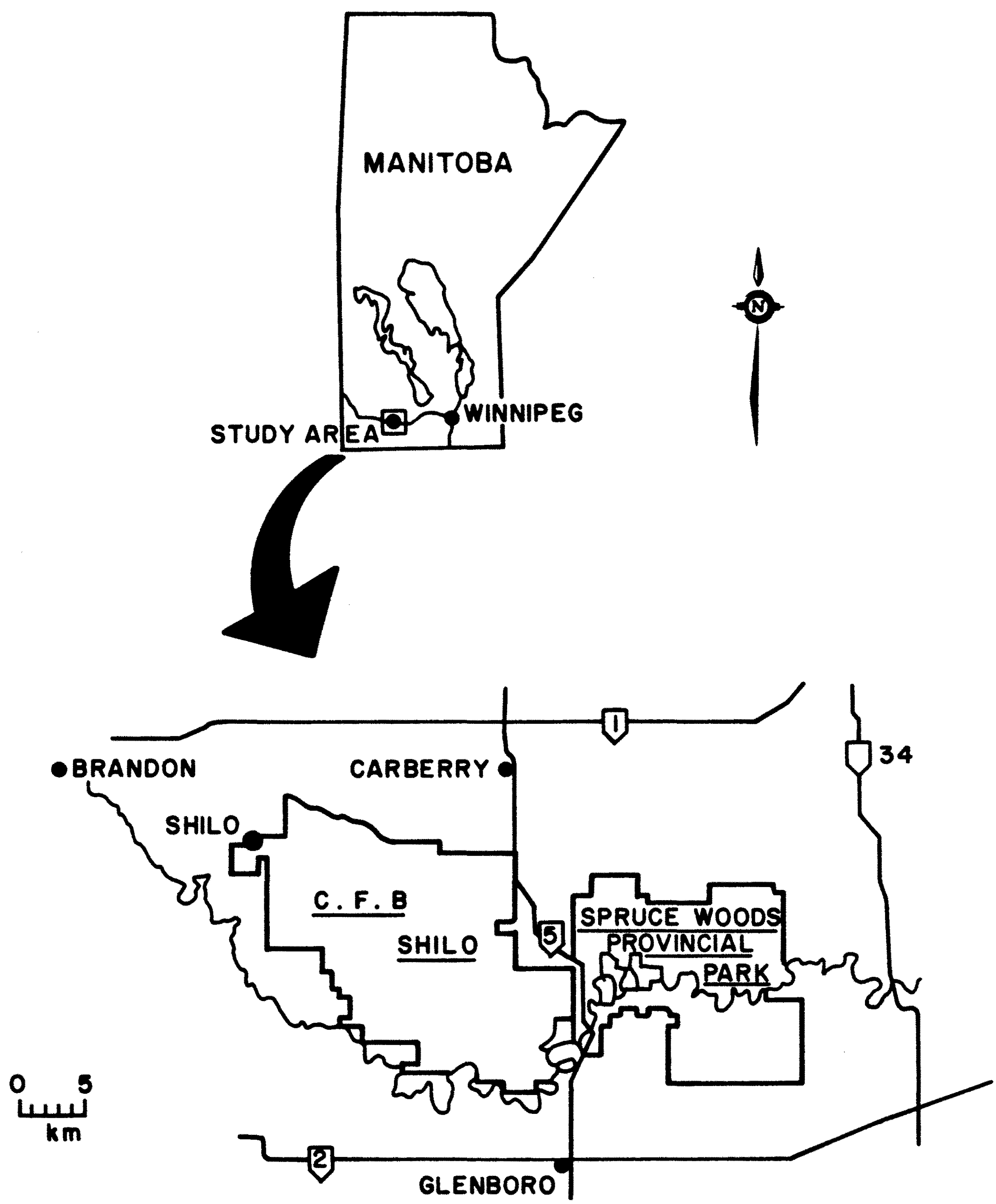

Figure 1.1. Carberry Sand Hills study area, Manitoba, Canada, (adapted from Strong 1981).

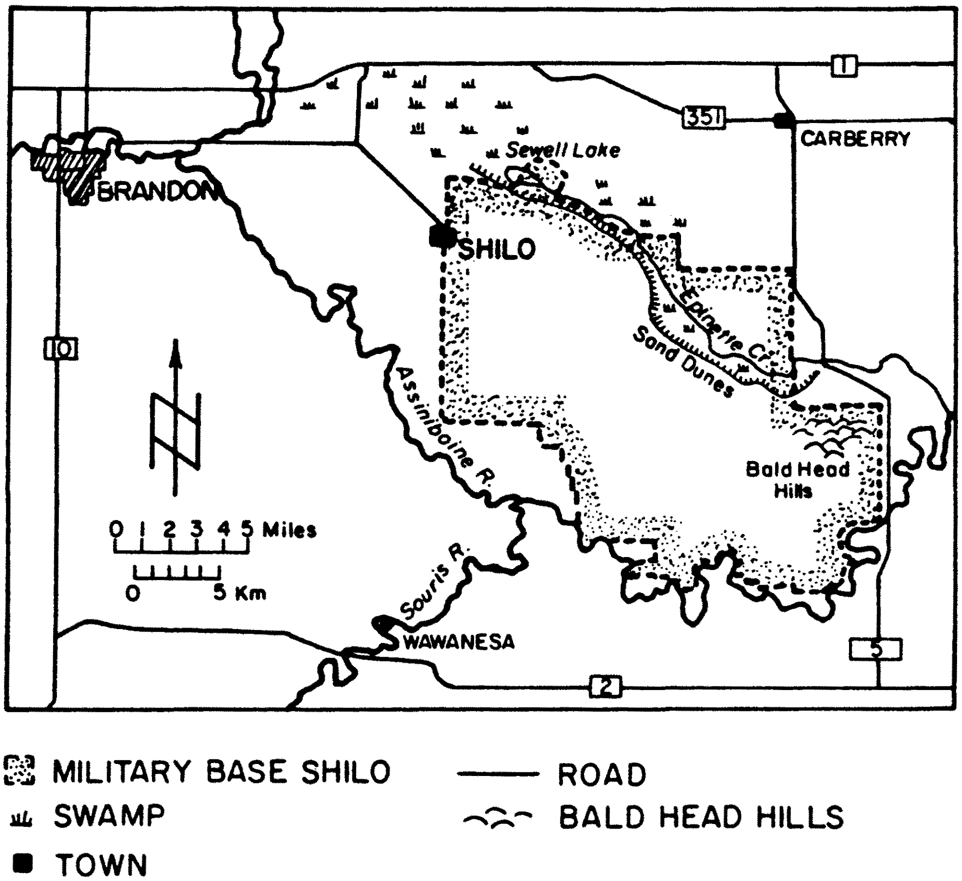

Fig. 1.2. Canadian Forces Base Shilo Military Reserve (adapted from Nilsson 1983).

CHARACTERISTICS OF SHARP-TAILED GROUSE LEKS

CHARACTERISTICS OF SHARP-TAILED GROUSE LEKS

INTRODUCTION

A lek is a communal display area where males congregate for the purpose of attracting and courting females, and to which females come for mating (Wilson 1975). Bradbury (1981) contended that leks develop only in situations where males contribute no parental care, male territories contain no limiting resources for females, females select a mate, and a mating arena exists.

Several studies have described environmental features of sharp-tailed grouse (Tympanuchus phasianellus) dancing grounds. Baumgartner (1939) described leks as open, grassy knolls or ridges, usually with sparse vegetation. Grange (1948) and Ammann (1957), reporting on display grounds in Wisconsin and Michigan, respectively, suggested that relatively open sites having low or sparse vegetation with terrain varying from flat to slightly higher than surrounding land were preferred. Hanson (1953) noted that sharptail dancing grounds in northern Ontario were on grass-sedge mats with slightly elevated hummocks that enhanced visibility.

Hart et al. (1950) found that most leks used by sharptails in Utah were on relatively higher elevation, ranging from small knolls to high hills, in a weed-grass cover type. In Saskatchewan and Idaho, respectively, Pepper (1972) and Ward (1984) found that unhindered visibility was characteristic of display sites. In Nebraska, Kobriger (1965) found that 90% of the display grounds sampled were in areas mowed or winter-grazed by livestock. Twedt (1974) and Sisson (1976) provided quantitative descriptions of sharp-tailed grouse leks in other Nebraska studies.

Bradbury and Gibson (1983) stated, however, that lek site characteristics were so diverse that habitat selection by males is an unlikely determinant of lek location. They proposed two behavioral models of lek location - males clumping at 'hotspots' through which the largest number of females are likely to pass; and females selecting mates at the largest aggregation of males over a given area. In both cases, however, Bradbury and Gibson (1983) cautioned that their models may be influenced by habitat suitability, predator defense, or other ecological determinants.

This paper describes characteristics of 10 active and 2 inactive sharp-tailed grouse leks in southwestern Manitoba.

STUDY AREA AND METHODS

The study was conducted in the Carberry Sand Hills, southwestern Manitoba from June 1983 through May 1985. The study area was aspen parkland vegetation type, consisting of trembling aspen (*Populus tremuloides*) thickets interspersed with open prairie grassland. Major grasses included blue grama (*Bouteloua gracilis*), prairie junegrass (*Koeleria cristata*), and porcupine needlegrass (*Stipa spartea*). Average annual precipitation is 48 ± 3 cm, with most occurring as rain (Man. Dep. Mines, Resour., and Environ. Manage. 1977).

Twenty study leks were located during spring and summer 1983-1984 (Fig. 2.1). During spring, binocular and acoustical observations were made during morning and evening display periods. Locations were verified by walking to the designated site and observing grouse and/or evidence of display activity, i.e., trampled vegetation, droppings, and/or feathers. During summer, transect lines 100 m apart were walked in habitat likely to contain leks. Sites possessing evidence of display were marked, and verified the following fall.

Lek locations were plotted on 1:50,000 NTS topographic maps of the study area. Spatial distribution was scaled from map measurements. Twelve leks (1-10, A,B) were selected for further investigation based on access, proximity, and similarity of location, i.e., agriculture situations were excluded. Site characteristics were measured in summer (June - July) and fall (Sept. - Nov.) 1983 and spring (Apr.-May) 1984.

Lek areas and general shapes were determined by eight evenly spaced measurements from lek center to edge. Lek center was defined as the most heavily trampled or most exposed location on the lek. Lek edge was defined as the first 5-m distance along a transect from lek center where visual evidence of display activity was no longer apparent. Four transect lines, oriented along and perpendicular to the longest axis, were staked from lek center to edge (display area = DA), and to a point 50 m beyond lek edge (display perimeter = DP), following Twedt (1974). Sampling points were at 5- and 10-m intervals along transects on display areas and display perimeters, respectively. Elevation, cover, and visibility were recorded at each sampling point, and compared for each lek between display areas and display perimeters using a _t_ test.

