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1 : Any update?

Greater sage-grouse *Centrocercus urophasianus* migration links the USA and Canada: a biological basis for international prairie conservation

JASON D. TACK, DAVID E. NAUGLE, JOHN C. CARLSON and PAT J. FARGEY

Abstract Migratory pathways in North American prairies are critical for sustaining endemic biodiversity. Fragmentation and loss of habitat by an encroaching human footprint has extirpated and severely truncated formerly large movements by prairie wildlife populations. Greater sage-grouse *Centrocercus urophasianus*, a Near Threatened landscape species requiring vast tracts of intact sagebrush *Artemisia* spp., exhibit varied migratory strategies across their range in response to the spatial composition of available habitats. We unexpectedly documented the longest migratory event ever observed in sage-grouse (> 120 km one way) in 2007–2009 while studying demography of a population at the north-east edge of their range. Movements that encompassed 6,687 km² included individuals using distinct spring and summer ranges and then freely intermixing on winter range in what is probably an obligate, annual event. The fate of greater sage-grouse in Canada is in part dependent on habitat conservation in the USA because this population spans an international border. Expanding agricultural tillage and development of oil and gas fields threaten to sever connectivity for this imperilled population. Science can help delineate high priority conservation areas but the fate of landscapes ultimately depends on international partnerships implementing conservation at scales relevant to prairie wildlife.

Keywords Canada, *Centrocercus urophasianus*, Near Threatened species, greater sage-grouse, transboundary conservation, migration, prairie, USA

Introduction

Migration is an adaptive behavioural trait that allows individual organisms to capitalize on resources that fluctuate in time and space. Despite energetically costly movements, selective forces increase individual fitness when resource scarcity or crowding by conspecifics makes

habitats more risky or less attractive (Dingle & Drake, 2007). Migration conjures up images of thousands of wildebeest *Connochaetes taurinus* thundering across the Serengeti (Boone et al., 2008) or pods of humpback whales *Megaptera novaeangliae* on their annual journey from Antarctica to Central America (Rasmussen et al., 2007). However, migratory pathways in prairie ecosystems that sustain endemic North American fauna are poorly conserved but equally important to global biodiversity. The loss of long-distance movements in North America's sole surviving endemic ungulate, the pronghorn *Antilocapra americana*, typify the inability of small prairie reserves to sustain migratory populations (Berger, 2004). Prairie conservation supports sedentary populations within a patchwork of fragments that, at times, result in inadvertent loss of stepping stones necessary to maintain migratory species. Maintaining connectivity in large and intact grasslands should be a primary conservation objective before opportunities to do so are lost.

Greater sage-grouse *Centrocercus urophasianus* (hereafter sage-grouse), categorized as Near Threatened on the IUCN Red List (BirdLife International, 2008), are representative of the struggle to maintain biodiversity in a landscape that bears the debt of ever-increasing demands for natural resources (Knick et al., 2003). Expansion of the human footprint (Leu et al., 2008) continues to fragment the once vast tracts of sagebrush (*Artemisia* spp.)-dominated grasslands that sage-grouse require for each stage of their life-history (Connelly et al., 2000). This association is strongest in winter when sage-grouse forage in large dense stands of sagebrush that remain above snow (Homer et al., 1993; Doherty et al., 2008). This behaviour accounts for a diet of > 94% sagebrush in winter (Remington & Braun, 1985) and results in high survival and weight gain for sage-grouse (Beck & Braun, 1978). Sage-grouse conservation has largely focused on protecting nesting and brood-rearing habitats adjacent to leks because tracking research has largely focused on habitat around nest sites and brood-use locations (Connelly et al., 2000; Hagen et al., 2007). However, recent findings show severe winter weather can decrease survival (Moynahan et al., 2006) and that human disturbance degrades otherwise suitable winter habitat (Doherty et al., 2008; Carpenter et al., 2010).

