Wildlife Monographs 175:1–38; 2011; DOI: 10.1002/wmon.1

Geographic Distribution of the Mid-Continent Population of Sandhill Cranes and Related Management Applications

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ABSTRACT The Mid-continent Population (MCP) of sandhill cranes (*Grus canadensis*) is widely hunted in North America and is separated into the Gulf Coast Subpopulation and Western Subpopulation for management purposes. Effective harvest management of the MCP requires detailed knowledge of breeding distribution of subspecies and subpopulations, chronology of their use of fall staging areas and wintering grounds, and exposure to and harvest from hunting. To address these information needs, we tagged 153 sandhill cranes with Platform Transmitting Terminals (PTTs) during 22 February–12 April 1998–2003 in the Central and North Platte River valleys of south-central Nebraska. We monitored PTT-tagged sandhill cranes, hereafter tagged cranes, from their arrival to departure from breeding grounds, during their fall migration, and throughout winter using the Argos satellite tracking system. The tracking effort yielded 74,041 useable locations over 49,350 tag days; median duration of tracking of individual cranes was 352 days and 73 cranes were tracked >12 months. Genetic sequencing of mitochondrial DNA (mtDNA) from blood samples taken from each of our random sample of tagged cranes indicated 64% were *G. c. canadensis* and 34% were *Grus canadensis tabida*. Tagged cranes during the breeding season settled in northern temperate, subarctic, and arctic North America (U.S. [23%, $n = 35$], Canada [57%, $n = 87$]) and arctic regions of northeast Asia (Russia [20%, $n = 31$]). Distribution of tagged cranes by breeding affiliation was as follows: Western Alaska–Siberia (WA–S, 42 ± 4% [SE]), northern Canada–Nunavut (NC–N, 21 ± 4%), West-central Canada–Alaska (WC–A, 23 ± 4%) and East-central Canada–Minnesota (EC–M, 14 ± 3%). All tagged cranes returned to the same breeding affiliation used during the previous year with a median distance of 1.60 km (range: 0.08–7.7 km, $n = 53$) separating sites used in year 1 and year 2. Fall staging occurred primarily in central and western Saskatchewan (69%), North Dakota (16%), southwestern Manitoba (10%), and northwestern Minnesota (3%). Space-use sharing indices showed that except for NC–N and WC–A birds, probability of finding a crane from one breeding affiliation within the home range of another breeding affiliation was low during fall staging. Tagged cranes from WC–A and EC–M breeding affiliations, on average, spent 25 and 20 days, respectively, longer on fall staging areas in the northern plains than did WA–S and NC–N birds. Cranes in the NC–N, WA–S, and WC–A affiliations spent 99%, 74%, and 64%, respectively, of winter in western Texas in Hunting Zone A; EC–M cranes spent 83% of winter along the Texas Gulf Coast in Hunting Zone C. Tagged cranes that settled within the breeding range of the Gulf Coast Subpopulation spent 28% and 42% of fall staging and winter within the range of the Western Subpopulation, indicating sufficient exchange of birds to potentially limit effectiveness of MCP harvest management. Harvests of EC–M and WC–A cranes during 1998–2003 were disproportionately high to their estimated numbers in the MCP, suggesting more conservative harvest strategies may be required for these subpopulations in the future, and for sandhill cranes to occupy major parts of their historical breeding range in the Prairie Pothole Region. Exceptionally high philopatry of MCP cranes of all 4 subpopulations to breeding sites coupled with strong linkages between crane breeding distribution, and fall staging areas and wintering grounds, provide managers guidance for targeting MCP crane harvest to meet management goals. Sufficient temporal or spatial separation exists among the 4 subpopulations on fall staging areas and wintering grounds to allow harvest to be targeted at the subpopulation level in all states and provinces (and most hunting zones within states and provinces) when conditions warrant. Knowledge gained from our study provides decision-makers in the United States, Canada, Mexico, and Russia with improved guidance for developing sound harvest regulations, focusing conservation efforts, and generating collaborative efforts among these nations on sandhill crane research and management to meet mutually important goals. © 2011 The Wildlife Society.

KEY WORDS breeding affiliation, Central Flyway, *Grus canadensis*, harvest, Mid-continent Population (MCP), sandhill crane, satellite telemetry, fall staging areas, subspecies, wintering grounds.

Distribución Geográfica de la Población Centro-Continental de la Grulla Canadiense y Aplicación de Gestiones Relacionadas

RESUMEN La Población Centro-continental (MCP) de grulla canadiense (*Grus canadensis*) es cazada ampliamente en Norte América y, para propósitos de manejo, está dividida en las Subpoblaciones de la Costa del Golfo y Oeste. Una gestión efectiva de la especie requiere un conocimiento detallado sobre la distribución de las áreas reproductivas de subespecies y subpoblaciones, la cronología del uso de las áreas de escala durante el otoño y de las áreas de invernada, así como la exposición y presión a la cacería. Para poder obtener estos conocimientos necesarios, marcamos 153 grullas canadienses con transmisores PTT (*Platform Transmitter Terminal*) entre el 22 de febrero y el 12 de abril de 1998 a 2003 en los valles del Central Platte River y North Platte River, localizados en la zona centro sur de Nebraska. Monitoreamos las grullas marcadas con transmisores PTT (en lo sucesivo grullas marcadas), desde su llegada hasta su partida a las zonas de reproducción, durante su migración de otoño y durante todo el período de invierno, utilizando el sistema de seguimiento por satélite ARGOS. Dicho seguimiento dio como resultado 74,041 localizaciones útiles de un total de 49,350 días; la duración mediana de seguimiento de individuos fue de 352 días y 73 grullas fueron rastreadas >12 meses. Las secuencias genéticas de ADN Mitocondrial en sangre, tomadas a

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Received: 26 December 2008; Accepted: 29 May 2010; Published: 20 April 2011.
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partir de muestras aleatorias de grullas marcadas, indicaron que el 64% eran *G. c. canadensis* y el 34% eran *Grus canadensis tabida*. Durante la estación reproductiva, las grullas marcadas se establecieron en las regiones templadas, subárticas, y árticas de Norte América (Estados Unidos [23%, $n = 35$], Canadá [57%, $n = 87$]) así como en las regiones árticas del nordeste de Asia (Rusia [20%, $n = 31$]). Las grullas marcadas, pertenecientes a diferentes afiliaciones reproductivas, se distribuyeron de la siguiente forma: Oeste de Alaska–Siberia (WA–S, 42 ± 4% [SE]), norte de Canadá–Nunavut (NC–N, 21 ± 4%), centro oeste de Canadá–Alaska (WC–A, 23 ± 4%) y centro este de Canadá–Minesota (EC–M, 14 ± 3%). Todas las grullas marcadas regresaron a la misma afiliación reproductiva del año anterior con una distancia mediana de 1.60 km (rango: 0.08–0.77 km, $n = 53$) de separación entre los sitios utilizados en el año 1 y en el año 2. Las áreas de escala otoñal se concentraron principalmente en el centro y oeste de Saskatchewan (69%), Dakota del Norte (16%), sudoeste de Manitota (10%) y noroeste de Minesota (3%). Los índices de compartimiento de espacio indicaron que a excepción de las aves NC–N y WC–A, la probabilidad de encontrar una grulla perteneciente a una afiliación reproductiva dentro del territorio de otra afiliación, era baja durante la escala otoñal. Las aves WC–A y EC–M pasaron respectivamente como promedio 25 y 20 días más en las áreas de escala otoñal de las grandes planicies, que las aves WA–S y NC–N. Las grullas pertenecientes a las afiliaciones NC–N, WA–S y WC–A pasaron el 99, 74 y 64% del invierno respectivamente, en el oeste de Texas en la Zona de Caza A; las grullas EC–M pasaron el 83% del invierno a lo largo de la Costa del Golfo de Texas en la Zona de Caza C. Las grullas marcadas que se asentaron en las áreas de reproducción de la Subpoblación de la Costa del Golfo, pasaron el 28% de la escala otoñal y el 42% del invierno dentro del territorio de la Subpoblación Oeste, indicando un intercambio de individuos lo suficiente grande como para potencialmente limitar el manejo efectivo de la MCP. La caza de aves EC–M y WC–A entre los años 1998 a 2003 fue desproporcionalmente alta en relación a los números estimados en la MCP, sugiriendo que se podrían requerir estrategias de manejo más conservadoras para estas subpoblaciones en un futuro, y para que la grulla canadiense pueda reocupar gran parte de su área reproductiva histórica en la región del *Prairie Pothole*. El hecho de que las 4 subpoblaciones de grullas pertenecientes a la MCP exhibieron una excepcional filopatría a los sitios de reproducción y de que existieron fuertes vínculos entre las distribuciones reproductivas de las grullas, las áreas de escala otoñal y las áreas de invernada, ofrece una orientación a los manejadores de la caza de grullas de la MCP para que puedan cumplir con las metas de gestión establecidas. Existe suficiente separación temporal y/o espacial entre las 4 subpoblaciones en las áreas de escala otoñal y en las áreas de invernada como para permitir la caza dirigida al nivel subpoblacional en todos los estados y provincias (y en la mayoría de las zonas de caza dentro de los estados y provincias) siempre y cuando las condiciones lo ameriten. El conocimiento obtenido a partir de este estudio proporciona a los responsables de decisiones en los Estados Unidos, Canadá, México y Rusia, una mejor dirección para desarrollar cuotas de caza razonables, enfocar los esfuerzos en materia de conservación y generar colaboraciones entre estas naciones en materia de investigación y gestión de la grulla canadiense, para poder cumplir metas importantes y a la vez comunes.