Elevation was recorded using a surveyor's level and rod. Lek slope was derived using a best-fit, linear, unbiased regression plot. Elevation was also measured at all points approximately > lek elevation ≤500 m from each lek.

Maximum vegetation height was measured in dm using a surveyor's rod. Ground cover (percent of shrubs, forbs, grasses, and bare ground) was measured using line-intercept (Canfield 1941) and 0.1-m^2 plots (Daubenmire 1959). Vegetation was identified to dominant genera.

Visibility was measured at sampling points using the density board technique (Jones 1968). In addition, visibility was estimated from lek center using a modification of the Robel et al. (1969) visual obstruction rod (VOR) technique. An observer at lek center, lying at grouse-eye level (approximately 20 cm) indicated the lowest point of a VOR rod that was visible at each sampling point. A best-fit, linear, unbiased regression of VOR visibility versus distance from lek center was estimated.

Distance to appropriate escape cover was estimated for each lek along 12 sight lines at 30°-intervals from North. Appropriate cover was determined by observing grouse flushing and roosting behavior during summer and fall 1983 and spring 1984. Distances to appropriate advertising or perching sites for females in spring were estimated by pacing from lek center. These sites were located by observing female aggregations during spring 1983 and 1984.

Data were analyzed using MANTES, SAS, and SPSS-X statistical packages on the University of Manitoba AMDAHL computer system.

RESULTS

Spatial Distribution

Active leks were an average of 2.2 km apart over 87.5 km^2, representing a density of 0.1/km^2 (Table 2.1). Inactive leks A and B were closer than average to an active lek. Approximate lek area ranged from 100 to 1220 m^2, with mean size being about 450 m^2. Inactive leks A and B were larger than average. Leks were not oriented in a consistent compass direction, although oval-shaped NW to SE orientations were most common.

Elevation

Lek elevations were generally higher than most surrounding terrain within 500 m. Locations within 500 m from each lek with elevations $\geq$ lek elevation ranged from 2 to 9 points per lek, with a mean of 4.7.

Lek centers were generally higher than surrounding areas of the lek to a distance of approximately 100 m. A best-fit, linear, unbiased regression estimate for lek slope was -0.010 $\pm$ .003 ($\bar{x}$ $\pm$ SE), indicating an approximate 1% drop in elevation over display areas.

Vegetation Characteristics

Vegetation height on leks was generally less on active display areas than on display perimeters (Table 2.2). Mean spring vegetation height on display areas was 10.4 ± 1.1 cm ($\bar{x}$ ± SE).

Ground cover of display areas differed from display perimeters (Table 2.3). Less shrubs and more bare ground were present on display areas. The Daubenmire and Canfield methods did not produce differences ($P > 0.10$) in ground cover type classification. Percent ground cover type did not vary ($P > 0.10$) among seasons (Table 2.4). Spring ground cover on display areas was dominated by grasses (68%), followed by approximately equal amounts (15%) of forbs and bare ground, and a small amount of shrubs (≤1%).

Vegetation on leks was no different than on surrounding areas. Dominant grasses were prairie junegrass (*Koeleria cristata*), blue grama (*Bouteloua gracilis*), and porcupine needlegrass (*Stipa spartea*), with prairie sand reed (*Calamovilfa longifolia*), and bluestem (*Andropogon spp.*) sometimes present; forbs were fringed common, and Louisiana sage (*Artemisia frigida*, *A. campestris*, *A. ludovincia*), three-flowered avens (*Geum triflorum*), field horsetail (*Equisetum arvense*), leafy spurge (*Euphorbia esula*), and black-eyed susan (*Rudbeckia hirta*); shrubs were prickly rose (*Rosa acicularis*), creeping juniper (*Juniperus horizontalis*), willows (*Salix spp.*), common snowberry (*Symphoricarpos albus*), and poison-ivy (*Toxicodendron radicans*).

Visibility and Escape Cover

Mean percent visibility on display areas was generally no different than on display perimeters in summer and fall, but greater in spring (Table 2.5). Visibility increased progressively from summer to fall to spring.

Visibility from lek center was reduced progressively along transects due to a combination of vegetation and topographical features (Fig. 2.2). A best-fit, linear, unbiased estimate showed that VOR readings increased by approximately 12 cm with each 10-m progression from lek center. Approximate mean obstruction height on display areas was 31 cm compared to 78 cm on display perimeters.

Distance to appropriate escape cover from study leks ranged from 200 to 3000 m. At all leks, at least one 30° sampling interval had suitable cover ≤500 m from lek center.

Distance to nearest female advertising or perching sites from study leks ranged from 200 to 600 m and averaged 400 m. Female perching sites were sometimes equidistant from 2 or more leks. These locations are, I believe, important to determination of lek location, and especially important in spring. Prior to and during early season dancing activity, groups of female sharptails congregated in 6-10 m aspen and oak trees and "gobbled". The gobble sound was audible on nearby leks and stimulated male dancing activity. Females remained associated in these locations during mornings for approximately 1 week in mid-April 1984 and 1985, and no females were observed on leks during this period. Since the female vocalization was audible on leks, I tested the audibility of male vocalizations to humans at the base of perching trees using tape recordings on leks. Only male 'coo' and 'chilk' notes could be heard at these locations.

DISCUSSION

Sharp-tailed grouse leks in the Carberry Sand Hills, Manitoba had several common environmental and ecological characteristics (Table 2.6). This constitutes the first attempt to provide a comprehensive, quantitative description of the components of the system which comprises a sharp-tailed grouse lek. Kobriger (1965), Pepper (1972), Twedt (1974), Sisson (1976), and Ward (1984) provided quantitative descriptions of some lek components, each in different habitat types, with fewer variables described.

Patterns of lek distribution over a unit of habitat may vary according to habitat type, habitat availability, population densities, or female home range size (Lumsden 1965, Sisson 1976, Bradbury and Gibson 1983). Average spacing between nearest leks (2.2 km) in my study was similar to Ammann's (1957) estimate of 2.4 km in Michigan, and Lumsden's (1965) estimate of ≥1.6 km in Ontario. Sisson (1976) estimated dancing grounds in Nebraska were much closer (0.8 km). The number of dancing grounds on a given area changes yearly as a result of population fluctuation (Lumsden 1965, Cannon and Knopf 1981, Wells 1985), possibly explaining inactivity at formerly active leks A and B. Leks A and B may also have been transient or satellite locations.

The density of 0.1 leks/km^2 was within the range reported by Sisson (1976) of 0.02 - 0.30/km^2 in Nebraska. Horkel and Silvy (1980) found lek densities as high as 6/km^2 for Attwater's prairie-chicken (_T. cupido attwateri_) in Texas, however, those leks were primarily on areas impacted by oil field operations. Contrary to Sisson's (1976) findings, however, leks on my study area clumped rather than randomly distributed. The common lek orientation (oval-shaped, NW to SE) has not been reported previously, but is likely a result of topographic features of the area. Lek area, noted to be highly variable by Lumsden (1965), Twedt (1974), and Sisson (1976), also varied in my study, and is probably not an important lek characteristic.

All study leks were generally at elevated locations, with flat to undulating surrounding topography. This characteristic has been the predominant descriptor of all open country avian leks for many years (Hjorth 1970). These locations obviously afford improved visibility and unrestricted movement, important to increased observability of mates and decreased predation (Koivisto 1965, Hjorth 1970, Wiley 1974, Wrangham 1980). More recently, Bradbury (1981) and Bradbury and Gibson (1983) suggested that an environmental component is necessary to either of their two general models (hotspots or large clumps of males) of determination of lek location. I suggest that the critical environmental determinant for sharptails is an elevated site affording the listed benefits to displaying individuals.

Study leks were relatively level, with <1% decrease in elevation over the display area. Twedt (1974) and Sisson (1976) also found slope on leks in Nebraska to be gentle, usually 8c35%. Terrain used by displaying grouse was confined to sites less than 2 m below the elevation at ground center of the lek (Twedt 1974). A greater slope might increase visual obstruction from surrounding landforms, thus counteracting benefits of improved visibility afforded by increased elevations.

Vegetation height on study leks during spring was relatively low (7-13 cm), primarily a result of grouse trampling, but also due to snow lodging. Other researchers have noted similar results in Utah (Marshall and Jensen 1937) and Nebraska (Kobriger 1965, Sisson 1976). Twedt (1974) reported mean vegetation height on eight dancing grounds in Nebraska at 8.5 cm, and Anderson (1969) indicated 12-15 cm for greater prairie-chickens (_T. cupido_) in Wisconsin. As noted by Hart et al. (1950), leks in Utah were in the shortest cover type available, probably a more appropriate description than actual measured height.

Leks can be characterized as predominantly grass covered (70%), with equal amounts (15%) of forbs and bare ground, and negligible shrubs. The prevalence of bare ground and absence of shrub cover on leks relative to surrounding areas is likely a function of grouse visibility. Shrub cover would restrict and bare ground would improve visibility, noted earlier as a necessary prerequisite for lek location. Whether sharptails select sites for leks because of cover composition or cause it through trampling (especially of shrubs) is unclear.

Visibility on lek display areas of approximately 70% during spring allows for improved observability of predators, mates, and other males. Vegetative growth on display areas during late spring results in reduced visibility from and of leks during summer and fall, periods of low or non-use. My results are similar to Ward's (1984) findings in Idaho that grouse preferred sites with 70-80% visibility during spring. The reduction of visibility from lek center toward the edge may indicate that the observation range for dominant males on each lek is confined to a certain distance, leaving peripheral males to function as sentinels for predator observation. Similarly, females may gain a selective advantage of increased safety from predation by searching for and mating with central males, whose subdominants will alert the mating pair of approaching danger.

The importance of suitable escape cover within a reasonable flight distance from the lek may explain the ≤500 m distance for this characteristic. Grouse prefer short flushing distances to escape danger, resulting in time and energy savings which may lead to benefits to the population through natural selection. Although no specific distances were presented, Twedt (1974), Sisson (1976), and Ward (1984) noted the importance of nearby escape cover.

The importance of nearby female advertising or perching sites is likely to facilitate optimal communication between sexes. All sounds audible to humans at these locations have been measured as low frequency sound waves (Kermott and Oring 1975, Sparling 1981). Given that the least attenuation occurs in grassland habitats for low frequency waves (Marten and Marler 1977), these sounds are likely serving a long-distance communication function. Along with advertising male location to females, these sites may afford females the opportunity to observe male activity and use this information to select a lek and/or a male for mating. Since vocalizations are important to successful mating in all tetraonines and many other species, I hypothesize that sharptail leks may be located so as to maximize sound transmission thereby optimizing mating opportunities for each sex. Thus, complexes consisting of elevated leks with wide-viewing horizons and female advertising sites, may be an appropriate model to explain the lek mating system. This model would be complementary to Bradbury and Gibson's (1983) hotspot and grouped male models, which require unspecified environmental components.