Divergent migratory strategies across the range of sage-grouse reflect the variation in distribution and abundance of available habitats. Non-migratory populations fulfil

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annual habitat requirements within overlapping seasonal ranges, while populations that are obligate or partial migrants occupy spatially distinct breeding, summer or winter ranges (Beck et al., 2006). Conservation plans often delineate bird concentration areas but lack the information on movement necessary to identify areas that support entire populations. One population in south-east Idaho travels c. 80 km between summer and winter (Connelly et al., 1988; Leonard et al., 2000) and individuals from a nearby population move < 5 km between fall and winter (Beck et al., 2006). Identifying migratory pathways provides the biological basis for maintaining connectivity and conveys to decision makers the size of prairie landscapes necessary to support migratory populations.

We report the discovery of the longest documented migration ever recorded for any prairie grouse species. We found that sage-grouse in this population nested and raised broods in plains silver sagebrush *Artemisia cana cana* habitats but were surprised when birds moved up to 122 km south to winter in Wyoming big sagebrush habitats *Artemisia tridentata wyomingensis*. Birds probably migrated from sparse silver sagebrush to tall dense stands of big sagebrush in search of a more reliable food source in winter. This study includes individuals captured in the largest remaining active lek (communal breeding ground) in Canada. Our objectives are to (1) demonstrate that the fate of sage-grouse in Canada partly depends upon conservation efforts in the USA, (2) identify human stressors that could sever connectivity between countries, and (3) pinpoint the northern Great Plains as a high conservation priority internationally.

Study area

Our study area covered portions of Phillips and Valley counties in Montana, USA, and south-central Saskatchewan, Canada (Fig. 1). North of the Milk River is a short grass prairie ecosystem with a predominately native understorey of western *Agropyron smithii* and northern *Agropyron dasytachyum* wheatgrass communities. Plains silver sagebrush occurs in dense patches along linear overflow areas in the banks of seasonal streams and in sparse clumps in upland grasslands. A similar grassland understorey is found south of the Milk River but with a dominant shrub cover of Wyoming big sagebrush. Big sagebrush is a denser, more ubiquitous shrub than silver sagebrush, with large tracts (> 100 ha) occurring in uplands. Mean minimum temperatures in winter are -6.3°C , with a mean snowfall of 400 mm.

Methods

We captured 80 female sage-grouse on leks in northern Valley County, Montana, and in the East Block of Grasslands

National Park, Saskatchewan, during the spring breeding seasons of 2007 and 2008 (Fig. 1). Sage-grouse were classified as yearlings or adults based on primary feather development (Eng, 1963). Females were fitted with a 22 g necklace-style radio collar with an 18 h mortality switch (Advanced Telemetry Systems; Isanti, USA). Females were then banded with a size 20, individually-numbered, aluminium band (National Band and Tag Co., Newport, USA). We intensively followed marked birds from March to September, and conducted six flights each winter between November and March in 2008 and 2009 to relocate radio-marked females from a fixed-wing aircraft at 300–600 m above ground level (AGL). We circled marked birds at 30–100 m AGL until we reached maximum signal strength, and recorded their location with a global positioning system (GPS). We had an independent source place 10 collars within the study area near known winter locations in habitat similar in vegetation and ruggedness to estimate location error. We calculated the distance between recorded and known locations of the training collars and used the maximum value (105 m) as our resolution to estimate locations.

This population used overlapping ranges during breeding and summer seasons and individuals were considered migratory if they made movements > 10 km from their capture location on leks to winter locations (Connelly et al., 2000). The distance to suitable winter habitat may be constrained by lek location and we stratified measurements for each lek where females were captured. We measured the distance individuals moved between consecutive flights to document movements within winter habitat and divided the measurement by the number of days between flights. We used a 100% minimum convex polygon to calculate the area encompassed by the outermost extent of radio-marked bird locations.

Juvenile sage-grouse may seasonally disperse further than adults in some landscapes (Dunn & Braun, 1985; Connelly et al., 1988; Beck et al., 2006). We could not test for differences in movements between juveniles and adults because females captured at leks had already survived more than one winter. However, juveniles may still be imprinting on winter ranges and could make larger movements than adults if they are still seeking high quality habitat. We tested whether yearling and adults differed in mean distances moved from summer to wintering range, and within their winter range, to explore this hypothesis.