Distribution Géographique de la Population des Grues du Canada Dans le Centre du Continent et Les Applications Relatives à Leur Gestion

SOMMAIRE La grue du Canada (*Grus canadensis*) est largement chassée en Amérique du Nord et elle se sépare entre la sous-population côtière du Golfe et la sous-population de l'Ouest afin de tel que défini. Pour administrer la population des grues efficacement, il est nécessaire d'avoir une connaissance détaillée de la répartition des colonies, des sous-espèces et des sous-populations. Il faut aussi une table chronologique des divers points de ravitaillements visités par ces grues et leur exposition aux dangers de la chasse au cours de leur migration. Pour répondre à ce besoin, nous avons étiqueté cent cinquante-trois (153) grues du Canada avec des bornes de transmission plate-forme (VTP), entre le 22 février et le 12 avril des années 1998 et 2003, au centre et au nord de la vallée de la Rivière Platte dans le sud-central du Nebraska. Grâce au système de repérage satellite ARGOS, nous avons contrôlé les bornes de transmission (VTP) des grues du Canada étiquetées, de leur arrivé jusqu'à leur départ des zones de reproduction, pendant la migration printanière et tout au long de la période hivernale. L'effort de repérage a localisé 74,041 lieux utilisés sur une période de 49,350 jours. Le suivi des grues individuelles était d'une durée médiane de 352 jours, dont 73 grues ont étés repérées sur une période de plus de douze mois.

Le séquençage génétique de l'ADNmt à partir de certains échantillons de sang prélevé sur des grues étiquetées au hasard a démontré que 64% étaient des *G. c. canadensis* et que 34% étaient des *Grus canadensis tabida*. Les grues étiquetées durant la saison de reproduction se sont installées majoritairement dans les régions tempérées, subarctiques et arctiques de l'Amérique du Nord (États-Unis [23%, $n = 35$], Canada [57%, $n = 87$]) ainsi que dans les régions de l'Arctique de l'Asie du Nord (Russie [20%, $n = 31$]). La répartition des grues étiquetées lors de la reproduction a démontré les affiliations suivantes: Ouest de l'Alaska–Sibérie (OA–S, 42 ± 4% [SE]), Nord du Canada–Nunavut (NC–N, 21 ± 4%), Centre-Ouest du Canada–Alaska (COC–A, 23 ± 4%) et Centre-Est du Canada–Minnesota (CEC–M, 14 ± 3%). Toutes les grues étiquetées sont retournées dans les mêmes groupes de reproduction que les années précédentes, quoiqu'une distance médiane de 1.60 km (gamme: 0.08–7.7 km, $n = 53$) séparait les sites entre les deux années étudiées.

Les relais automnaux des grues étudiées sont principalement situés dans le centre et l'ouest de la Saskatchewan (69%), au Dakota du Nord (16%), dans le sud-ouest du Manitoba (10%) et dans le nord-ouest du Minnesota (3%). Les indices de partage d'espace ont démontré qu'à l'exception des grues du NC–N et du COC–A, les probabilités de trouver une grue dans le domaine vital d'une autre affiliation de reproduction que la sienne est très faible lors de la saison d'accouplement. Les grues étiquetées provenant des zones de reproduction du COC–A et du CEC–M passent, respectivement, en moyenne 25 et 20 jours de plus en automne dans les plaines du nord que les oiseaux des régions OA–S et du NC–N. Les grues se situant dans les affiliations du NC–C, de l'OA–A et du COC–A ont respectivement passé 99, 74, et 64% de leur hiver dans l'ouest du Texas, zone de chasse A. Les grues du CEC–M ont passé 83% de leur hiver le long de la région de la Côte du Golfe du Texas, dans la zone de chasse C. Les grues étiquetées qui se sont installées dans la zone d'accouplement de la sous-population côtière du Golfe, ont passé entre 28 et 42% de la saison d'accouplement et de la saison hivernale dans la région de la sous-population de l'Ouest. Cela indique qu'un échange suffisant entre les deux populations de grues peut potentiellement limiter l'effet de la gestion de la reproduction. L'étude des grues du CEC–M et du COC–A en 1998 et 2003 a démontré une disproportion vis-à-vis du nombre estimé de la PGCC, suggérant que de nouvelles stratégies conservatrices sont nécessaire pour que les sous-populations de grue du Canada réoccupent la majorité de leur territoire historique de la région des cuvettes des prairies. Les quatre sous-populations de grues de la PGCC ressentent une philopatrie exceptionnelle entre leurs sites de reproduction respectifs, leurs sites d'élevage, leurs lieux de rassemblement automnaux et leurs relais hivernaux. Cette philopatrie offre aux chasseurs une cible incroyable pour gérer et atteindre leurs objectifs quand vient la saison de la chasse. Parmi les quatre sous-populations, une séparation temporelle et spatiale suffisante existe entre les aires de repos automnales et hivernales. Quand les conditions le permettent, cette séparation permet aux grues des sous-populations d'être la cible des chasseurs durant la saison de chasse dans tous les états et toutes les provinces (et dans la plupart des zones de chasses). Les connaissances acquises lors de cette étude permettent aux États-Unis, au Canada, au Mexique et à la Russie de pouvoir améliorer leurs lois en ce qui à trait à la saison de la reproduction. Elle aide aussi ces pays à diriger leurs efforts sur la conservation des grues et de leur territoire. Finalement, elle génère une nouvelle collaboration entre ces quatre nations en matière de recherche et de gestion sur les grues du Canada, pour répondre à ces objectifs mutuels.

Географическое Распространение Средне-Континентальной Популяции Канадских Журавлей и Мероприятия по ее Управлению в Этой Связи

АННОТАЦИЯ Средне-континентальная Популяция (СКП) канадского журавля (*Grus canadensis*) подвержена интенсивной охоте в Северной Америке; в управленческих целях она подразделяется на две субпопуляции - Галф Коуст и Западную. Эффективное управление СКП требует подробных сведений о распределении подвидов и субпопуляций в ареале гнездования, хронологии использования ими территорий осенних транзитных остановок и зимовок, а также об объеме добычи вида как объекта охоты. В целях получения соответствующей информации, с 22 февраля по 12 апреля 1998–2003 мы установили спутниковые передатчики (PTTs) на 153 канадских журавля отловленных на территории центральной и северной долины реки Платт юго-центральной Небраски. Далее мы отслеживали меченых PTT журавлей с начала прибытия на места размножения и до отлета, в период осенней миграции и в течение всего зимнего сезона с помощью спутниковой системы слежения АРГОС. Мероприятия по космическому слежению позволили выявить 74041 местоположение за 49350 дней, средняя продолжительность слежения за отдельными птицами составила 352 дня, за 73 журавлями – более 12 месяцев. Генетическое секвенирование митохондриальной ДНК (mtDNA) полученной из образцов крови меченых журавлей показало, что 64% журавлей принадлежали к *G. c. canadensis,* 34% - к *G. c. tabida.* Меченые журавли во время сезона размножения пребывали в северных умеренных, субарктических и арктических районах Северной Америки (США [23%, $n = 35$], Канады [57%, $n = 87$]) и арктических регионах северо-восточной Азии (Россия [20%, $n = 31$]). Распределение меченых журавлей по принадлежности к местам размножения было следующим: Западная Аляска/Сибирь (ЗА–С, 42 ± 4% [*SE*]), северная Канада/Нунавут (СК–Н, 21 ± 4%), западно-центральная Канада/ Аляска (ЗК–А, 23 ± 4 %) и восточно-центральная Канада/Миннесота (ВК–М, 14 ± 3 %). Все меченые птицы вернулись на территории размножения, используемые ими в предыдущем году, со средним расстоянием 1,6 км (0,08–7,7 км, $n = 53$) между участками первого и второго года. Места осенних транзитных остановок были сосредоточены в основном в центральном и западном Саскачеване (69%), Северной Дакоте (16%), юго-западной Манитобе (10%), и северо-западной Миннесоте (3%). Индекс «совместного использования пространства» показал, что за исключением птиц из СК-Н и ЗК-А, вероятность нахождения особей из одной территории размножения в пределах индивидуальных участков (home range) птиц из других территорий размножения была низкой во время осенних миграций. Меченые птицы с гнездовых территорий ЗК–А и ВК–М в среднем провели на 25 и 20 дней соответственно больше на осенних стоянках в северных равнинах, чем птицы из ЗА–С и СК–Н. Журавли с территорий СК–Н, ЗА–С и ЗК–А провели 99%, 74% и 64% соответственно зимнего времени в западном Техасе в Охотничьей Зоне А; птицы из ВК–М провели 83% зимнего периода на побережье Техасского Залива в Охотничьей Зоне С. Меченые журавли, пребывавшие на территории размножения субпопуляции Галф Коуст, провели 28% времени осенней транзитной остановки и 42% времени зимовки внутри ареала Западной субпопуляции, что указывает на обмен птицами между этими субпопуляциями, достаточный для потенциального уменьшения эффективности управления добычей СКП. Добыча птиц из ВК–М и ЗК–А за 1998–2003 гг. была несоразмерно высока по сравнению с их расчетной численностью в СКП, что предполагает возможность требования более консервативных стратегий изъятия этих субпопуляций в будущем, для того чтобы канадские журавли могли вновь занять свои основные исторические районы размножения в Регионе Прерии Потхоул. Исключительно высокая филопатрия журавлей СКП всех 4 субпопуляций к территориям размножения, наряду с сильными связями между распределением на местах размножения, осенних транзитных остановок и зимовок предоставляют возможность определить объемы добычи журавлей СКП, и осуществлять задачи по управлению. Существует достаточное временное и пространственное разделение между 4-мя субпопуляциями на осенних и зимних местообитаниях, чтобы разрешить изъятие на субпопуляционном уровне во всех штатах и провинциях (и большинстве охотничьих зон в границах штатов и провинций) при благоприятных условиях. Знания, полученные благодаря нашей работе, дают возможность руководителям, ответственным за принятия решений в Соединенных Штатах, Канаде, Мексике и России, усовершенствовать разработку четкого регулирования по прореживанию популяции, фокусируя совместные усилия по охране, инициируя проведение общих исследований по канадскому журавлю и управлению его популяциями, чтобы решить обоюдно важные цели.