MANAGEMENT IMPLICATIONS

Although this study provided descriptions of quantitative characteristics of sharp-tailed grouse leks, the data should be viewed with caution. All leks were located in a relatively uniform habitat type. Measurements might vary in different locations. Characteristics were measured over three sampling seasons, and might be altered by varying environmental conditions. More important to management for the species and other lekking grouse are the general patterns described quantitatively. The measurements which I recorded agree with the general descriptions available in the literature. These data will be useful not only to species management, but also for better understanding of the lek mating system, which will assist in developing new theories of sexual selection and mate choice.

Sharptail management should include the importance of leks as part of species habitat management. Although likely not a limiting factor, the habitat components required for a lek are essential to maintaining or introducing a population in an area. In addition, loss of leks may have negative effects on an existing population.

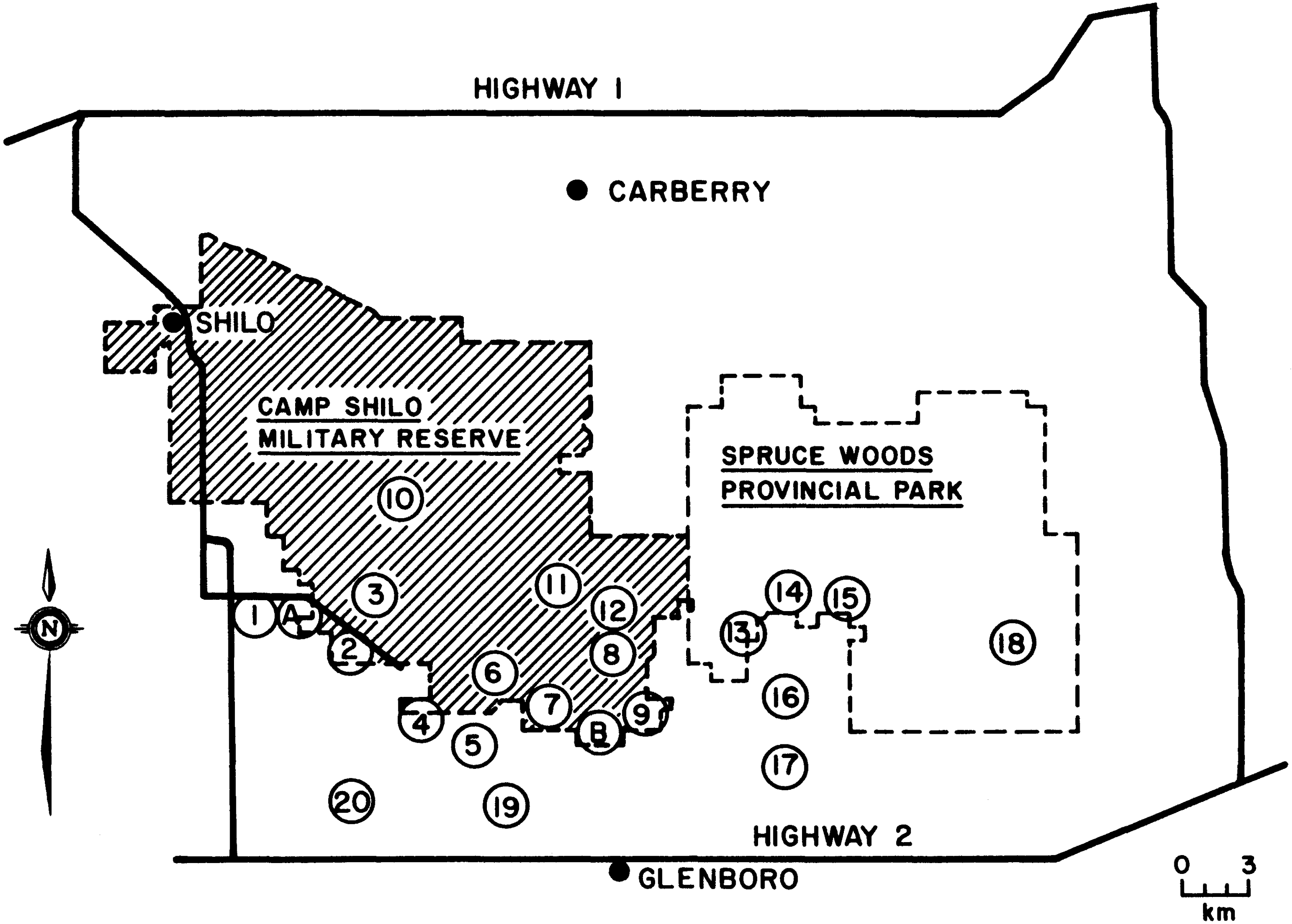

Fig. 2.1. Locations of sharp-tailed grouse leks in the Carberry Sand Hills Area, 1983-85.

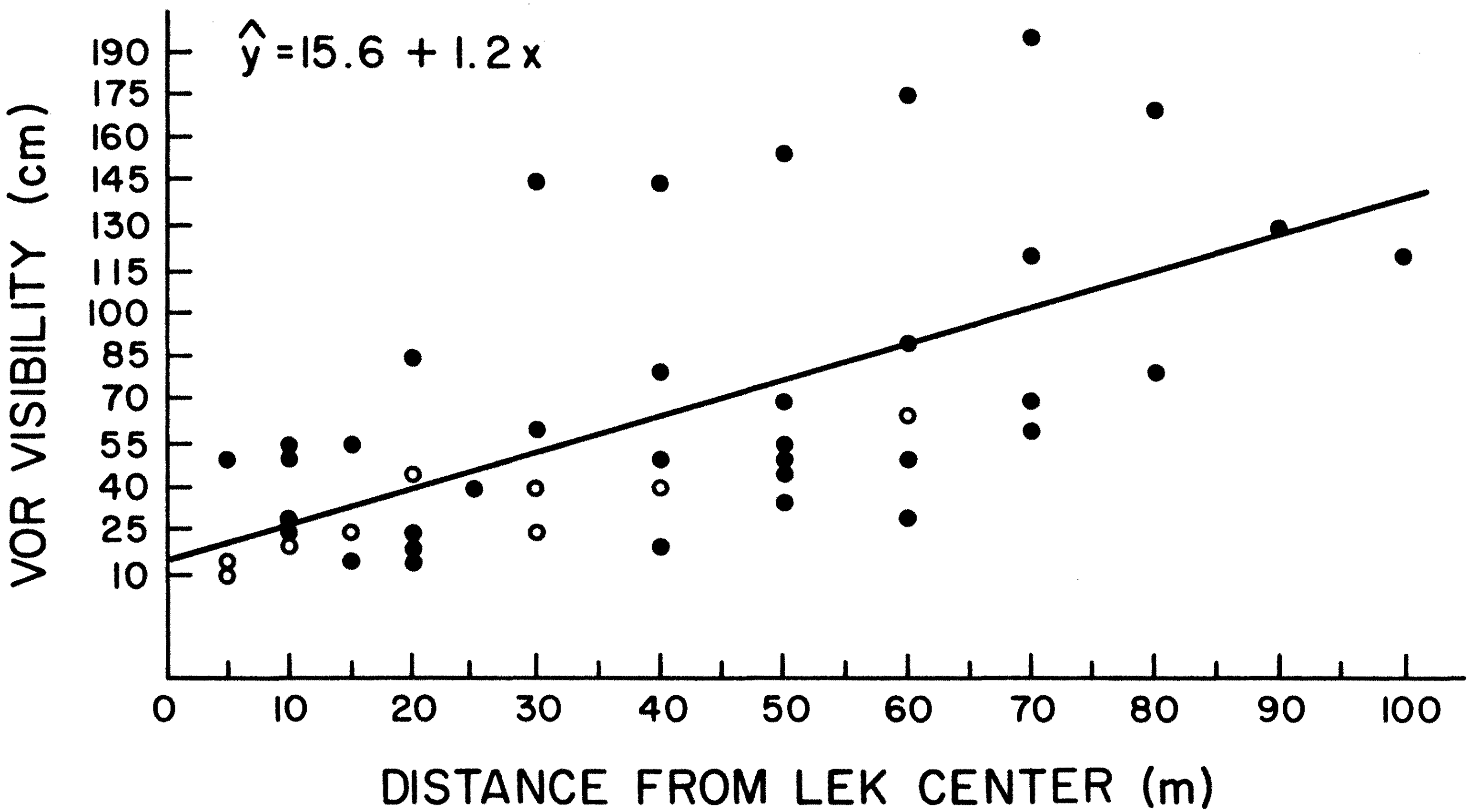

Fig. 2.2. Regression plot of VOR visibility (cm) vs. distance from lek center (m) for all study leks.

Table 2.1 Distribution, area, and orientation of study area leks.

Lek number	Nearest active lek (km)	Area (m^2)	Orientation (°N of longest axis)
1	2.9	220	352
2	2.4	250	338
3	2.4	315	86
4	1.7	205	350
5	1.7	105	357
6	2.1	100	342
7	1.8	160	295
8	1.8	1055	339
9	2.4	835	294
10	2.8	1220	270
Mean	2.2	446	
A	1.1	1150	292
B	1.1	930	76

Table 2.2 Mean of maximum vegetation heights (cm) for study lek display areas (DA) vs. display perimeters (DP), 1983-84

Lek number	Summer (July-Aug.) 1983			Fall (Oct.-Nov.) 1983			Spring (April -May) 1984		
	DA	*t* test *P*	DP	DA	*t* test *P*	DP	DA	*t* test *P*	DP
1							9.7	0.07	16.2
2							11.4	0.08	19.6
3	35.3	0.02	46.0	38.2	0.04	48.5	13.3	0.05	21.8
4				32.1	0.08	39.8	8.3	0.06	17.9
5							8.1	0.06	16.7
6	41.1	0.01	64.4	35.8	0.01	86.7	14.3	0.04	23.1
7	34.2	0.02	45.5	38.3	0.03	49.6	11.8	0.09	16.9
8	27.0	0.32	29.9	24.5	0.05	31.0	10.6	0.04	17.1
9	41.4	0.06	46.6	40.3	0.02	48.6	7.9	0.03	17.7
10	30.9	0.03	45.5	34.1	0.71	35.8	8.1	0.03	17.4
Mean	35.0	0.04	46.3	34.8	0.03	48.6	10.4	0.08	18.4
A	33.1	0.09	39.1				11.9	0.18	16.7
B	26.7	0.64	28.3	24.0	0.91	24.3	14.3	0.84	16.6

Table 2.3. Type of ground cover for study lek display areas (DA) vs. display perimeters (DP) using Daubenmire and Canfield methods, summer 1983.

Method and location	N [a]	Ground cover type (%) Shrub	Forb	Grass	Bare ground
Daubenmire-DA	98	1.0	19.1	67.7	12.2
Daubenmire-DP	117	4.4	20.8	69.6	5.2
t test P		0.07	0.36	0.72	0.04
Canfield-DA	25	1.6	15.8	62.1	20.5
Canfield-DP	25	5.5	19.7	59.5	15.2
t test P		0.08	0.19	0.63	0.05

[a] N refers to sampling points for Daubenmire method; 100-m transect lines for Canfield method.