Results

We obtained 209 locations from 39 individuals on 12 flights between 26 January 2008 and 3 March 2009. Each radio-marked individual moved > 21 km from summer to winter ranges and 122 km was the longest documented movement (Table 1). All but five of the 209 locations were south of the Milk River in big sagebrush habitat (Fig. 1). We recorded

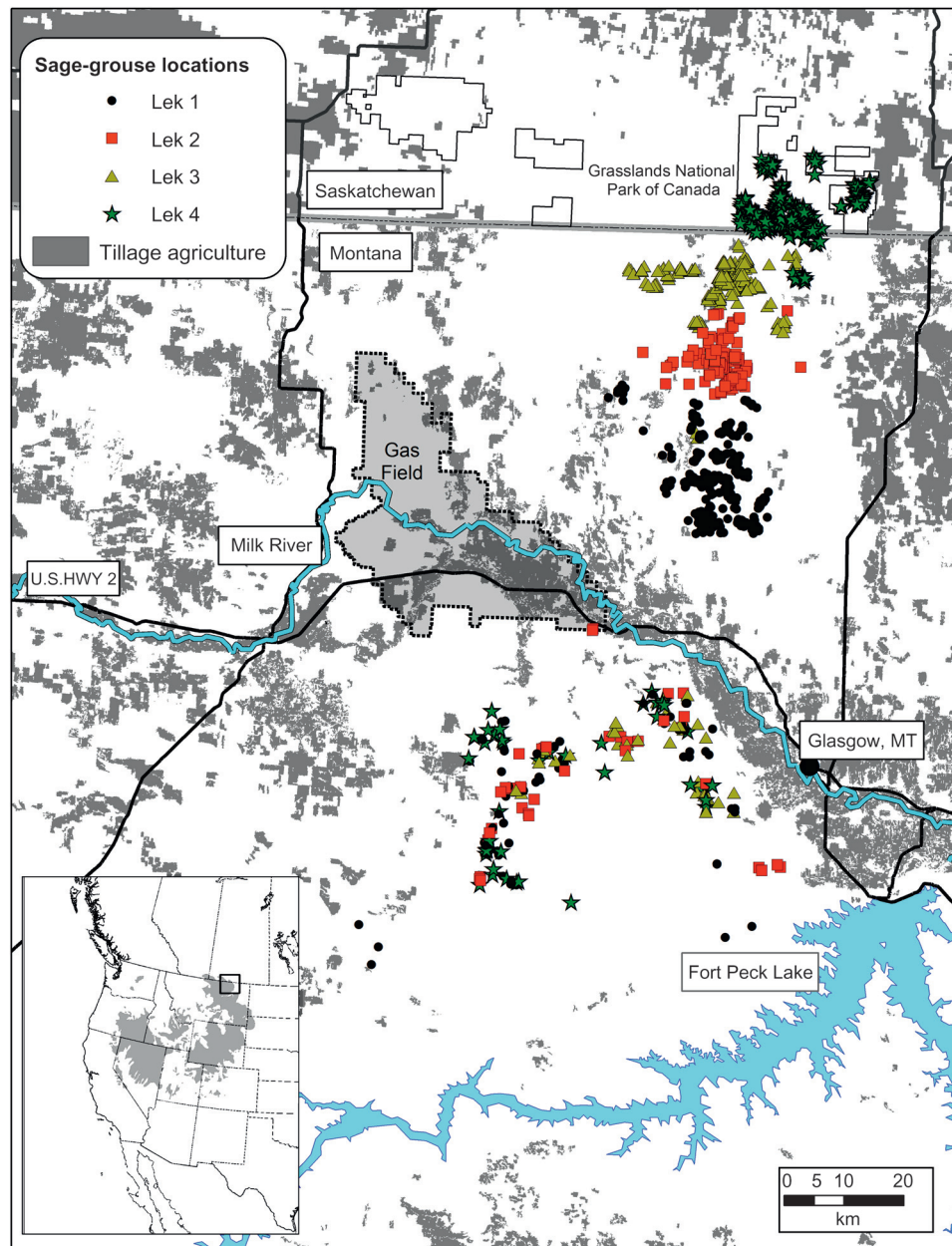


Fig. 1 Female greater sage-grouse *Centrocercus urophasianus* locations in spring and summer (north of Milk River) and winter (south of Milk River) in north-eastern Montana and the East Block of Grasslands National Park, Saskatchewan. The rectangle on the inset depicts the current occupied range of the species (Schroeder et al., 2004).