Contents

INTRODUCTION

Sport hunting of the Mid-continent Population (MCP; see Appendix A for an index of all acronyms and abbreviations) of sandhill cranes occurs in 11 states in the United States, 2 provinces in Canada, and 3 states in Mexico (Sharp et al. 2007). Hunting and harvest of the MCP is centered in the plains states of North Dakota, Kansas, Oklahoma, Texas, and the prairie provinces of Saskatchewan and Manitoba. In the 1960s, sport hunting of the MCP was introduced, in part, to alleviate crop depredation problems, particularly in the northern plains (Lewis 1977). Over the past 5 decades, hunting seasons for sandhill cranes have been implemented in 9 of 10 states that form the Central Flyway. Along with a growing interest and expansion of sandhill crane hunting, season lengths, number of crane hunters, and harvest have increased (Kruse et al. 2008). By 2000–2005, total harvest (including birds shot in Canada and the estimated unretrieved kill) averaged approximately 33,000 birds annually (Sharp et al. 2007). Rapid growth in annual harvest has resulted in a concern that insufficient information is available to prevent overharvest of key segments of the population, ultimately leading to diminished hunting opportunities.

State and federal wildlife agencies in the Central Flyway have taken a lead in seeking detailed quantitative information on the MCP to provide diverse recreational opportunities consistent with the welfare of the MCP, international treaties, and socio-economic constraints while maintaining MCP crane abundance at 1982–2005 levels (Central Flyway Webless Migratory Game Bird Technical Committee 2006, Sharp et al. 2007). Because sandhill cranes have the lowest annual recruitment rate of game birds in North America (Drewien et al. 1995), a high potential exists for overharvest. Therefore, greater precision is required when making decisions concerning where and when to target harvest than is required for most species. The MCP is separated into the Gulf Coast and Western subpopulations for management purposes (Tacha and Vohs 1984, Tacha et al. 1994). Ranges of these subpopulations were delineated based upon limited information on where MCP sandhill cranes of known breeding origins staged during fall or spent winter. To ensure that harvest strategies for the MCP are conservative, detailed insight is required regarding the breeding origins of MCP sandhill cranes using specific fall staging areas and wintering grounds, chronology of use of these areas, knowledge of approximate numbers of cranes in each subpopulation, and distribution and size of the harvest by subpopulation.

Three subspecies are recognized in the MCP based on differences in crane morphometry: greater sandhill crane (*Grus canadensis tabida*), Canadian sandhill crane (*G. c. rowani*), and lesser sandhill crane (*G. c. canadensis*; Tacha et al. 1994). Four recent studies analyzing mitochondrial DNA (mtDNA) of these 3 subspecies concluded that genetic variation was insufficient to warrant classifying the Canadian sandhill crane as a separate subspecies from the greater sandhill crane (Rhymer et al. 2001, Glenn et al. 2002, Peterson et al. 2003, Jones et al. 2005). However, results of microsatellite and mtDNA lineage data for greater sandhill crane also eliminated the possibility of these birds being simply an alternate body form of greater sandhill crane (Jones et al. 2005). Rather, results suggested that the Canadian sandhill crane morphotype is intermediate in morphometry, geography, and genetics, with a gradation in morphometric and nuclear DNA variation from arctic-nesting lesser sandhill crane to non-arctic greater sandhill crane. To allow researchers and managers to relate our results to existing literature but also gain insight into the implications of current genetic research, we present our results, where possible, in relation to taxonomy based on crane morphometry and genetic analyses.

Developing sound hunting regulations that will ensure a long-term maximum sustainable harvest requires knowledge of subpopulation sizes and a balance of annual mortality with annual recruitment for each subpopulation. Detailed knowledge of distribution of MCP sandhill cranes of each breeding affiliation by date, along with information on their turnover rates and length of stay on fall staging areas and wintering grounds is required to evaluate distribution of harvest by subpopulation in states and provinces of the Central Flyway where the species is hunted. Currently, distribution of harvest by subspecies and subpopulation is not known (Kendall et al. 1997). Also, information is needed on extent of overlap of the MCP range with other populations (i.e., the Eastern Population [EP] and Rocky Mountain Population [RMP]) of greater sandhill cranes and the Pacific Flyway Population (PFP) of lesser sandhill cranes. Knowledge of extent of overlap with other populations is most needed in regions where cranes from the MCP are hunted because the EP, RMP, and PFP are smaller in size with either no sport hunting permitted (EP) or limited sport hunting allowed (RMP, PFP).

We used satellite telemetry as the primary tool to address identified information needs. We attached Platform Transmitting Terminals (PTTs) to a representative sample of MCP cranes and systematically monitored their locations from arrival on their breeding grounds to departure, during fall migration, and throughout winter. We monitored tagged MCP cranes to establish their breeding affiliations and to link cranes of known breeding origin to their fall staging areas and wintering grounds. We coupled information collected on chronology of use by tagged MCP cranes of known breeding affiliation at sites where they were exposed to hunting with knowledge of hunting frameworks for states and provinces where recreational hunting occurs, thus providing a sound basis for estimating annual harvest by breeding affiliation.

STUDY AREA

Our study area encompassed the breeding grounds, fall migration corridors, fall staging areas, and wintering grounds of the MCP as determined by systematically monitoring locations and movements of tagged sandhill cranes using satellite telemetry. Breeding grounds of the MCP encompassed most of the central and western arctic of Canada eastward to Hudson Bay and westward along the Arctic Ocean to Yukon Territory, Alaska, and northeastern Russia (Tacha et al. 1994). The southern edge of the breeding range extended from northwestern Minnesota through southeastern and central Manitoba, central Saskatchewan, central Alberta, northeastern British Columbia, and central and southwestern Alaska. This vast area included temperate grassland, mixed coniferous and deciduous forest, parkland, boreal forest, and tundra. The winter range included parts of the south-central and southwestern United States and northern Mexico. We trapped and tagged all sandhill cranes we monitored with PTTs in the Central Platte River Valley (CPRV) and North Platte River Valley (NPRV) of south-central Nebraska during 22 February to April 1998–2003 (Fig. 1). Virtually the entire MCP staged in the CPRV and NPRV during