Table 2.4. Type of ground cover on study lek display areas by season (Daubenmire method).

Date	N	Ground cover type (%) Shrub	Forb	Grass	Bare ground
Summer 1983	98	1.0	19.1	67.7	12.2
Fall 1983	145	1.6	18.4	65.2	14.8
Spring 1984	183	0.8	15.3	68.0	15.9

Table 2.5. Mean % visibility (cover board technique) for study lek display areas (DA) vs. display perimeters (DP), 1983-84.

Lek number	Summer (July-Aug.) 1983			Fall (Oct.-Nov.) 1983			Spring (April.-May) 1984		
	DA	*t* test *P*	DP	DA	*t* test *P*	DP	DA	*t* test *P*	DP
1							72.1	0.01	22.8
2							69.2	0.02	33.2
3	20.8	0.38	16.7	37.5	0.32	32.3	76.3	0.09	57.7
4				39.6	0.81	40.1	55.1	0.18	44.4
5							65.2	0.01	42.8
6	17.1	0.04	6.3	32.1	0.53	21.7	68.3	0.03	49.7
7	32.1	0.01	8.9				74.6	0.02	53.4
8	40.8	0.41	37.3	62.9	0.55	60.0	84.0	0.02	76.4
9	13.2	0.31	16.7	22.3	0.64	24.0	71.5	0.05	64.3
10	49.3	0.55	46.4	52.9	0.52	56.8	81.5	0.07	77.2
Mean	28.9	0.33	22.1	41.2	0.59	39.2	71.8	0.04	52.2
A	40.4	0.04	24.3				61.4	0.62	59.2
B	46.1	0.98	46.0	50.5	0.38	53.7	67.3	0.49	63.7

Table 2.6. Environmental characteristics of study leks, Carberry Sand Hills, Manitoba.

Component	Measurement
Nest nearest lek	1.7 - 2.9 km, $\bar{x}$ = 2.2 km
Orientation	NW to SE
Area	100-1220 m^2, $\bar{x}$ = 446 m^2
Surrounding terrain	Flat to undulating, generally lower elevation
Slope	≤1% over display area
Vegetation height in spring	7 - 13 cm, $\bar{x}$ = 10.4 cm
Ground cover in spring	
shrub	<1%
forb	15%
grass	70%
bare ground	15%
Visibility	Unrestricted in all directions, 70-80% on display area.
Distance to escape cover	≤500 m
Distance to perching trees	≤400 m

TOLERANCE OF SHARP-TAILED GROUSE TO LEK DISTURBANCE

TOLERANCE OF SHARP-TAILED GROUSE TO LEK DISTRUBANCE

INTRODUCTION

Alteration of habitat has adversely affected prairie grouse (Hamerstrom et al. 1952, Crawford and Bolen 1976a, Johnston and Smoliak 1976, Vance 1976, Drobney and Sparrowe 1977, Brown 1978, Miller and Graul 1980, Robel 1980, Kessler and Bosch 1982). For sharp-tailed grouse (Tympanuchus phasianellus), altered habitat has caused reductions in populations and distribution (Buss and Dziedzic 1955, Ammann 1963, Aldrich 1966, Evans 1968, Kirsch et al. 1973, Kobriger 1975, Sisson 1976, Kantrud 1981, Mattise et al. 1982, Nielsen and Yde 1982). Because sharptails exhibit seasonal selection of habitat type (Ammann 1957, Sisson 1976), meeting seasonal habitat preferences is important to maintaining a population. A component of sharptail habitat in spring is the traditional dancing ground or lek (East 1952, Ammann 1963, Lumsden 1965, Evans 1968, Hjorth 1970, Robel 1972, Rippin and Boag 1974, Kermott 1977, Moyles and Boag 1981).

A difference of opinion exists, however, regarding the importance of leks to a viable population of grouse. Eng et al. (1979) reported that sage grouse (Centrocercus urophasianus) may be sensitive to loss of leks. Tate et al. (1979) speculated that a sage grouse lek can be destroyed without affecting reproductive potential. Work with prairie-chickens has shown a similar division of opinion regarding the importance of leks (Douglass 1942, Kirsch 1974, Crawford and Bolen 1976b). As with some lekking grouse, sharptails exhibit an apparent year-round, as well as year-to-year, attachment to their dancing grounds (Twedt 1974).

Effects of lek disturbance on sharp-tailed grouse have not been well documented, although some observations have been reported in the course of other studies. Hjorth (1970) reported that agricultural tillage caused a shift in location of sharptail leks. The extent of movement was not documented, however. Sexton and Gillespie (1979) noted that fire, which removed grass and forb cover, induced sharptails to return to a previously abandoned lek. Heavy cattle grazing contributed to declines of sharp-tailed grouse in several locations (Marshall and Jensen 1937, Hart et al. 1950, Pepper 1972, Hillman and Jackson 1973, Kohn 1976, Sisson 1976, Nielsen and Yde 1982), but influence on lekking behavior was not clearly determined. Other disturbances, such as strip mining and road construction, are also thought to affect grouse leks. Leks have been described as ideal testing grounds for current theories of sexual selection and mate choice (Bradbury and Gibson 1983), and interruption of this process by human disturbance may contribute to evaluation and advancement of existing hypotheses.

The purpose of this study was to measure tolerance of sharp-tailed grouse to lek disturbance. I tested the hypothesis that sharptails will be displaced from leks by disturbance. I also predicted that displaced sharptails would randomly disperse from the traditional lek. I further hypothesized that disturbance would result in long-term (>10 days) displacement during the mating period.

STUDY AREA AND METHODS

The study was conducted in the Carberry Sand Hills, southwestern Manitoba, from June 1983 to May 1985. The study area was aspen parkland vegetation type, consisting of trembling aspen (Populus tremuloides) thickets interspersed with open prairie grassland. Major grasses included blue grama (Bouteloua gracilis), prairie junegrass (Koeleria cristata), and porcupine needlegrass (Stipa spartea). Average annual precipitation is 48 ± 3 cm, with most occurring as rain (Man. Dep. Mines, Resour., and Environ. Manage. 1977).

Eight leks (Fig. 3.1) were used to monitor grouse response to disturbance during spring (Mar. - June) and fall (Sep - Nov.) 1984, and spring (Mar. - May) 1985. Lek #3 was designated as an alternate to be used in the event of abandonment of any other study lek.

Grouse were captured on leks in spring using two rectangular 1.8 x 3.7 m traps per lek. Traps were constructed with aluminum conduit frames (1.25-cm dia.), welded wire mesh (5.1 x 2.5 cm) sides, and nylon mesh (2.5 x 2.5 cm) tops, following K. M. Giesen (pers. commun.). Each side panel (1.2 x 0.9 or 1.8 m) had a 15 cm^2 opening with an inverted, woven wire funnel. Woven wire (0.9 x 50 m) leads were extended from each opening; but their use was discontinued after April 1984, because they did not improve trapping success. Trapping extended for a maximum of three mornings and evenings per lek, with trap positions alternated regularly.

Although K. M. Giesen (pers. commun.) reported success capturing male sharptails using traps with tape-recorded vocalizations, and placed at lek edges between leks and escape cover, I was unsuccessful using this approach. Males from my study leks would walk around or fly over traps and/or leads to regain their territories. Therefore, I repositioned traps regularly on each lek to cover the maximum number of male territories during a 3-day trapping period. To increase coverage, I supplemented the large rectangular traps with four smaller, circular, welded-wire mesh traps (0.9-m dia. x 0.5 m) having nylon mesh tops and a funnel entrance. Although these traps caught fewer grouse, they appeared to create confusion on leks and may have been responsible for increasing success in the larger traps.

Male decoys and tape-recorded vocalizations were used in each trap in March and April 1984. Female decoys in precopulatory position were used after April 1984, and they enhanced trapping success and reduced trapping effort. Woven wire leads were not required with female decoys.

Seventy-two male (45 adults, 27 juveniles) and six female (five adults, one juvenile) sharp-tailed grouse were trapped and banded. Grouse were classified as to sex using crown feather and tail covert patterns, and to age using the proximal primary technique (Wishart 1977). Twenty-five radio transmitters (22 solar-powered, three battery-powered) attached to ponchos (Amstrup 1980) were placed on grouse to ensure relocation of ≥2 males per lek using a hand-held Yagi antenna and receiver.

A variety of methods of lek disturbances or obstructions (snow fencing, parked vehicles (running or not), propane 'bangers', scarecrows, scarecrows and tape-recorded voices, radio sounds, leashed dogs, human presence) were pre-tested at three leks for ≥2 days in May 1984 to determine the most effective disturbance i.e., that which prevented lek use. Experimental treatments of varying duration of the most effective disturbance were then assigned to leks in spring and fall 1984 and spring 1985 (Table 3.1).

During 1984 experiments, periodic transmitter relocations were made during peak display times. During spring 1985 experiments, grouse position was determined using transmitter relocations at 10-minute intervals during peak morning (2 hr ≥ sunrise ≥ 1 hr) and evening (1 hr ≥ sunset ≥ 1 hr) display times. In all cases, an initial radio transmitter relocation, followed by observation with binoculars, allowed each male to be located as to direction and distance from original lek. In addition, in spring 1985, each observation was further classified by type of habitat selected (prairie, shrub, woodland, prairie-woodland edge, and unknown) and grouse activity (sitting, displaying, cooing, walking, pecking, flying, and unknown). Effects of disturbance on females was obtained through direct observation of female presence relative to undisturbed control leks.

Data were analyzed using MANTES, SAS, and SPSS-X statistical packages on the University of Manitoba AMDAHL computer system. Number of male sharp-tailed grouse attending leks before and during disturbance were compared using _t_ tests. Patterns of male sharptail displacement were determined using Chi-squared tests.

RESULTS

Methods of Disturbance

Male sharptails were tolerant of all tested lek disturbances except human presence (Table 3.2). For all other methods of disturbance, there was no difference ($\underline{P} > 0.10$) in numbers of males attending before and during disturbance. On the first morning of disturbance, males would initially flush, but most returned to the traditional lek ≤15 minutes, seemingly to resume normal display activity. During the first morning of human disturbance, male grouse would attempt to land on or near the lek in ≤15 minutes if not flushed off again. Male grouse continued to attempt to regain their positions on leks with humans present at 5 - 10 minute intervals for approximately 1 hour, followed by periodic return attempts for ≥2 hours. On the second and subsequent mornings, the above pattern continued for the human disturbance treatment. For other disturbances, however, males did not flush from the lek at any time but exhibited normal display activity for the entire morning.

Female sharptails were not observed at any leks during any treatment, but were present at undisturbed control leks. Due to military use of leks #8 and #9 which restricted access, it was not possible to determine if females attended these leks post-disturbance. Females were observed in attendance at lek #1 post-disturbance.