our last summer locations on 9 and 15 September in 2007 and 2008, respectively. All sage-grouse had migrated by our earliest winter flight on 17 November 2008 and were still on winter range on 16 March 2009. We documented females attending leks north of the Milk River as early as 22 March 2008. Dispersal distances were similar between yearlings and adults and therefore we combined estimates by lek (Table 1). Distances migrated by lek differed because some leks were further north of the winter range. We also pooled individual movements between winter locations because yearling and adult movements were similar ($P = 0.31$). We assumed movements between females from

different leks were similar once individuals had reached winter habitat.

Females on winter range moved an average of 250 m per day, assuming straight-line uniform movements between flight intervals, with some movements estimated > 2.5 km per day. We relocated eight females more than two times each winter. Three of the eight females overlapped a portion of areas used in both winters and the remaining five females were located 1–25 km from the previous year's location. Females mixed freely with individuals from other capture leks (Fig. 1). During flights we relocated several flocks that contained radio-marked females from multiple capture

TABLE 1 Mean distance (with range) moved by radio-marked female greater sage-grouse *Centrocercus urophasianus* from four breeding leks (Fig. 1) to their winter range in north-eastern Montana and south-central Saskatchewan in 2007–2009.

Lek	No. of individuals	No. of locations	Mean distance of lek to winter location (range), km
1	16	77	58.3 (21.5–98.1)
2	8	39	77.4 (53.9–100.1)
3	9	45	78.7 (70.6–93.7)
4	11	45	97.3 (61.1–122.1)

leks. The outermost extent of radio-marked bird locations recorded was 6,687 km².

Discussion

The migratory movements we documented are probably annual obligate movements, not dependent on extreme winter weather events. We recorded all individuals moving > 20 km in consecutive seasons including a winter with the lowest snowfall recorded in 30 years (Opheim 12 SSE Weather Station, U.S. National Climatic Data Center). Migratory movements we observed are not a mechanism for dispersal because adult females returned to leks north of the Milk River in subsequent years. We cannot infer the same for males or juveniles because females captured at leks had already survived more than one winter. We may be missing an age- or sex-specific trait of dispersal by examining only females that survived more than one winter over 2 years. Genetic evidence suggests that populations north and south of the Milk River are distinct but a few individuals from south of the Milk River assigned to leks in Alberta, Canada (Bush et al., 2011).

Sage-grouse probably migrated because breeding areas lack sufficient sagebrush cover in winter. Females breeding in silver sagebrush habitats north of the Milk River used distinct areas on breeding and summer ranges (Fig. 1). Sage-grouse migrated to winter range in big sagebrush habitat south of the Milk River by early November, where birds captured from different leks mixed freely with each other in wintering areas (Fig. 1). Sage-grouse in nearby Alberta, Canada, use silver sagebrush habitats in winter with high apparent survival (73–88%; J. Carpenter, pers. comm.). Silver sagebrush in Alberta has larger remaining tracts and higher densities of silver sagebrush in uplands than Saskatchewan.

We are concerned that expanding human development could degrade otherwise suitable winter habitat. Expanding agricultural tillage results in loss of sagebrush habitat and wintering sage-grouse avoid otherwise high quality winter habitat as well density from oil and gas development increases (Doherty et al., 2008). Agricultural tillage continues to encroach upon sagebrush habitat along the Milk

River and radio-marked females spent the winter near a developed portion of the Bowdoin gas field south of Hinsdale, Montana (Fig. 1). Winter habitat will be reduced if agricultural tillage continues along the Milk River or if oil and gas development expands into authorized leases south of U.S. Highway 2 (Fig. 1). Understanding how and when sage-grouse migrate is pivotal in understanding the mechanisms of large movements and the role of transitional habitat in facilitating long and presumably costly movements. Maintaining connectivity between seasonal ranges requires knowing if and how sage-grouse use transitional habitats. Habitat use along migratory pathways remains unknown because VHF technology cannot keep pace with the timing and distance of migratory movements.