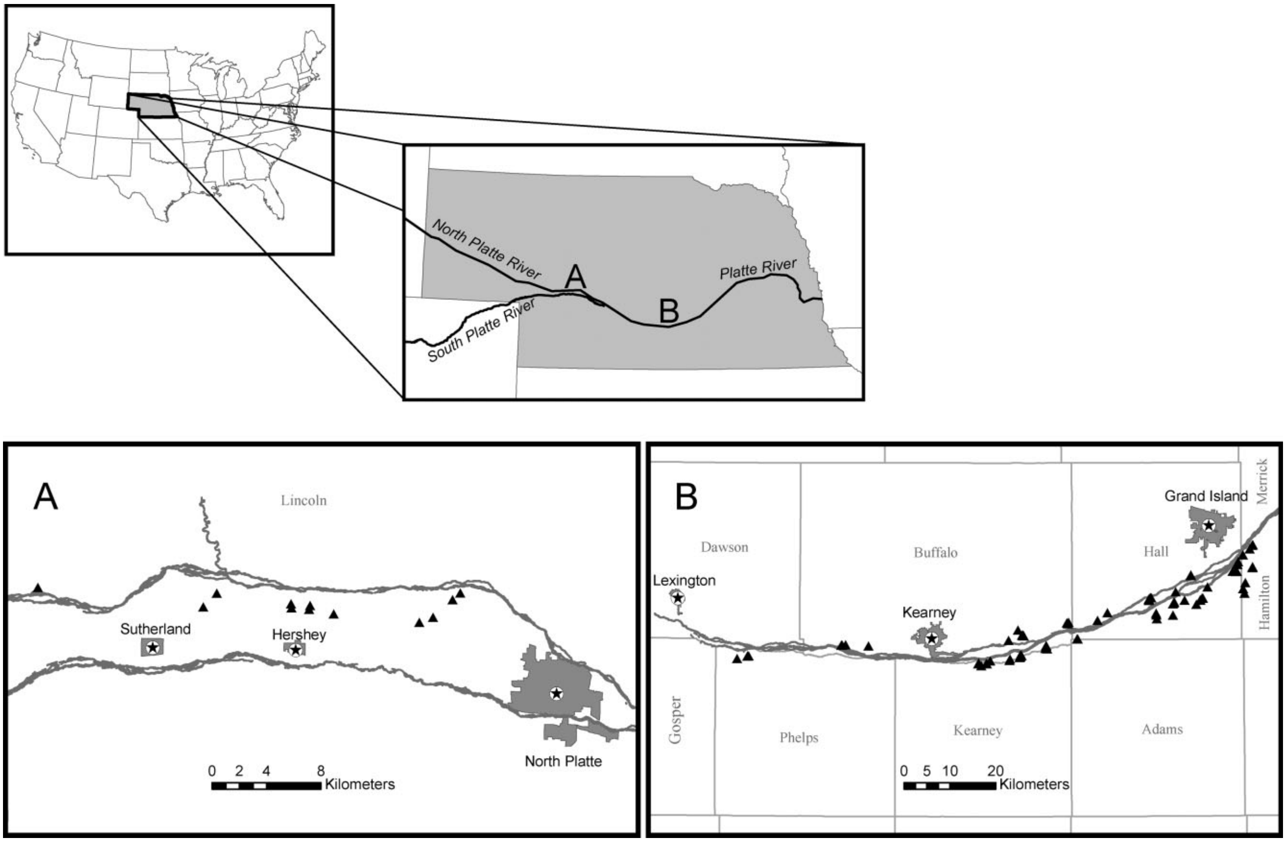

Figure 1. Locations (indicated by triangles) in (A) North Platte River Valley, and (B) Central Platte River Valley Nebraska where we captured and tagged 153 sandhill cranes of the Mid-continent Population with Platform Transmitting Terminals (PTTs) during February–April, 1998–2003.

early spring, staying an average of 26 days (G. Krapu, U.S. Geological Survey, unpublished data). Detailed descriptions of the CPRV (U.S. Fish and Wildlife Service 1981, Krapu et al. 1982) and NPRV (Krapu et al. 1987, Iverson et al. 1987) have been presented previously.

METHODS

Trapping and Transmitter Deployment

It was important from both a scientific and management perspective to capture and monitor a sample of cranes that would allow us to make inferences concerning the entire MCP. We took several steps to help ensure that our sample of tagged cranes was representative of the MCP with regard to geographic distribution and chronology of use of fall staging areas and wintering grounds, including sites where most hunting occurred. Sandhill cranes begin arriving in the CPRV and NPRV in mid-February; a rapid buildup follows from early to mid-March, and the population generally peaks in the last week of March (U.S. Fish and Wildlife Service 1981). As a result, we scheduled our trapping efforts accordingly by capturing birds throughout the period they were arriving in Nebraska. Magnitude of trapping effort increased as the percentage of the MCP present increased. Trapping effort and numbers of birds captured and tagged with PTTs were distributed approximately proportional to the number of birds using each section of the river.

We conducted trapping and tagging at numerous sites in the CPRV and NPRV (Fig. 1), specifically in the Chapman to Lexington reach of the CPRV, and in the Hershey area of the NPRV, from late February to early April 1998–2003. Trapping sites generally were located in grasslands (pastures) and hay lands in the CPRV and NPRV, often in areas that functioned as secondary roosts (i.e., where birds congregate in the morning after leaving the nocturnal roosts, where they return in mid-day immediately after feeding in adjacent agricultural fields, or where they occur before moving on to nocturnal roosts). We captured birds by positioning taxidermy-mounted sandhill cranes as small flocks in areas previously used and where we could fire well-hidden rocket-propelled nets over cranes drawn within the capture zone of the net (Wheeler and Lewis 1972). We set nets before the expected arrival of cranes, accounting for areas of concentrated crane activity. We concealed net setups by raking surrounding vegetation and covering all components, taking care to provide total visual concealment and minimal vertical obstruction. We fired rocket nets remotely (Fig. 2) with radio-controlled detonators held by field personnel concealed within 300 m of the net.

We removed captured cranes immediately and placed them into burlap bags to restrain movement during processing. Upon capture, we took the following linear measurements (mm) of all captured cranes: post-nares culmen (Fig. 3A), tarsus length (Fig. 3B), and flattened wing chord (Fig. 3C). Based upon these measurements, we later categorized birds by morphometry as greater sandhill crane, Canadian sandhill crane, or lesser sandhill crane using the discriminant methods of Johnson and Stewart (1973). We selected adults for PTT attachment, marking ≤ 2 cranes from each throw of the net based on social status (e.g., family groups or pairs) or location under the net (e.g., pairs at opposite ends). We established these criteria to limit the chance of sampling related birds. Also, minimizing capture group size shortened the stress period associated with capture and handling.

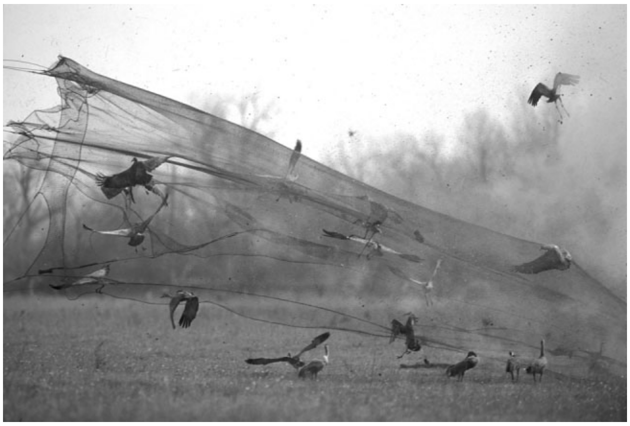

Figure 2. Capture of sandhill cranes for Platform Transmitting Terminal (PTT)-tagging in the Central Platte River Valley, Nebraska during March 2002 using concealed rocket-propelled nets fired remotely with radio-controlled detonators. We used crane taxidermy mounts to attract groups of cranes to capture sites.

We sought a sample consisting of primarily breeding adults, so we avoided sub-adults by tagging cranes with plumage characteristic of adults. Adult characteristics included a bare, brightly colored reddish forehead, lores, and crowns. We avoided tagging cranes with tawny feathers on the crown, occiput, nape, or tawny plumage on the body coverts and wing coverts, which are plumage traits characteristic of juveniles (Lewis 1979).

We drew a blood sample from each crane selected to receive a PTT from the metatarsal vein just below the tibio-tarsus joint of the right leg (Fig. 3D) and placed it into a storage lysis buffer (0.1 M Tris, 0.1 M EDTA, 5% SDS, 0.01 M NaCl; Longmire et al. 1991) for later extraction to determine sex and mtDNA lineage. We followed protocols for DNA isolation from the Promega Wizard Genomic DNA Purification Kit (Promega Corp., Madison, WI). We determined sex using polymerase-chain-reaction (PCR) methods of Duan and Fuerst (2001). We diagnosed mtDNA lineage using a modified PCR restriction-fragment-length-polymorphism (RFLP) methodology of Glenn et al. (2002). We substituted MSE I for HAE III, as it better discriminated between the 2 mtDNA lineages.

We attached a PTT (Microwave Telemetry Inc., Columbia, MD; North Star Science and Technology LLC, Baltimore, MD) to the left leg of each crane using a 2-piece leg band (Fig. 4). Leg bands consisted of a pair of 7.62-cm, semi-circular, flanged halves of color-coated polyvinyl chloride (PVC) (Haggie Engraving, Crumpton, MD) of which one half had 2 superimposed 2.5-cm numeric or character codes engraved in it (Fig. 4). These 2 pieces together formed a band with an inside diameter approximately equivalent to U.S. Geological Survey Bird Banding Laboratory band sizes 8 and 9. Manufacturers attached PTTs to the blank band half with various methods. Band halves were lined with 1-mm-thick closed-cell neoprene to prevent abrasion and for insulation from ambient cold and heat conduction from the package. We mounted PTT leg bands on the left tibia above the tibio-tarsus with the antenna pointing down. Preliminary results indicated these PTTs arrangements resulted in acceptable levels of signal reception and less stress to birds than did backpack harnesses (Ellis et al. 2001).