Human Presence

From 18 May to 1 June and from 4 to 29 October 1984, human presence on leks displaced all male sharptails during morning and evening display times. Within 1 hour of sunrise, male grouse would approach the lek in flight, attempt a landing if not flushed, and return to their point of origin. These approaches by displaced males averaged 3.5/morning in spring (*N* = 3 leks) and 1.6/morning in fall (*N* = 6 leks). Females were not observed at treated leks during spring or fall disturbances, but were recorded periodically during spring at undisturbed controls.

Human disturbance at leks displaced all male sharptails regularly during spring 1985 (Table 3.3). Therefore, I rejected the null hypothesis of no measurable change in sharptails attending the original lek due to disturbance ($P < 0.01$). The null hypothesis pertaining to permanency (>10 days) of displacement could not be rejected; male grouse often returned to the lek within minutes of cessation of disturbance.

Displacement Distance and Direction.

Displacement distance for 22 radio-marked males averaged slightly > 400 m from the traditional lek during all human disturbances in spring 1985 (Table 3.4). All males remained <2000 m from the traditional lek at all times during disturbance. Mean displacement distance did not change ($P > 0.10$) between morning and evening. The null hypothesis that displacement distance was random was rejected (Poisson distribution test for randomness, $P < 0.001$), indicating a clumped or aggregated distribution.

For individual leks, mean displacement distance ranged from approximately 240 to 765 m (Table 3.5). In all but one case, mean distance was <370 m. Median distances were generally 200 or 300 m. Displacement distance was distributed in a clumped fashion, (Poisson distribution test for randomness, $P < 0.001$).

Male sharptails selected at least one specific displacement site at each lek during human disturbance. Grouse did not change these locations during morning and evening disturbances at any lek.

Cover Selection by Displaced Male Grouse

Cover selection by radio-marked male sharptails during human disturbance in spring 1985 was predominantly prairie habitat (90%) (Table 3.6). Other cover types were rarely selected. No difference ($P > 0.10$) was found in choice of cover type between morning and evening disturbances, although woodland cover was selected slightly more during evenings. Cover type selection varied slightly among individual leks, but was dominated by prairie in all cases (Table 3.7).

Activity of Displaced Male Grouse

Activity of radio-marked male sharptails during human disturbance during spring 1985 was dominated by sitting motionless (70%) (Table 3.8). A relatively large proportion (15%) of all observations were classified as 'unknown,' because observers were unable to accurately assess an individual bird's activity. No difference ($P > 0.10$) existed between morning and evening activity relative to disturbance, although display activity was negligible during evenings.

Response to Burning

Two large (approximately 4500 ha) controlled burns occurred over the area encompassing lek #'s 6, 7, 8, and 9 on 5 April 1984, and lek #'s 7, 8, 9, and B on 30 April 1985. Although not an experimental treatment of my study, observations of grouse activity were made at each affected lek the morning immediately after burning. In all cases, all radio transmitters were functioning and mean number of displaying males was no different ($P > 0.10$) from the 5-day pre-burn mean. Display activity at all burned leks continued through spring 1984 and 1985. No activity was observed at lek B pre- or post-burning in spring 1984 and 1985.

DISCUSSION

Sharp-tailed grouse were tolerant of all tested experimental lek disturbances (snow fencing, parked vehicles - running or not, propane 'bangers', scarecrows, scarecrows with tape-recorded voices, radio sounds, leashed dogs), except human presence. Males attempted to return to leks in the wake of each disturbance, likely to resume normal display activity. Only human disturbance efforts i.e., flushing, prevented males from regaining their territorial positions.

Female sharptails were not observed on any lek during treatments with any experimental disturbance; however, mating did occur on undisturbed control leks during the same time period. Thus, I suspect that females were affected in some way by all disturbances, even though males were tolerant of most.

K. M. Giesen (pers. commun.) and Grosz (1985) reported no apparent disturbance to sharptail mating activity from barbed wire fences crossing leks in Colorado and North Dakota. Snow fences used in my study did alter positions of males on leks and reduced their visibility, and may have decreased sound transmission, but had no detected effect on male display activity. Vehicular disturbance to mating activity is generally recognized by many grouse researchers to be negligible (K. M. Giesen, D. E. Sexton, pers. commun.), so it was not surprising to observe male sharptails on leks with vehicles present. Profera and Braun (1985) reported that this concept is being used by the Colorado Division of Wildlife in developing sage grouse viewing tours, although presence of females was apparent in their observations. No disturbance to male activity from propane 'bangers', scarecrows, and/or radio sounds was surprising, and not documented by other studies. Perhaps grouse in the study area were accustomed to noise and activity (including soldier silhouettes) from military training, and were therefore not displaced from leks. This finding requires additional study in non-military areas. Assuming the leashed dog to be similar to the effect from a natural predator such as a coyote, no displacement of males has also been noted by Twedt (1974) and R. E. Jones (pers. commun.).

Although not tested, observations at leks on agricultural areas as well as leks subjected to tank traffic, lead me to reject Hjorth's (1970) contention that tillage will cause a shift in location of sharptail leks. As Crawford and Bolen (1976b) noted, agricultural activity may not always lead to lek abandonment, but destruction of the lek and/or surrounding habitat will foster irregular use of a lek. Eng et al. (1979) and Tate et al. (1979) noted that strip mining operations will displace sage grouse from leks by eliminating advantages of the lek location. On the other hand, roadways, oil drilling pads, and even housing development on traditional leks have been reported not to affect grouse display activity (Udvary 1977, Taylor 1979, Horkel and Silvy 1980). In all cases, the improved visibility afforded by a raised landform or rooftop was suggested as the reason for lek maintenance at the disturbed location.

Although sharp-tailed grouse populations in Manitoba were generally considered to be low at the time of the study, the population that I worked with at CFB Shilo appeared to be high. A contributing factor to the apparently high population may be the schedule of military exercises; most begin in mid-May, generally after peak of sharptail mating. Training usually begins at 0800 and ends by 1500 hours, after and before peak morning and evening lek use times, respectively. The area is also closed to hunting. More important to the success of sharptails, however, is the regular pattern of burning which helps maintain an optimal habitat condition. Kirsch and Kruse (1973) reported that prairie fires were essential to maintaining the proper cover type for sharptail broods. Sexton and Gillespie (1979) noted that fire rekindled grouse use of a previously abandoned lek site by improving visibility. Fires on the study area probably help maintain much of the aspen parkland habitat in an equal mix of woodland versus grassland cover. Suppression of fires in other aspen parkland areas of Manitoba may have lead to declining habitat quality for sharptails because ecological succession has created mature stands of aspen.

My observation of female avoidance of treated leks during disturbance has not been previously reported. Although possibly coincidental or due to female recognition of observers in blinds, I suggest that this finding lends support to the female choice process of sexual selection and mate choice (Bradbury and Gibson 1983). Females did not mate with males on leks having potentially harmful disturbances. Females may have mated at other leks or not mated at all. Any choice made by a female was likely designed to increase her inclusive fitness. The limited effect on males of experimental disturbance could support either of Bradbury and Gibson's (1983) preferred models of lek formation. The 'hotspot' theory would be supported since males should attempt to remain at the maximum points of overlap of female home range, regardless of cost. Female home ranges may not have been affected since leks only were disturbed. The female preference for grouped males model would also be supported, since males of the affected generation should continue to clump at the location most favorable for mating in the past. Female avoidance of disturbed leks implies, however, that disturbed leks will contribute no genetic material to future generations.

Male sharp-tailed grouse displaced from traditional leks by human disturbance selected specific locations about 400 m from the traditional lek in a prairie or grassland cover type, and remained inactive during disturbance. Males from leks disturbed by human presence lose reproductive opportunity during the period of disturbance, and perhaps longer, depending on effects of disturbance on females. Continued disturbance at leks over several seasons could bring about population declines or a loss of genetic diversity. Although Tate et al. (1979) suggested that a sage grouse lek could be destroyed without affecting reproductive potential, my findings indicate that males from the affected lek may not reproduce. Reproductive potential of the population might only be maintained if females select another lek which affords them opportunities for mating or mate off lek.

The male response to lek disturbance for sharp-tailed grouse seems peculiar in terms of natural selection. Why do males simply appear to 'wait out' the disturbance? Were they able to mate with females at other times or off lek? Other than Sexton's (1979) report, no authors have indicated that mating in prairie grouse populations occurs other than on the lek ±1 hour from sunrise.

I suggest that leks of sharp-tailed grouse and other species are critical habitat components to individuals who traditionally use them. Males lose their reproductive opportunity when their traditional sites are disturbed, while females lose at least the genetic makeup from the males so affected.

MANAGEMENT IMPLICATIONS

Sharp-tailed grouse exhibit strong attachment to leks not only during spring mating but throughout the year (Twedt 1974). Although difficult to achieve, sharptails were displaced from traditonal leks by different experimental disturbances. Displaced males lose the reproductive opportunity by attempting to wait out the disturbance in close proximity to the traditional lek, but return to it upon cessation of the disturbance. Females, however, were not observed on treated leks at any time during disturbance.

Wildlife managers should consider the apparent impact on lekking grouse which occurs due to disturbance vs. the real effect on the population. Although grouse may continue to be observed at disturbed leks during spring, monitoring of mating activity may indicate that the site is reproductively inactive, since females avoid it consistently. Left to natural events, the lek population could disappear within 2 - 3 years. Consequences may include not only a loss of a lek population and genetic diversity, but also a decrease in a regional population of sharptails.

Lek sites which may be altered or eliminated through man-made events should be carefully surveyed prior to and during habitat alteration. If development can be realigned to avoid the lek, the population in the area may be maintained, provided that other necessary habitat components are not eliminated.