New GPS technology provides the ability to identify potential habitat pathways between seasonal ranges. Large deciduous trees line the banks of the Milk River and there is c. 10 km wide strip of agricultural tillage running the length of the river (Fig. 1), both inhospitable habitats to the sagebrush-dependent sage-grouse (Doherty et al., 2008). If there are corridors that sage-grouse rely upon to connect summer and winter habitats, these may be at risk from conversion to agriculture or increased development of oil and gas fields (Fig. 1). Identifying potential bottlenecks that restrict movement will be paramount to conserving this unique migratory event. Migratory movements add urgency to maintaining populations that transcend international boundaries because sage-grouse are an endangered species in Canada under the federal Species at Risk Act.

Extraordinary movements point to an important wintering area for sage-grouse that is a high priority for transboundary conservation. The winter range we observed is probably used by a large population of sage-grouse south of the Milk River, an area with some of the highest sage-grouse densities in their eastern range (Doherty et al., 2010). Our winter locations overlapped leks in big sagebrush, and several times we observed radio-marked individuals in flocks of > 100 birds, abundances probably higher than the entire Saskatchewan population of sage-grouse. Conservation of sage-grouse habitat in Montana will in part affect the viability of endangered sage-grouse in Canada.

The number of species that make disproportionately large movements has initiated a rethink regarding the land area necessary to conserve biodiversity in the northern Great Plains. The migratory sage-grouse population we studied encompasses 6,687 km², an area 30 times larger than the East Block of Grasslands National park (218 km²; Fig. 1). Similarly, reintroduced swift fox *Vulpes velox* dispersal distances (190 km) in Montana, Alberta and Saskatchewan (Ausband & Moehrenschrager, 2009) exceeds that of other populations, prairie rattlesnakes *Crotalus viridis viridis* in south central Alberta migrate farther (> 52 km) than any other terrestrial snake (Jorgensen et al., 2008), and pronghorn regularly migrate > 100 km

between Saskatchewan and Montana (A. Jakes, unpubl. data). Science can help decision makers identify the size and location of landscapes to prioritize for conservation. Nevertheless, the fate of remaining large and intact prairie landscapes ultimately depends on our ability to foster partnerships that result in implementation of long-term conservation.