Figure 3. We took the following linear measurements (mm) on each captured sandhill crane to be tagged with a Platform Transmitting Terminal (PTT): (A) post-nares culmen length, (B), flattened wing chord and (C) tarsus length. We later used these measurements to categorize birds to subspecies based on their morphometry using the discriminant methods of Johnson and Stewart (1973). (D) We drew a blood sample from the metatarsal vein just below the tibio-tarsus joint of the right leg of each captured bird to determine sex and assign subspecies based on mtDNA lineage. We measured and tagged cranes in the Central Platte River Valley and North Platte River Valley of south-central Nebraska during February–April, 1998–2003.

Figure 4. Platform Transmitting Terminal (PTT)-tagged sandhill crane with plastic leg band on the left tarsus above the tibio-tarsus. The PTT is fused to one half of a 2-part leg band and is located on the underside in this photo; numeric code on leg band is to allow visual identification of each individual in the field. We tagged MCP cranes in the Central Platte River Valley and North Platte River Valley of south-central Nebraska during February–April 1998–2003.

We released most captured birds simultaneously within 30 min (range 15–60 min) of capture to maintain potential group and family bonds. We released cranes captured in the evening under enough ambient light to enable visual navigation to river roosts, usually before sunset. All capture and marking procedures conformed to recommendations of the American Ornithologists' Union (1997) and followed the protocol contained in Study Plan 169.02 which was approved on 13 July 1998 by the Chairman of the Animal Care and Use Committee at Northern Prairie Wildlife Research Center.

We programmed PTTs at the time of manufacture to follow 1 of 4 duty cycles (Table 1). We structured duty cycles to give more-frequent locations during migration and less-frequent locations during periods when cranes were more sedentary (i.e., while on breeding and wintering grounds). Improved technology allowed us to increase frequency of locations as the study progressed, but the overall strategy of transmission frequency relative to the annual crane cycle remained consistent. We simultaneously activated PTTs prior to deployment to ensure

Table 1. Programmed transmission schedules by annual cycle for Platform Transmitting Terminals (PTTs) we deployed on sandhill cranes captured in the Central Platte River Valley and North Platte River Valley, Nebraska, 1998–2003. Numbers represent transmission to the satellites every *n*th day.

Program	*n*	Spring staging	Spring migration	Breeding grounds	Fall migration	Winter grounds	Second spring migration
A	61	4	4	7	4	10	5
B	9	5	2	8	4	10	4
C	17	5	1	8	2	9	4
D	66	1.5	1	4	1.5	4	3

synchronization of duty cycles and transmissions. Life span of PTTs was projected to be 16 months to enable an evaluation of level of philopatry to breeding sites used the previous year (we programmed North Star PTTs to shut off during early June after reaching the breeding grounds for the second year).

We used the Argos satellite system (Service Argos 2008) to determine locations of tagged cranes throughout the annual cycle. The Argos system consists of ultra-high-frequency (UHF) receivers carried on 5 polar-orbiting National Oceanic and Atmospheric Administration (NOAA) weather satellites that receive PTT transmissions within their field of view. Locations are calculated from the Doppler shift in the received frequency as the satellite passes over the transmitter. Information is transferred to Earth-based processing centers that make the data available to users through personal computers within a few hours of acquisition. Along with location, data from sensors built into the PTTs that provided temperature of the PTT, battery voltage, activity, and current duty cycle were also resolved during transmission and relayed to processing centers. We received data from Service Argos via daily E-mail. Fancy et al. (1988) and Harris et al. (1990) provided a more detailed description of the Argos system and its application in tracking wildlife.

Data Processing and Analyses

Argos assigns a quality code (Location Class [LC]) for each location denoting its relative accuracy based upon satellite telemetry and transmitter geometry during the satellite pass, number of messages received during the pass, and transmitter frequency stability. Quality assessment by Argos has shown that assuming isotropic error, the accuracy defined by each LC code represents one standard deviation around the true PTT latitude and longitude. Argos states accuracy by LC as follows: LC-3 = < 250-m radius; LC-2 = 250–500-m radius; LC-1 = 500–1,500-m radius; LC-0 = > 1,500-m radius; LC-A, LC-B, or LC-Z = no accuracy assessment (Service Argos 2008, Section 3.4).

Service Argos estimates accuracy of their standard locations using high-power PTTs under ideal ambient conditions. Empirical tests of low-power wildlife PTTs under a variety of environmental settings have reported slightly poorer accuracies for the standard location classes (Harris et al. 1990, Vincent et al. 2002). Keating et al. (1991) and Clark (1989) showed that a 68% distribution (1 SD) does not always hold true for smaller PTTs used in wildlife tracking. Although Argos gives no accuracy ratings for LC-0, LC-A, or LC-B, the calculated location was shown to be within 11.5 km, 6.8 km, and 98.5 km, respectively, of the true location 68% of the time for PTTs similar to those we used (Britten et al. 1999). In our opinion, magnitudes of errors like these are acceptable for interpreting continental-scale migration.

Filtering methods can improve robustness of the Argos auxiliary locations, but most published algorithms are for marine and terrestrial species that are far less mobile than birds (McConnell et al. 1992, Keating 1994, Hays et al. 2001, Austin et al. 2003). We used the Douglas Argos-Filter Algorithm version 6.5 (Alaska Science Center 2010) developed by D. Douglas (U.S. Geological Survey). The Douglas filter extracts locations from the Argos diagnostic format files and provides output as a number of filtered data sets including all locations (no filtering), minimum-redundant-distance (MRD) filtered locations, distance-angle-rate (DAR) filtered locations, and a hybrid of both. The MRD algorithm allows the user to set a maximum distance from each location beyond which all other locations are rejected within a set time frame. The DAR algorithm determines whether to accept a location by determining the angle of divergence away from the path created by connecting 3 consecutive locations with the location under evaluation. The hybrid filter uses both the MRD and DAR algorithms. User inputs include a limit on the plausible rate of travel and the acceptable angle of divergence. The filter default does not remove LC-3 locations but this limit may be set lower. We used the hybrid filter with the LC limit set at 1 (LC-1, LC-2, and LC-3 always retained), and we set the maximum rate of travel 100 km/hr, maximum redundancy value to 30 km, and the angle of divergence parameter to ignore all angles >125°. For more detailed information on how the filter works, see Alaska Science Center (2010).

We ran all resolved satellite locations through the filter, which marks records for deletion that do not meet the user-defined criteria for inclusion. We then manually scrutinized the resulting output as a geographic information system (GIS) layer and made subjective decisions as to the legitimacy of removing each individually marked as well as any unmarked locations that appeared unrealistic or improbable. This processing resulted in a final dataset of crane locations that contained only those locations that passed through this stepwise sequential geospatial algorithm and subjective manual review.

We initially imported the final filtered data into MapInfo Professional software (TETRAD Computer Applications Inc., Bellingham, WA) for viewing and summary. We attached annual cycle attributes (Platte River, Breeding Area, Fall Migration, and Wintering Area) post hoc to each location based upon manual inspection of arrival and departure to and from appropriate discrete geographic areas. We designated Breeding Area to locations from arrival at the geographic terminus of spring migration through a major departure from that area. We assigned Fall Migration to locations from departure from breeding grounds through arrival at Wintering Area. Wintering Area was any location in a state (U.S. or Mexico) where a tagged bird generally terminated its fall migration in any year. During the breeding season (Jun-Aug), most cranes were confined to a small area, suggesting a breeding status. We created one breeding-season location for each monitored crane by calculating a weighted mean of all breeding ground locations. We weighted each observation by a numeric representation of the Argos Location Class (LC-3 = 4, LC-2 = 3, LC-1 = 2, LC-0 = 1, LC-A = 1, LC-B = 1, LC-Z = 1) to reflect the decreasing accuracy of these LCs and to theoretically arrive at a more precise estimate of the activity center.

We assigned the MCP to 4 breeding affiliations based upon breeding-ground locations and locations of cranes' fall staging areas in the northern plains (Fig. 5). The 4 breeding affiliations were East-central Canada–Minnesota (EC–M), West-central Canada–Alaska (WC–A), Western Alaska–Siberia (WA–S), and northern Canada–Nunavut (NC–N). To assess whether our tagged sample reliably represented the distribution of cranes by breeding affiliation in the CPRV, we compared the percent distribution of our tagged sample of sandhill cranes by bridge section with estimates of percent crane distribution by bridge section obtained from aerial infrared videography while cranes were gathered on nocturnal roosts. We conducted aerial infrared surveys of cranes on or near the fourth Tuesday of March 2000–2003 (Kinzel et al. 2006). We assumed that we sampled breeding affiliations of cranes in proportion to their abundance in each bridge section. We next adjusted numbers of PTT-tagged cranes by bridge section to reflect the proportion of roosting cranes of each breeding affiliation in each bridge section using estimates available from infrared videography.