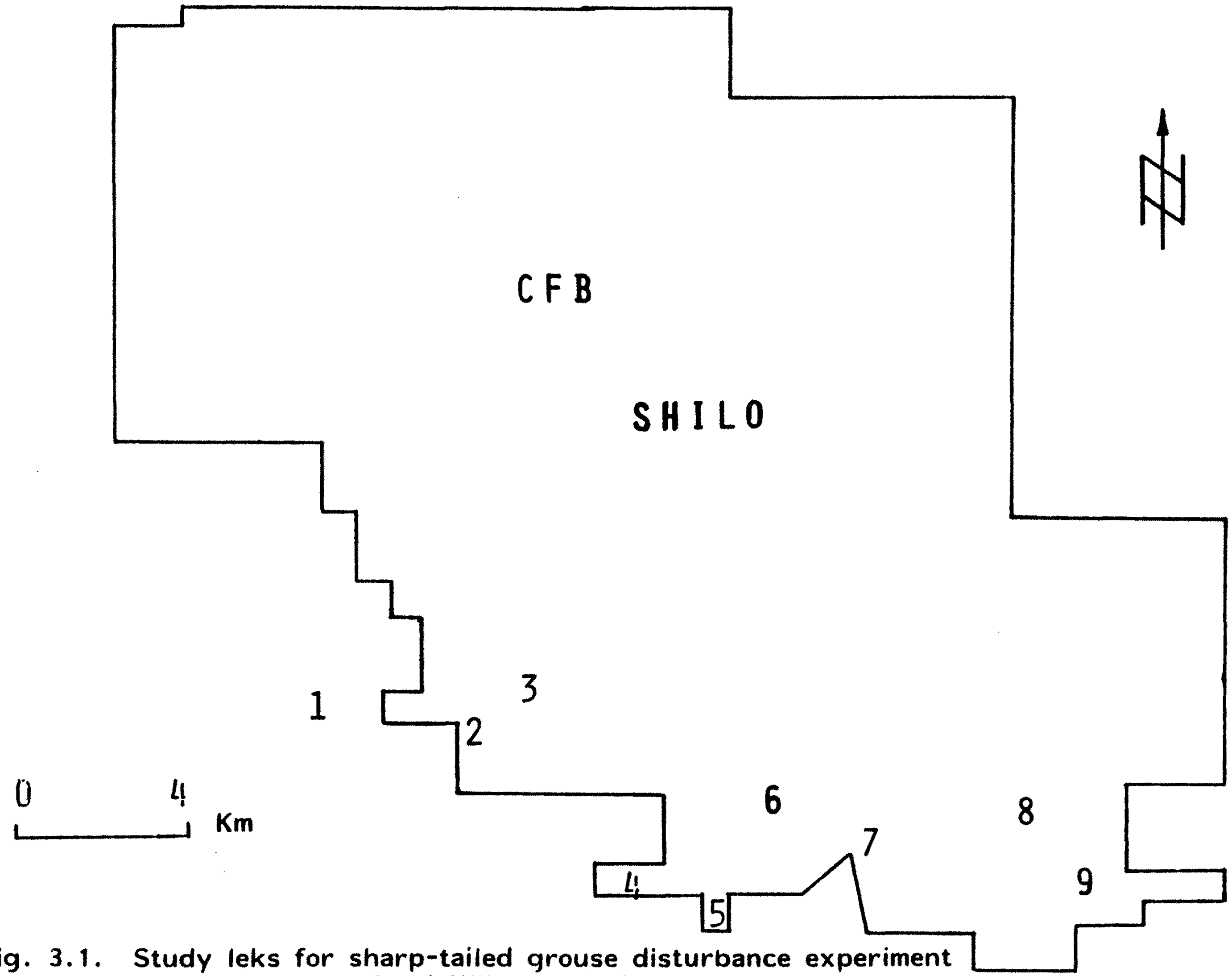

Fig. 3.1. Study leks for sharp-tailed grouse disturbance experiment in the Carberry Sand Hills, Manitoba, 1983-85.

Table 3.1. Experimental treatments for sharp-tailed grouse lek disturbance by human presence, 1984-85.

Lek number	Disturbance duration (days)		
	Spring 1984 (May-June)	Fall 1984 (Oct.-Nov.)	Spring 1985 (Apr.-May)
1	14	9	18
2	9	9	14
4	5	9	9
5 (control)	0	0	0
6 (control)	0	0	0
7	0	0	9
8	5	9	14
9	5	0	14

Table 3.2. Maximum number of displaying male sharp-tailed grouse per morning at study leks during spring 1984 disturbance treatments.

Treatment	Pre-disturbance[a]		Disturbance[b]	
	Range	Mean	Range	Mean
Snow fencing	9-16	13.0	7-15	12.0
Parked vehicle-engine on	12-16	13.8	12-15	13.0
Parked vehicle-engine off	10-17	13.8	10-13	12.0
Parked vehicle-radio on	4-16	12.0	7-13	10.5
Propane banger	6-18	13.0	9-15	11.5
Scarecrow	11-16	13.0	10-14	11.5
Scarecrow & taped voices	7-17	13.8	10-14	11.5
Radio on	11-15	12.0	11-14	12.0
Leashed dog	9-17	12.0	8-14	10.5
Human presence[c]	11-15	13.0	0	0.0
Undisturbed control	9-12	10.5	8-12	8.8

[a] 5-day pre-disturbance period at ≥ 2 study leks per treatment.
[b] ≥ 2-day disturbance period at ≥ 2 study leks per treatment.
[c] t test: $P < 0.01$.

Table 3.3. Maximum number of displaying male sharp-tailed grouse per morning at study leks during spring 1985 human lek disturbance.

Lek number	Pre-disturbance [a]		Disturbance [b]		*t* test *P* [c]
	Range	Mean	Range	Mean	
1	11-12	11.2	0	0.0	0.001
2	5-12	7.2	0	0.0	0.001
4	9-16	13.0	0	0.0	0.001
5[c]	4-10	5.0	2-8	4.3	0.825
6[c]	0-5	4.0	3-6	4.3	0.916
7	3-9	7.0	0	0.0	0.001
8	14-16	15.4	0	0.0	0.001
9	17-26	21.0	0	0.0	0.001

[a] 5 -day pre-disturbance period.
[b] *N* = days of treatment from Table 3.1.
[c] Pre-disturbance vs. disturbance means

Table 3.4 Displacement distance from traditional lek for radio-marked sharp-tailed grouse during spring 1985 lek disturbance.

Distance intervals(m)	Percent of observations		
	Total[a] (N=3214)	A.M.[b] (N=2208)	P.M.[c] (N=1006)
100	5.8	7.7	1.5
100-199	8.6	8.5	8.7
200-299	20.8	22.3	17.4
300-399	9.8	17.7	21.0
400-499	18.7	17.7	21.0
500-599	12.9	11.7	15.5
600-699	7.0	6.3	8.8
700-799	3.5	2.7	5.2
800-899	0.0	0.0	0.0
900-999	0.1	0.0	0.2
1000	10.9	10.6	11.5
Unknown	1.9	2.3	1.0
Totals	100	100	100
Mean	432.5	412.2	476.7
C V[d]	0.78	0.79	0.74
Median	400	400	400
Mode	200	200	400
Distribution type[e]	C	C	C

[a] The combination fo 3-hour morning and 2-hour evening distrubances.
[b] The 3-hour morning disturbance.
[c] The 2-hour evening distrubance.
[d] Coefficient of variation.
[e] C = clumped, Poisson distribution test for randomness, $P < 0.001$

Table 3.5. Mean and median displacement distances from study leks for radio-marked male sharp-tailed grouse during spring 1985 lek disturbance.

Lek number	$\bar{x}$(m)	C V[a]	Distribution type[b]	Median
1	356.2	0.52	C	300
2	288.6	0.74	C	200
4	765.0	0.59	C	600
5 (control)	0.0		C	
6 (control)	0.0			
7	239.5	0.55	C	200
8	263.1	0.59	C	300
9	367.8	0.45	C	400

[a] Coefficient of variation
[b] C = clumped, Poisson distribution test for randomness, $\underline{P}$ <0.001.

Table 3.6. Cover selection by displaced male sharp-tailed grouse during spring 1985 lek disturbance.

Cover type	Percent of observations		
	Total[a] (N=3214)	A.M.[b] (N=2208)	P.M.[c] (N=1006)
Prairie	90.2	92.1	86.1
Woodland	4.8	2.8	9.1
Shrub	0.3	0.2	0.5
Woodland-prairie edge	1.3	1.1	1.7
Unknown	3.5	3.9	2.5
Totals	100	100	100

[a] The combination of 3-hour morning and 2-hour evening disturbances.
[b] The 3-hour morning disturbance.
[c] The 2-hour evening disturbance.

Table 3.7. Cover selection by displaced male sharp-tailed grouse at individual leks during spring 1985 lek disturbance.

Lek number	Percent of observations[a] Prairie	Woodland	Shrub	Woodland-Prairie edge	Unknown	Totals %
1	86.7	7.3	0.8	0.3	3.9	100
2	97.8	2.2	0	0	0	100
4	92.3	3.5	0	0.5	3.7	100
7	90.4	5.3	0	0.9	3.4	100
8	95.0	1.8	0	2.9	0.3	100
9	79.5	7.1	0	8.2	5.2	100

[a] The combination of 3-hour morning and 2-hour evening disturbances.

Table 3.8. Activity patterns of displaced male sharp-tailed grouse during spring 1985 lek disturbance.

Activity	Percent of observations		
	Total[a] (N=3214)	A.M.[b] (N=2208)	P.M.[c] (N=1006)
Sitting	69.9	67.1	76.2
Displaying	5.4	7.8	0.1
Cooing	2.4	3.5	0.0
Walking	4.6	5.0	3.9
Pecking	1.8	2.4	0.3
Flying	0.6	0.5	0.7
Unknown	15.3	13.7	18.8
Totals	100	100	100

[a] The combination of 3-hour morning and 2-hour evening disturbances.
[b] The 3-hour morning disturbance.
[c] The 2-hour evening disturbance.

REPLACEMENT LEKS FOR DISPLACED SHARP-TAILED GROUSE

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INTRODUCTION

Loss of appropriate habitat for sharp-tailed grouse (*Tympanuchus phasianellus*) has been widely recognized as a major contributing factor to population and range reduction (Buss and Dziedzic 1955, Ammann 1963, Aldrich 1966, Evans 1968, Kirsch et al. 1973, Kobriger 1975, Sisson 1976, Brown 1978, Miller and Graul 1980, Kantrud 1981, Mattise et al. 1982, Nielsen and Yde 1982). As suggested by Ammann (1957) and Sisson (1976), meeting seasonal habitat requirements is essential to a successful sharptail population or transplant. Spring habitat selection by male sharp-tailed grouse is dominated by the traditional dancing ground or lek (East 1952, Ammann 1963, Lumsden 1965, Evans 1968, Hjorth 1970, Robel 1972, Rippin and Boag 1974, Kermott 1977, Moyles and Boag 1981). Loss of lek microhabitat may result in elimination of reproductive opportunities for male and female sharptails dependent on a particular location (Twedt 1974).

For other tetraonines, relocations of leks from areas of high human impact have been suggested or attempted, with some success in establishing breeding populations (Crawford and Bole 1976*b*, Eng et al. 1979, Taylor 1979, Horkel and Silvy 1980). Tate et al. (1979) speculated, however, that a sage grouse (*Centrocercus urophasianus*) lek can be destroyed without destroying reproductive potential. They claimed that protective measures designed to reclaim other sage grouse habitat components would be more useful.

The objective of this study was to test the feasibility of attracting displaced sharp-tailed grouse to replacement leks. I tested the hypothesis that replacement leks would attract ≥50% of the mean daily number of sharptails from leks experimentally disturbed. I also predicted that replacement leks would attract female sharptails attempting to select a mate for breeding.