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References

- AUSBAND, D. & MOEHRENSCHLAGER, A. (2009) Long-range juvenile dispersal and its implication for conservation of reintroduced swift fox *Vulpes velox* populations in the USA and Canada. *Oryx*, 43, 73–77.
- BECK, J.L., REESE, K.P., CONNELLY, J.W. & LUCIA, M.B. (2006) Movements and survival of juvenile greater sage-grouse in south-eastern Idaho. *Wildlife Society Bulletin*, 34, 1070–1078.
- BECK, T.D. & BRAUN, C.E. (1978) Weights of Colorado sage-grouse. *Condor*, 80, 241–243.
- BERGER, J. (2004) The last mile: how to sustain long-distance migration in mammals. *Conservation Biology*, 18, 320–331.
- BirdLife International (2008) *Centrocercus urophasianus*. In *IUCN Red List of Threatened Species v. 2010.4*. <http://www.iucnredlist.org>, accessed 8 April 2011.
- BOONE, R.B., THIRGOOD, S.J. & HOPCRAFT, J.G. (2008) Serengeti wildebeest migratory patterns modelled from rainfall and new vegetation growth. *Ecology*, 87, 1987–1994.
- BUSH, K., DYTE, C., MOYNAHAN, B., ALDRIDGE, C., SAULS, H., BATTAZO, A.M. et al. (2011) Population structure and genetic diversity of greater sage-grouse (*Centrocercus urophasianus*) in fragmented landscapes at the northern edge of their range. *Conservation Genetics*, 12, 527–542.
- CARPENTER, J., ALDRIDGE, C. & BOYCE, M. (2010) Sage-grouse habitat selection during winter in Alberta. *Journal of Wildlife Management*, 74, 1806–1814.
- CONNELLY, J.W., BROWERS, H.W. & GATES, R.J. (1988) Seasonal movements of sage-grouse in south-eastern Idaho. *The Journal of Wildlife Management*, 52, 116–122.
- CONNELLY, J.W., SCHROEDER, M.A., SANDS, A.R. & BRAUN, C.E. (2000) Guidelines to manage sage-grouse populations and their habitats. *Wildlife Society Bulletin*, 28, 967–985.
- DINGLE, H. & DRAKE, V.A. (2007) What is migration? *Bioscience*, 57, 113–121.
- DOHERTY, K.E., NAUGLE, D.E., COPELAND, H., POCEWICZ, A. & KIESECKER, J. (2011) Energy development and conservation trade-offs: systematic planning for greater sage-grouse in their eastern range. *Studies in Avian Biology*, in press.
- DOHERTY, K.E., NAUGLE, D.E., WALKER, B.L. & GRAHAM, J.M. (2008) Greater sage-grouse winter habitat selection and energy development. *Journal of Wildlife Management*, 72, 187–195.
- DUNN, P.O. & BRAUN, C.E. (1985) Natal dispersal and lek fidelity of sage-grouse. *The Auk*, 102, 621–627.
- ENG, R.L. (1963) Observations on the breeding biology of male sage-grouse. *The Journal of Wildlife Management*, 27, 841–846.
- HAGEN, C.A., CONNELLY, J.W. & SCHROEDER, M.A. (2007) A meta-analysis of greater sage-grouse *Centrocercus urophasianus* nesting and brood-rearing habitats. *Wildlife Biology*, 13, 42–50.
- HOMER, C.G., EDWARDS, JR, T.C., RAMSEY, R.D. & PRICE, K.P. (1993) Use of remote sensing methods in modelling sage-grouse winter habitat. *The Journal of Wildlife Management*, 57, 78–84.
- JORGENSEN, D., GATES, C. & WHITESIDE, D. (2008) Movements, migrations, and mechanisms: a review of radiotelemetry studies of prairie (*Crotalus v. viridis*) and western rattlesnakes (*Crotalus oreganus*). In *The Biology of Rattlesnakes* (eds W.K. Hayes, M.D. Cardwell, K.R. Beamen & S.P. Bush), pp. 303–316. Loma Linda University Press, Loma Linda, USA.
- KNICK, S.T., DOBKIN, D.S., ROTENBERRY, J.T., SCHROEDER, M.A., VANDER HAEGEN, W.M. & VAN RIPER, III, C. (2003) Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *The Condor*, 105, 611–634.
- LEONARD, K.M., REESE, K.P. & CONNELLY, J.W. (2000) Distribution, movements and habitats of sage-grouse *Centrocercus urophasianus* on the Upper Snake River Plain of Idaho: changes from the 1950s to the 1990s. *Wildlife Biology*, 6, 265–270.
- LEU, M., HANSER, S.E. & KNICK, S.T. (2008) The human footprint in the west: a large-scale analysis of anthropogenic impacts. *Ecological Applications*, 18, 1119–1139.
- MOYNAHAN, B.J., LINDBERG, M.S. & THOMAS, J.W. (2006) Factors contributing to process variance in annual survival of female greater sage-grouse in Montana. *Ecological Applications*, 16, 1529–1538.
- RASMUSSEN, K., PALACIOS, D.M., CALAMBOKIDIS, J., SABORÍO, M.T., DALLA ROSA, L., SECCHI, E.R. et al. (2007) Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. *Biology Letters*, 3, 302.
- REMINGTON, T.E. & BRAUN, C.E. (1985) Sage-grouse food selection in winter, North Park, Colorado. *The Journal of Wildlife Management*, 49, 1055–1061.
- SCHROEDER, M.A., ALDRIDGE, C.L., APA, A.D., BOHNE, J.R., BRAUN, C.E., BUNNELL, S.D. et al. (2004) Distribution of sage-grouse in North America. *The Condor*, 106, 363–376.

Biographical sketches

JASON TACK has worked on sage-grouse habitat and conservation issues for the past 4 years in Montana and Saskatchewan, and DAVID NAUGLE's applied research focuses on creating conservation planning tools for focal species in the mid continent and western grasslands of the USA. Together, they are creating conservation planning tools for sage-grouse populations range-wide. JOHN CARLSON is a wildlife biologist and PAT FARGEY a species-at-risk biologist, and for the past 10 years they have been helping guide research to effectively manage transboundary conservation issues in the northern Great Plains.