We investigated areas that cranes of each breeding affiliation occupied on fall staging areas in the northern plains and on the wintering grounds in Texas to gain insight into spatial relationships among the 4 breeding affiliations. Given the large spatial scale of our coverage, we converted all locations to meters using a cylindrical equal area map projection to minimize area distortion (Yildirim and Kaya 2008). Because multiple locations with minimal temporal separation are often resolved during one PTT transmission event, we calculated an average location, weighted by LC, for each individual bird and satellite overpass using all resolved locations in the final database. We created kernel density estimates using ArcMap software. We set the grid-cell parameter to the mean error estimate from all locations in our final dataset (12.231 km) based upon *NQ* (0–3) observed by Keating et al. (1991) and LC-A and LC-B reported in Soutullo et al. (2006). We used an interactive average-nearest-neighbor approach in setting the bandwidths (*k*) for the analyses, integrating average-nearest-neighbor values for *k* until nominal coverage and actual coverage of 50%, 75%, and 95% kernel density estimates (KDEs) were similar. We found that the 5th average-nearest-

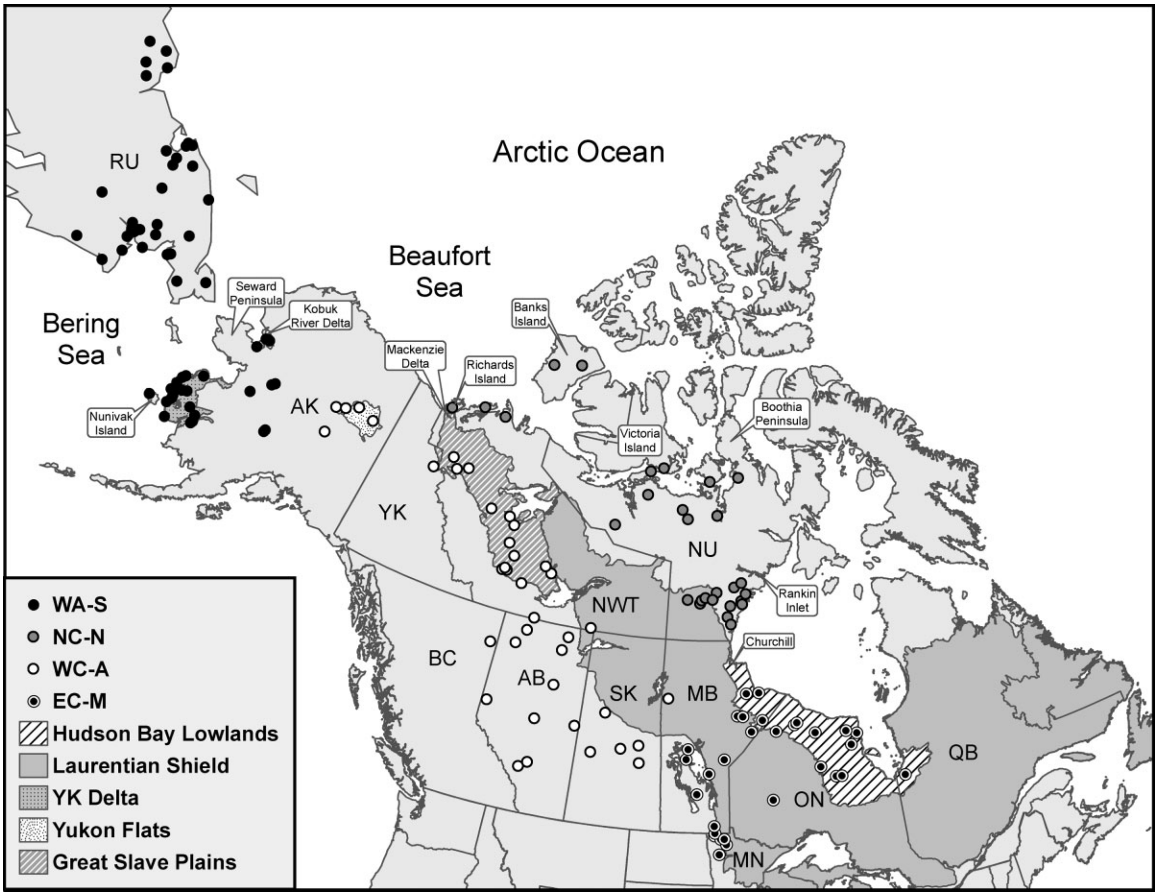

Figure 5. Locations where Platform Transmitting Terminal (PTT)-tagged sandhill cranes (*n* = 153) of the Mid-continent Population settled on breeding grounds in the United States, Canada, and Russia, 1998–2004. Locations are by breeding affiliation, that is, Western Alaska–Siberia (WA–S), Northern Canada–Nunavut (NC–N), West-central Canada–Alaska (WC–A), and East-central Canada–Minnesota (EC–N). Abbreviations of states, provinces, and territories are as follows: AK = Alaska, AB = Alberta, BC = British Columbia, MB = Manitoba, MN = Minnesota, NU = Nunavut, NWT = Northwest Territories, ON = Ontario, QB = Quebec, SK = Saskatchewan, YT = Yukon Territory.

neighbor distance (9,687 m) fit the fall staging data well and the 11th average-nearest-neighbor distance (10,296 m) fit the wintering area data well.

We used grid-cell counts based on the average size of our errors to summarize the area used by each breeding affiliation and to estimate the utilization distribution (UD) for each. We computed 5 overlap indices (Fieberg and Kochanny 2005) for each pair of breeding affiliations. We used 3 of these metrics, 2 for interpreting overlap via probabilities of co-occurrence ($\mathrm{PHR}_{i,j}$ and $\mathrm{PHR}_{j,i}$) and 1 for quantifying space-use sharing (i.e., the UD overlap index [UDOI]). Probability of breeding affiliation *j* being located in an area used by breeding affiliation *i* ($\mathrm{PHR}_{i,j}$) accounts for how much a cell was used. We computed $\mathrm{PHR}_{i,j}$ by summing the probability of use by breeding affiliation *j* across cells used by both breeding affiliations *i* and *j*. We needed to compute $\mathrm{PHR}_{i,j}$ separately for the overlap of breeding affiliation *i* with *j* and the overlap of breeding affiliation *j* with *i*, which resulted in 2 values for each overlap index for each pair of breeding affiliations. The UDOI is non-directional and we only needed to compute it once for each pair of breeding affiliations. The utilization distribution overlap index equals zero for 2 breeding affiliations with no overlap and equals 1 for 2 breeding affiliations if both UDs are uniformly distributed and have complete overlap; however, UDOI can also exceed 1 if the UDs of 2 breeding affiliations are non-uniformly distributed and have a high degree of overlap.

To estimate crane exposure to hunting seasons, we eliminated all locations from the final dataset except for those dates where hunting was allowed under the Federal framework for sandhill crane hunting seasons in accordance with the Migratory Bird Treaty Act (1 Sep–10 Mar). For each tagged crane, we summarized the dates when it occurred in a state or a zone within a state for that time frame. Some cranes were located in multiple states or zones within a state on the same day and we assigned exposure to each. We then compared specific season dates where crane hunting was allowed within each state and any hunting zones within a state for each year to the defined exposure period for each crane. If that date or span of dates fell within the defined hunting season, we assigned exposure to hunting. If a tagged crane was located in a state or hunting zone within a state that allowed hunting but no season was in effect for that period, or if a crane was located in a state that did not have a crane hunting season, we assigned exposure to the non-hunting category. We summarized these data for descriptive presentation as mean exposure to hunting and non-hunting by state and province, by hunting unit within state, and by breeding affiliation.

We estimated harvest of the MCP by breeding affiliation by assigning harvest in proportion to the exposure of tagged cranes of each breeding affiliation within each state or province. For Saskatchewan, Manitoba, North Dakota, and Texas, where nearly 80% of the annual crane harvest occurred, we used smaller-scale calculations (county level for states, and 1° latitude by 2° longitude for provinces) to estimate use and harvest. We then multiplied proportional use by each breeding affiliation by the average annual harvest during the same years as our study (1998–2003) to arrive at an estimated harvest by breeding affiliation.

RESULTS

We attached PTTs to 153 cranes in the CPRV and NPRV of Nebraska and monitored the birds via receivers on NOAA weather satellites for 7 years between 1 April 1998 and 30 May 2004. We tagged 131 sandhill cranes (86%) with PTTs in the CPRV and 22 (14%) in the NPRV. We excluded the 2003 sample of tagged cranes from analyses that required a random sampling of the entire population because in that year, we focused on capturing and tagging a representative sample of greater sandhill cranes to gain more insight into life history of this less plentiful but important component of the MCP. We tracked an average of 35 cranes (range = 4–56) annually (Table 2); median duration of tracking of individual cranes was 352 days, and we tracked 73 cranes >12 months. Overall, tracking effort yielded 74,041 Argos-determined locations over 49,350 tag-days (Table 2). We used these locations for analyses after we applied the filter algorithm and manually scrutinized the location data. Number of cranes monitored each month and number of days they carried functioning PTTs peaked in spring shortly after tagging and declined through late winter (Table 3).