STUDY AREA AND METHODS

The study was conducted in the Carberry Sand Hills, southwestern Manitoba, from June 1983 to May 1985. The study area is aspen parkland vegetation type, consisting of trembling aspen (*Populus tremuloides*) thickets interspersed with open prairie grassland. Major grasses include blue grama (*Bouteloua gracilis*), prairie junegrass (*Koeleria cristata*), and porcupine needlegrass (*Stipa spartea*). Average annual precipitation is 48 ± 3 cm, with most occurring as rain (Man. Dep. Mines, Resour., and Environ. Manage. 1977).

Eight study leks, each having one replacement lek (Fig. 4.1), were used to determine grouse use of replacement leks during morning (2 hr ≥ sunrise ≥ 1 hr) and evening (1 hr ≥ sunset ≥ 1 hr) disturbances. Lek #3 was designated as an alternate lek to be used in the event of abandonment of any other study lek. Human presence was selected as the most effective disturbance treatment to be used throughout this experiment.

Grouse were captured on leks in spring using two rectangular 1.8 x 3.7 m traps per lek. Traps were constructed with aluminum conduit frames (1.25-cm dia.), welded wire mesh (5.1 x 2.5 cm) sides, and nylon mesh (2.5 x 2.5 cm) tops, following K. M. Giesen (pers. commun.). Each side panel (1.2 x 0.9 or 1.8 m) had a 15 cm^2 opening with an inverted, woven wire funnel. Woven wire (0.9 x 50 m) leads were extended from each opening; but their use was discontinued after April 1984, because they did not improve trapping success. Trapping extended for a maximum of three mornings and evenings per lek, with trap positions alternated regularly.

Although K. M. Giesen (pers. commun.) reported success capturing male sharptails using traps with tape-recorded vocalizations, and placed at lek edges between leks and escape cover, I was unsuccessful using this approach. Males from my study leks would walk around or fly over traps and/or leads to regain their territories. Therefore, I repositioned traps regularly on each lek to cover the maximum number of male territories during a 3-day trapping period. To increase coverage, I supplemented the large rectangular traps with four smaller, circular, welded-wire mesh traps (0.9 m dia. x 0.5 m) having nylon mesh tops and a funnel entrance. Although these traps caught fewer grouse, they appeared to create confusion on leks and may have been responsible for increasing success in the larger traps.

Male decoys and tape-recorded vocalizations were used in each trap in March and April 1984. Female decoys in precopulatory position were used after April 1984, and they enhanced trapping success and reduced trapping effort. Woven wire leads were not required with female decoys.

Seventy-two male (45 adults, 27 juveniles) and six female (five adults, one juvenile) sharp-tailed grouse were trapped and banded. Grouse were classified as to sex using crown feather and tail covert patterns, and to age using the proximal primary technique (Wishart 1977). Twenty-five radio transmitters (22 solar-powered, three battery-powered) attached to ponchos (Amstrup 1980) were placed on grouse to ensure relocation of ≥2 males per lek using a hand-held Yagi antenna and receiver.

Disturbance and replacement treatments were randomly assigned to leks during spring 1984 and 1985 and fall 1984. Disturbance length was dependent on availability of field assistants. Sharptail decoys of male grouse and female grouse in precopulatory position were constructed from study skins. Sharptail vocalizations were recorded on continuous loop casette tapes.

Replacement lek sites were established in spring seasons at test distances of 200 or 400 m from traditional leks. Each designed replacement lek resembled the traditional site as closely as possible, with particular attention to specific criteria (Table 4.1). The replacement area was dependent on traditional lek area. Surrounding topography was flat to undulating. A location was selected where the elevation was approximately equal to or slightly greater than at the traditional lek. Although initially thought to be important for male grouse to observe predators and/or females, the elevated location probably provided improved visibility of replacement leks by displaced grouse. Each replacement lek was in full view from the traditional lek. Slopes at replacement leks were <1% on display areas. A lawn mower was used to mow vegetation to the spring measurement mean (approximately 10 cm). Visibility on replacement display areas was unrestricted in all directions. Ground cover was manipulated through removal where necessary to ensure the specified composition was achieved. Replacement locations were also selected to ensure minimum distances to escape cover and perching trees were met.

Some replacement leks were positioned in random directions at test distances. This technique of random placement was used to test whether decoys and tapes were responsible for attracting males to replacement leks as opposed to increasing the attractiveness of a designed site.

Data were analyzed using MANTES, SAS, and SPSS-X statistical packages on the University of Manitoba AMDAHL computer system. Use of replacement leks by displaced sharptails was analyzed using *t* tests.

RESULTS

Spring 1984

Male sharptails displaced from traditional leks from 8 May to 1 June 1984 were attracted only to replacement leks having the combination of male decoys, female decoys in precopulatory position, and tape-recorded grouse vocalizations (Table 4.2). Attracted males remained on replacement leks for varying lengths of time, some danced and displayed and attempted copulation with female decoys, but only if the human disturbance remained on the traditional lek. If disturbance ceased, displaced males returned to the traditional lek within 5 minutes. No males were attracted to the replacement lek near the undisturbed control lek, nor to replacement leks with only male decoys and tape-recorded vocalizations.

Although displaced males used replacement leks, attraction success was not complete (Table 4.2). Most displaced males would fly over or near the replacement lek at least once each morning, but were not counted as 'users' of the replacement lek unless they landed. Reduced counts from control lek #5 showed that mating activity was waning as the experiment progressed.

Similarly, few females (two on different mornings to replacement lek #1, and one to replacement lek #2) attended replacement leks where males were present. These females approached the replacement leks after perching in nearby trees, landed near the edge thereby inciting male activity, walked rapidly around the perimeter of the replacement, and flew back to escape cover within approximately 3 minutes. No copulations were observed on any leks in the study area after 15 May 1984, when the experiment was in progress, although females attended some other leks until at least 8 June 1984.

Fall 1984

Male sharptails displaced from traditional leks from 4 to 29 October 1984 were attracted during morning display periods only to designed replacement leks having male decoys, female decoys in precopulatory position, and tape-recorded grouse vocalizations (Table 4.3). No males were attracted to replacement leks that were near undisturbed control leks, nor to a randomly located replacement containing the same combination of decoys and tapes. When decoys and tapes were not set on replacement leks, no male sharptails were attracted. No females were observed at replacement or traditional leks during fall disturbance.

No success was achieved in attracting male sharptails to two previously abandoned leks (A and B) from 13 September to 1 October 1984. These leks were last recorded as active in spring 1983. Three, 5-day attraction periods using the same combination of decoys and tapes that was effective on replacement leks resulted in no sharptails attending these sites.

Spring 1985

Male sharptails displaced from traditional leks from 18 April to 24 May 1985 were attracted to five replacement leks, three of which were located at designed sites and two at random sites (Table 4.4). All successful replacement leks contained female and male decoys and tape-recorded grouse vocalizations. Use of two designed replacement leks (#'s 1 and 8) was greater ($\underline{P} < 0.05$) than for other replacement leks. Male sharptails were not attracted to replacement leks near undisturbed control leks, nor to one randomly located replacement. Mean number of sharptails per day attending leks was reduced from 1984 (Table 4.4).

Females were rarely observed at replacement leks during morning display periods, but allowed rejection of the null hypothesis of no female attendance. Female attendance incited increased male display activity. The general pattern of females was to land near the edge of the replacement lek, sit motionless for ≤2 minutes, walk onto the replacement lek, run across the replacement lek with ≥1 male in pursuit, and then flush to aspen cover ≤500 m distant. No copulations were observed on replacement leks, although males often mounted female decoys and attempted copulation.

Although use of some replacement leks by male sharp-tailed grouse appeared to be regular during experimental treatments, attendance time was limited (Table 4.5). Males tended to select replacement leks more often during morning than evening disturbance periods. Activity of male sharptails on replacement leks was dominated by sitting motionless, then displaying (Table 4.6). Activity patterns on replacement leks did not change between morning and evening. More display activity occurred on replacement leks than elsewhere off the traditional lek. (Table 4.7).

Yearly Comparison

Some replacement leks attracted ≥50% of the predisturbance mean number of sharptails per day, thus allowing rejection of the null hypothesis of <50% attendance (Tables 4.2 to 4.4). These replacement leks were always at designed locations and contained male decoys, female decoys in precopulatory position, and tape-recorded vocalizations. No randomly located nor control replacement leks attracted sufficient sharptails to allow rejection of the above null hypothesis for these cases. Replacement leks which attracted displaced males in spring 1984 were also used in fall 1984 and spring 1985.

DISCUSSION

Replacement leks were developed for sharp-tailed grouse that were unable to use their traditional location. The probability of success in attracting displaced males was <0.50, and much less for females. Although this success rate may appear rather low, no researchers have ever approached this level in past mitigation efforts.

Rogers (1985) attempted using male sharptail decoys and an audio system placed on an open site to simulate an artificial lek to increase success of sharptail releases in Kansas. In all cases, released birds remained ≤300 m from the artificial lek on the first morning. Rogers (1985) speculated that the number (20-25) of decoys and their aggregated position on the artificial site may have reduced the released males to subdominant birds. Clear evidence of established territories on the lek site was never obtained. Dominance hierarchies were apparently established on at least two replacement leks in my study, with juvenile males seeming to assume central positions. At these locations, marked juvenile males were the first to arrive at the replacement each day, and successfully defended the entire lek by chasing off approaching single males. Eventually, several males approached the replacement from different directions, and each was able to gain and subsequently defend a position peripheral to the original juvenile male. The fewer decoys (maximum of four) and use of precopulatory-position female decoys apparently improved success of replacement leks, however, the importance of proper placement of the new site cannot be discounted. Although Rogers (1985) selected an open site, little attention was paid to other important lek site criteria.

Two studies of sage grouse in Montana and Wyoming drew opposite conclusions from attempted mitigation of strutting ground loss by attracting displaced birds to alternative sites. Eng et al. (1979) reported success in relocating a lek about 3.2 km from the traditional site, with the assistance of silhouette decoys and tape-recorded sounds. Tate et al. (1979), however, had little success attracting sage grouse to an artificial lek. Displaced males selected a satellite lek rather than the totally new, albeit well-chosen, location. Although untested, movement of sharptail leks as far as 3.2 km seems highly unlikely, especially given the difficulty attracting birds to 200 or 400 m locations. Streeter et al. (1979) indicated that behavioral plasticity or adaptability of most wildlife species is not well known, especially for raptors and grouse, whose nests and leks have been moved no more than a few hundred meters. Unless the area ≤400 m from the traditional lek will be completely destroyed or disturbed for virtually 24 hours per day during spring mating, I recommend positioning replacement leks in these locations.

Work on prairie-chickens suggested that artificial leks, which simulate disturbed sites resulting from oil exploration and development, could be used to enhance populations (Crawford and Bolen 1976b, Taylor 1979, Horkel and Silvy 1980). None of the authors tested their strategies for constructing artificial leks, but their ideas were consistent with my findings. Use of elevated sites with unrestricted viewing horizons is essential to create viable artificial leks. I suggest that decoy and sound inducements would increase success in establishing continued use of the appropriate location.