Analysis of mtDNA genotypes for 129 tagged cranes (we did not perform mtDNA analysis on 4 birds tagged in 1998) indi-

Table 2. Satellite-tracking effort by year, as measured by the number of Platform Transmitter Terminal (PTT)-tagged sandhill cranes and number of days that sandhill cranes were carrying functioning PTTs from March 1998 to June 2004, in mid-continent and northwestern North America, and northeastern Asia.

	Year of study						
	1998	1999	2000	2001	2002	2003	2004
Tagged cranes (*n*)	4	18	41	54	56	50	20
Tag-days (*n*)	1,036	4,654	6,914	11,019	12,749	10,970	2,008

Table 3. Satellite-tracking effort by month, as measured by the number of individual Platform Transmitter Terminal (PTT)-tagged sandhill cranes that transmitted successfully during each month of each calendar year from deployment to last successful transmission while in mid-continent and northwestern North America, and northeastern Asia. Tag-days represent the total number of days that sandhill cranes were carrying functioning PTT tags each month from March 1998 to June 2004, inclusive.

	Month of study											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Tagged cranes (*n*)	86	89	196	221	211	193	166	138	129	114	98	92
Tag-days (*n*)	2,718	2,361	4,189	6,484	6,374	5,489	4,792	4,168	3,679	3,393	2,872	2,831
% of total days	5.5	4.8	8.5	13.1	12.9	11.1	9.7	8.5	7.5	6.9	5.8	5.7

cated 83 (64%) were lesser sandhill crane and 46 (36%) were greater sandhill crane. Based on morphometry, 56%, 38%, and 5% of tagged cranes ($n = 133$) were lesser sandhill crane, the Canadian sandhill crane morph, and greater sandhill crane. The tagged sample of 20 sandhill cranes from 2003 were all *G. c. tabida* based on mtDNA lineage and 30% greater sandhill crane and 70% Canadian sandhill crane based on morphometry.

Geographic Distribution During Breeding Season

MCP-tagged adult cranes captured in the CPRV ($n = 131$) and NPRV ($n = 22$) settled on breeding grounds on 2 continents (North America, Asia) and 3 nations (U.S., 23% [$n = 35$]; Canada, 57% [$n = 87$]; and Russia, 20% [$n = 31$]; Fig. 5). Of tagged cranes, 97% spent the breeding season on the continental land masses of North America ($n = 117$) and Asia ($n = 31$), and 3% ($n = 5$) spent the breeding season on arctic islands off the coast of continental North America on Richards Island ($n = 1$), Banks Island ($n = 2$), and Victoria Island ($n = 1$) in Canada and on Nunivak Island ($n = 1$) in Alaska. In the United States, tagged cranes settled in Minnesota (3%) and Alaska (20%); in Canada they settled in Quebec (<1%), Ontario (7%), Manitoba (9%), Saskatchewan (3%), Alberta (7%), Nunavut (15%), British Columbia (<1%), Northwest Territories (14%), and Yukon Territory (<1%); in Russia, they settled in northeastern Siberia (20%; Fig. 5). Annual movements and geographic distribution of MCP sandhill cranes that breed in northeastern Russia, their ecology, estimated harvest, and factors influencing recent breeding range expansion will be addressed in a separate publication (G. L. Krapu, unpublished data).

Tagged cranes of the EC–M breeding affiliation settled primarily in the Hudson Bay Lowlands near James Bay in northeastern Manitoba, northern Ontario and western Quebec, the Interlake region of central Manitoba, and northwestern Minnesota and adjacent parts of southeastern Manitoba (Fig. 5). Of 30 tagged cranes that settled in East-central Canada and northwestern Minnesota during spring, 93% ($n = 28$) were greater sandhill crane, 3% ($n = 1$) were lesser sandhill crane, and 3% ($n = 1$) were unclassified based on results from mtDNA analyses, whereas 70% ($n = 20$) were Canadian sandhill crane and 30% ($n = 10$) were greater sandhill crane based on morphometry. From the smaller, randomly trapped sample of 19 tagged EC–M cranes (excluding 2003 cranes), which represented an estimated 14 ± 3% of the MCP, 42% settled in central and southeastern Manitoba, central Ontario, and northwestern Minnesota, and 58% settled in northeastern Manitoba, northern Ontario, and western Quebec (Fig. 5).

Sandhill cranes of the WC–A breeding affiliation settled in central Saskatchewan, across central and northern Alberta, northeastern British Columbia, the Great Slave Plains in the Northwest Territories, and in the Yukon Flats of east-central Alaska (Fig. 5). Of 39 WC–A tagged cranes, 85% ($n = 33$) were greater sandhill crane and 15% ($n = 6$) were lesser sandhill crane based on mtDNA, whereas 90% ($n = 35$) were Canadian sandhill crane, 8% ($n = 3$) were greater sandhill crane, and 2% ($n = 1$) were lesser sandhill crane based on morphometry. Of 30 randomly tagged cranes, representing an estimated 23 ± 4% of the MCP that settled in west-central Canada and interior Alaska, 66%, mostly Canadian sandhill cranes, settled from interior Alaska eastward to the Northwest Territories, and 33%, also mostly Canadian sandhill cranes, settled primarily in Saskatchewan and Alberta (Fig. 5).

Cranes of the WA–S breeding affiliation settled in western Alaska from the Yukon-Kuskokwim Delta northward to the Seward Peninsula and in northeastern Russia. Of the 56 tagged sandhill cranes that settled in western Alaska and northeastern Russia, 92% ($n = 52$) were lesser sandhill crane, 4% ($n = 2$) were greater sandhill crane, and 4% ($n = 2$) were unclassified based on results from mtDNA analyses. Based on morphometry, 88% ($n = 49$) were lesser sandhill crane and 12% ($n = 7$) were Canadian sandhill crane. This group of tagged cranes represented an estimated 42 ± 4% (SE) of the MCP. Of tagged cranes that stayed in western Alaska, 64% settled on the Yukon-Kuskokwim Delta; remaining tagged WA–S cranes in Alaska settled northeast near Nikolai, along the inner reaches of the Yukon River and northward to the Seward Peninsula and Selawik National Wildlife Refuge (NWR) near the Kobuk River Delta (Fig. 5).

Sandhill cranes of the NC–N breeding affiliation were distributed from near the Arctic Ocean in the Yukon Territory eastward to the Boothia Peninsula, in parts of the Canadian Archipelago (i.e., Richards Island, Banks Island, and Victoria Island), and on the northwest side of Hudson Bay (Fig. 5). Based on their mtDNA, 96% of PTT-tagged NC–N cranes ($n = 27$) were lesser sandhill crane and 4% ($n = 1$) were unclassified based on results from mtDNA analyses; 83% ($n = 25$) were lesser sandhill crane and 17% ($n = 3$) were Canadian sandhill crane, based on morphometry. Our NC–N sample represented an estimated 21 ± 4% of the MCP, and 50% settled along the western and central Arctic coast and high Arctic islands versus 50% along the northwest side of Hudson Bay (Fig. 5). In the western Canadian Arctic, tagged cranes settled principally on or near the MacKenzie Delta and on Banks Island. In the central Canadian Arctic, PTT-tagged cranes settled near the Arctic Ocean eastward from near Bathhurst Inlet to the southwest edge of Boothia Peninsula (Fig. 5). Along the northwest side of Hudson Bay, cranes were distributed across approximately 50,000 km^2 from near Rankin Inlet southward to near the Manitoba border at 60°N, a distance of approximately 260 km (Fig. 5).

We found only marginal differences between the percentage of tagged cranes of each breeding affiliation by bridge section in the CPRV based on our adjusted tagged sample and the percentage obtained after adjusting for any disparities in distribution based on crane estimates from aerial infrared videography (see Totals by breeding affiliation, Table 4). The largest difference between the 2 estimates was for EC–M, which averaged 1.0% less after adjusting for population distribution based on results from infrared videography (Table 4). A potential cause for this difference, based on knowledge gained from related work, is that EC–M cranes, on average, leave the CPRV 6, 8, and 10 days earlier than cranes from WC–A, NC–N, and WA–S (G. Krapu, unpublished data) so a higher proportion of cranes from this breeding affiliation may have left by the dates of the surveys. Of the 22 cranes we captured and tagged in the NPRV, 90% were WA–S cranes. When we added these birds to tagged cranes from the CPRV, WA–S became the most numerous breeding affiliation (56 of 133), accounting for 42.1% of the MCP (Table 4).

Table 4. Distribution of sample of 133 Platform Transmitter Terminal (PTT)-tagged sandhill cranes by river section and breeding affiliation in the Central Platte Valley and North Platte Valley, Nebraska, compared with distribution of cranes on nocturnal roosts obtained by infrared videography (IR) during 2000–2003 (Kinzel et al. 2006). Data in IR columns represent the estimated number of cranes by breeding affiliation that would have been PTT-tagged if capture proportions by river segment had been equivalent to crane breeding affiliation composition based on IR distribution.