MANAGEMENT IMPLICATIONS

A strategy to mitigate habitat loss of sharp-tailed grouse is needed wherever the species is facing population reductions. The technique described herein is a simple, low-cost approach to maintaining an important habitat requirement for sharptails, and appears applicable to other lekking grouse species. Although this technique was developed in an experimental context, it should be applicable as either a short- or long-term mitigation tool in cases of habitat alteration.

For example, strip mining may eliminate a lek site which could be temporarily relocated using the following criteria:

1. Replacement leks should be developed and maintained in the fall immediately preceding the first spring of desired use.
2. Replacement leks should resemble the traditional lek as closely as possible, especially with respect to orientation, observable landmarks, and flight lanes.
3. Replacement leks should be located as close to the traditional lek as possible, preferably <400 m.
4. Replacement lek elevation should be similar to traditional lek elevation, with a gentle slope (<1%) over the display area.

5. Vegetation height should be regularly maintained at ≤10 cm by mowing.
6. Visibility should be unrestricted in all directions.
7. Escape cover and trees for perching should be about 400 m from the replacement lek.
8. Male decoys and female decoys in precopulatory position should be constructed using mounted birds (Rogers (1985) suggested photographic posters of displaying males attached to plywood silhouettes) and maintained on the replacement from early February until late May.
9. Grouse vocalizations should be used on replacement leks for 3 hours each morning and evening by means of a continuous loop casette tape-recorder and a mechanized switching system.

Success of the technique is not certain, but it is recommended for use in situations where population reductions are occurring (certainly where the species is threatened or endangered). I estimate approximately 20 person-days per year during spring (two half-days per week) would be required to establish and maintain a replacement lek. Little equipment is required (tape recorder, tapes, speakers, mower, decoy equipment) and cost should not exceed $500 per lek per season. Cost-savings in staff time would be realized if a group of replacement leks were established near each other. I also recommend using the replacement lek procedure in transplant or re-establishment operations, where success has generally been limited due to dispersal of introduced birds (Johnsgard 1983).

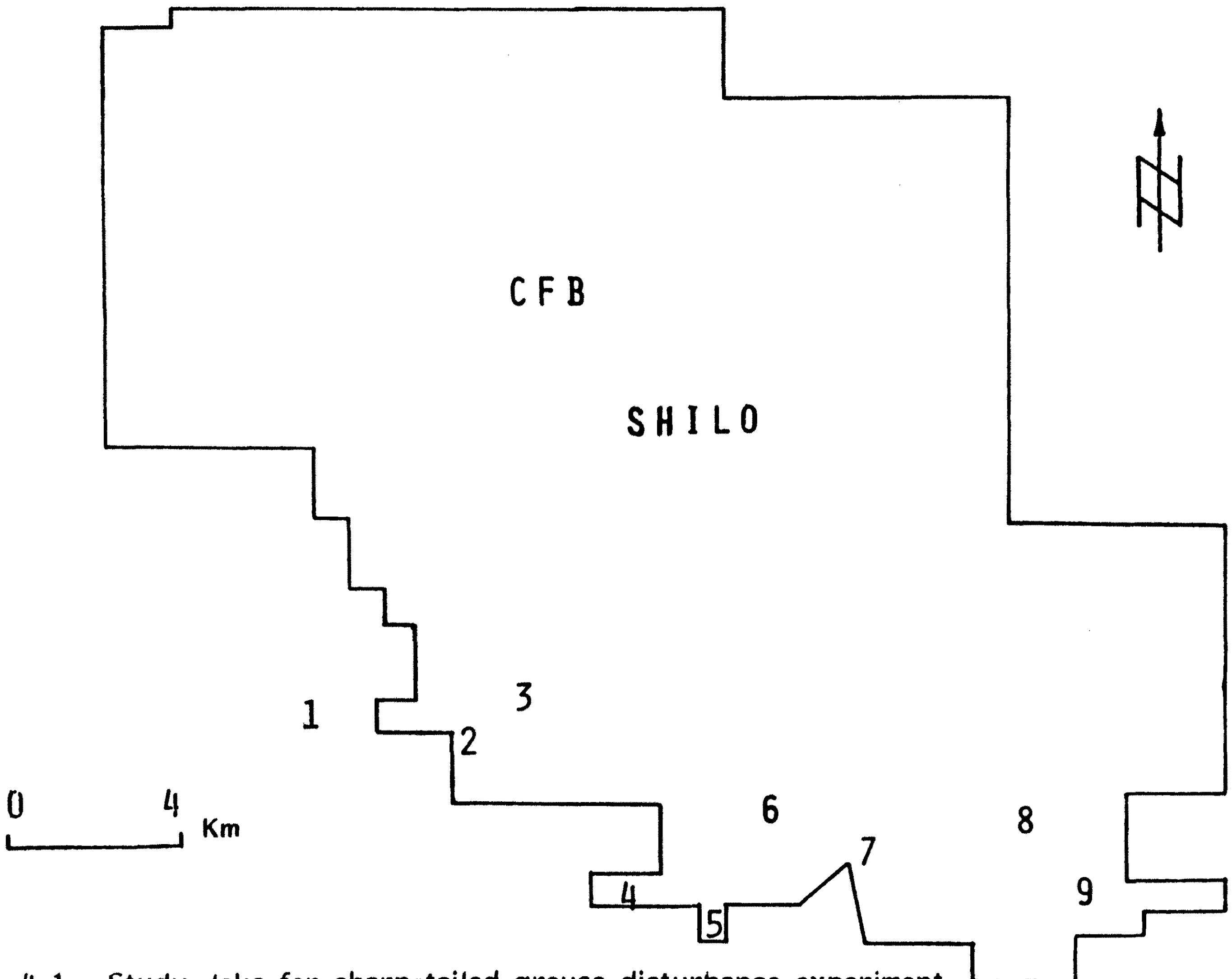

Fig. 4.1. Study leks for sharp-tailed grouse disturbance experiment in the Carberry Sand Hills, Manitoba, 1983-85.

Table 4.1 Environmental characteristics of study leks used in design of replacement leks.

Component	Measurement
Nest nearest lek	1.7 - 2.9 km, $\bar{x}$ = 2.2 km
Orientation	NW to SE
Area	100-1220 m^2, $\bar{x}$ = 446 m^2
Surrounding terrain	Flat to undulating, generally lower elevation
Slope	≤1% over display area
Vegetation height in spring	7 - 13 cm, $\bar{x}$ = 10.4 cm
Ground cover in spring	
shrub	≤1%
forb	15%
grass	70%
bare ground	15%
Visibility	Unrestricted in all directions, 70-80% on display area.
Distance to escape cover	≤500 m
Distance to perching trees	≤400 m

Table 4.2. Use of replacement leks by displaced sharp-tailed grouse during spring 1984 lek disturbance.

Lek number	Replacement location[a]	Replacement characteristics[b]	Disturbance (days)	Replacement use[c]	
				A.M.[d]	P.M.[e]
1	200	F	14	11(63)	10(48)
2	200	F	9	6(50)	1(2)
4	200	M	5	0	0
5 (control)	200	F	0	0	0
8	400	M	5	0	0
9	400	M	5	0	0

[a] All replacements located by design at approximate distance (m) from traditional lek.
[b] M = male decoys and tape-recorded vocalizations; F = female & male decoys & tape-recorded vocalizations.
[c] Days used and (% disturbance/predisturbance mean number males); predisturbance counts at traditional lek, disturbance counts at replacement.
[d] Use during 2 hr $\geq$ sunrise $\geq$ 1 hr.
[e] Use during 1 hr $\geq$ sunset $\geq$ 1 hr.

Table 4.3. Use of replacement leks by displaced sharp-tailed grouse during fall 1984 lek disturbance.

Lek number	Replacement location[a]	Disturbance (days)	Replacement use(days)[b]	% males[c]
1	D-200	9	7	49
2	D-200	9	5	42
4	R-200	9	0	0
5 (control)	D-200	0	0	0
8	D-400	9	6	13
9 (control)	R-400	0	0	0

[a] R = replacement located at random; D = replacement located by design; number refers to distance (m) from traditional lek. All replacements had male and female decoys and tape-recorded vocalizations.

[b] Use during 2 hr $\geq$ sunrise $\geq$ 1 hr.

[c] % disturbance/predisturbance mean number of males.

Table 4.4. Use of replacement leks by displaced sharp-tailed grouse during spring 1985 lek disturbance.

Lek number	Replacement location [a]	Disturbance (days)	Replacement use[b] A.M.[c]	Replacement use[b] P.M.[d]
1	D-200	18	16[e](47)	5(26)
2	D-200	14	4(14)	0
4	R-200	9	0	0
5 (control)	D-200	0	0	0
6 (control)	R-400	0	0	0
7	R-400	9	1(6)	0
8	D-400	14	6[f](30)	3(27)
9	R-400	14	4(4)	0

[a] R = replacement located at random; D = replacement located by design; number refers to distance (m) from traditional lek. All replacements had male and female decoys and tape-recorded vocalizations.

[b] Days used and (% disturbance/predisturbance mean number males); predisturbance counts at traditional lek, disturbance counts at replacement.

[c] Use during 2 hr ≥sunrise ≥ 1 hr.

[d] Use during 1 hr ≥sunset ≥ 1 hr.

[e] Female sharptail attendance on 3 days.

[f] Female sharptail attendance on 2 days.

Table 4.5. Percent use time of replacement leks by radio-marked sharp-tailed grouse males during spring 1985 lek disturbance.

Lek number	Percent of disturbance time Total[a]	A.M.[b]	P.M.[c]
1	21.0	25.4	11.8
2	4.7	6.9	0.0
7	1.8	2.5	0.0
8	38.8	37.5	41.3
9	5.2	7.9	0.0

[a] Use during the combination of 3-hour morning and 2-hour evening peak-display periods.
[b] Use during 2 hr ≥ sunrise ≥ 1 hr.
[c] Use during 1 hr ≥ sunset ≥ 1 hr.

Table 4.6. Activity of radio-marked male sharp-tailed grouse while on replacement leks during spring 1985 lek disturbance.

Lek number	A.M.[a] Sitting	A.M.[a] Displaying	P.M.[b] Sitting	P.M.[b] Displaying
1	88.4	11.6	100.0	0
2	100.0	0		
7	100.0	0		
8	41.4	58.6	100.0	0
9	28.6	71.4		

[a] Percent of time while on replacement from 2 hr ≥ sunrise ≥ 1 hr.
[b] Percent of time while on replacment from 1 hr ≥ sunset ≥ 1 hr.

Table 4.7. Display activity at individual leks by displaced male sharp-tailed grouse during spring 1985 lek disturbance.

Lek number	% display activity on replacement	% display activity off replacement
1	100.0	0
2	0	100.0
4	0	100.0
7	50.0	50.0
8	71.3	28.7
9	71.4	28.6
Mean	66.6	33.3

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