	River segment								Totals			
	Lexington to Kearney		Kearney to Shelton		Shelton to Chapman		North Platte[b]		PTTs		IR	
Breeding affiliation[a]	PTTs	IR	PTTs	IR	PTTs	IR	PTTs	IR	No.	%	No.	%
WA–S	9	6.0	13	16.9	14	13.0	20	20	56	42.1	56.0	42.1
NC–N	6	4.0	12	15.6	8	7.4	2	2	28	21.1	29.1	21.9
WC–A	1	0.7	7	9.1	22	20.5	0	0	30	22.6	30.3	22.7
EC–M	0	0	0	0	19	17.7	0	0	19	14.3	17.7	13.3
Combined	16	10.7	32	41.7	63	58.6	22	22	133		133	

[a] WA–S = Western Alaska–Siberia, NC–N = Northern Canada–Nunavut, WC–A = West-central Canada–Alaska, EC–M = East-central Canada–Minnesota.

[b] Estimates are not available on percentage of MCP cranes that occupied the North Platte section from IR. However, the 16.5% (22/133) of our PTT-tagged sample that came from the North Platte section would represent an estimated 99,000 cranes in an MCP numbering 600,000 birds. This estimate is only marginally higher than the 93,225 cranes estimated for the North Platte section based on aerial surveys conducted by the U.S. Fish and Wildlife Service and Nebraska Game and Parks Commission (J. Solberg, U.S. Fish and Wildlife Service, personal communication; M. Vrtiska, Nebraska Game and Parks Commission, personal communication).

Philopatry and Chronology of Use of Breeding Grounds

All 53 tagged sandhill cranes returning to breeding grounds in the second year after tagging settled at sites near those occupied during the previous year (Table 5), with 38% at sites averaging <1 km from the previously occupied locations. All returning birds were located <8 km from the activity center occupied during the previous breeding season (median distance = 1.6 km). No tagged birds switched breeding affiliation between years.

Mean arrival dates for cranes of the 4 breeding affiliations on their breeding grounds varied by up to 32 days, with the EC–M affiliation being the first to arrive followed by WC–A, WA–S, and NC–N affiliations (Table 6). Cranes of the EC–M affiliation spent the most time on their breeding grounds followed by cranes in the WC–A, WA–S, and NC–N affiliations (Table 6). In autumn, cranes from the WC–A affiliation were the first to depart from the breeding grounds, followed by cranes from EC–M, WA–S, and NC–N affiliations (Table 6).

Fall Migration Routes

Cranes of WC–A affiliation breeding in northern Alberta, northeastern British Columbia, the Northwest Territories, Yukon Territory, and Alaska migrated southeastward on flight paths to their fall staging areas in central Saskatchewan (Fig. 6A). Cranes of WC–A affiliation breeding in Saskatchewan required short flights to reach their fall staging areas in central Saskatchewan. When departing from their fall staging areas, WC–A cranes migrated southeast across southeastern Saskatchewan and through central and western North Dakota, South Dakota, Nebraska, Kansas, and Oklahoma, en route to wintering grounds located primarily in western, central, and coastal Texas (Fig. 6A). Only 5 of 29 cranes (17%) stopped in North Dakota for any period of time (range 3–7 days).

All EC–M cranes breeding in Manitoba, Ontario, and Quebec ($n = 22$) migrated in September to fall staging areas in southwestern Manitoba and North Dakota (Fig. 6B). Of those, 36% ($n = 8$) went first to southwestern Manitoba then continued on to North Dakota, whereas 27% ($n = 6$) staged exclusively in Manitoba and 36% ($n = 8$) proceeded directly to North Dakota. Four EC–M cranes breeding east of the Inter-lakes Region of central Manitoba and 1 crane that spent the breeding season in the Interlake Region staged 9–21 days between Lake Winnipeg and Lake Manitoba before continuing to staging areas in southwestern Manitoba and eastern North Dakota (Fig. 6B). All EC–M cranes breeding in northwestern Minnesota ($n = 4$) staged during fall in northwestern Minnesota and migrated southwestward to their wintering grounds without stopping in North Dakota or southwestern Manitoba. One EC–M crane breeding in southeastern Manitoba near the Minnesota border staged in eastern North Dakota.

When departing from fall staging areas, EC–M cranes migrated southward within a narrow migration corridor that approximately followed the route of U.S. Highway 281 through the plains states (Fig. 6B) and mostly east of WC–A, which migrated across a wider corridor that extended from the central to near the western borders of the plains states (Fig. 6A). About 48% of EC–M cranes ($n = 11$) utilized areas in Kansas (especially Kirwin NWR, Quivira NWR, and Cheyenne Bottoms Wildlife Area) and Oklahoma (especially along the Red River on the Texas–Oklahoma border) before continuing on to more southerly destinations. Of EC–M cranes, 22% ($n = 5$) terminated fall migration

Table 5. Median and mean distances in kilometers separating locations on the breeding grounds during successive years for Platform Transmitting Terminal (PTT)-tagged sandhill cranes of the Western Alaska–Siberia, Northern Canada–Nunavut, West-central Canada–Alaska and the East-central Canada–Minnesota breeding affiliations, 1998–2004. We did not include birds with <5 locations on the breeding grounds in a year.

Breeding affiliation	n	Median	$\bar{x}$	SE
Western Alaska–Siberia	13	1.81	3.16	0.76
Northern Canada–Nunavut	4	0.99	1.64	0.91
West-central Canada–Alaska	18	1.13	1.97	0.50
East-central Canada–Minnesota	18	1.78	2.06	0.47

Table 6. Mean arrival date, departure date, and length of stay of Platform Transmitting Terminal (PTT)-tagged sandhill cranes by breeding affiliation on the breeding grounds. We captured PTT-tagged sandhill cranes while they were on spring staging areas in the Central Platte River Valley and North Platte River Valley of Nebraska, 1998–2003. We calculated dates using mid-points of appropriate previous and successive locations.

	Arrival date[a]			Departure date[a]			Length of stay (days)		
Breeding affiliation	***n***	$\bar{x}$	**SE (days)**	***n***	$\bar{x}$	**SE (days)**	***n***	$\bar{x}$	**SE**
Western Alaska–Siberia	69	17 May	1.0	40	3 Sep	1.6	40	108	2.1
Northern Canada–Nunavut	32	25 May	1.8	20	8 Sep	1.5	19	107	3.1
West-central Canada–Alaska	57	30 Apr	1.5	35	20 Aug	2.8	35	113	3.9
East-central Canada–Minnesota	47	23 Apr	1.8	25	30 Aug	2.9	25	127	4.0

[a] We did not include cranes with location intervals >10 days between previous and successive locations.

in areas north of or along the Red River on the Texas–Oklahoma border. By mid-December, EC–M cranes had largely arrived at their final winter destination either on the Texas Gulf Coast, western Texas, or east-central Texas or remained at sites in Oklahoma or Kansas.

Cranes of WA–S affiliation departing from the Yukon-Kuskokwim Delta breeding grounds migrated northeastward in early September and converged in central Alaska with cranes coming from Russia (Fig. 6C). After migration paths of cranes from western Alaska and Russia merged, the birds flew southeast within a narrow corridor (30–50 km wide), mostly following the Tanana River. In southeastern Alaska, the birds crossed over to the Pelly River Valley and continued southeastward across Yukon Territory, northeastern British Columbia, and northwestern, central, and southeastern Alberta to their primary fall staging area in southwestern Saskatchewan, adjacent to the western reaches of the South Saskatchewan River (Fig. 6C).

Cranes of WA–S affiliation departed in mid-October from western Saskatchewan after staging for approximately 1 month, migrating southeast across central and eastern Montana, eastern Wyoming, eastern Colorado, and northeastern New Mexico en route to their primary wintering grounds in western Texas. The eastern edge of the fall migration corridor of WA–S cranes extended into western South Dakota, Nebraska, Kansas, and the panhandle of Oklahoma (Fig. 6C). When WA–S cranes within the primary migration corridor reached northeastern New Mexico, 76% continued to western Texas, whereas 24% took direct routes to wintering areas in central New Mexico, southeastern Arizona, and northern Mexico (Fig. 6C). Three cranes (9%) initially utilized wintering areas in western Texas but ultimately migrated into northern Mexico. Two cranes initially migrated to northern Mexico and then moved east back into western Texas; one ultimately settled in Coahuila (Fig. 6C). Tagged WA–S cranes made no major stops during migration from fall staging areas to wintering grounds.

Tagged NC–N cranes during the breeding season were distributed from near the coast in Yukon Territory eastward across the Arctic to near Churchill, Manitoba on Hudson Bay (Fig. 6D). As a result of this wide breeding distribution, several migration routes were followed when moving from major breeding grounds to primary fall staging areas in central and east-central Saskatchewan, and northwestern and central North Dakota. Tagged cranes breeding on Banks Island migrated southeast through the central part of the Northwest Territories and continued on a southeasterly course across northeastern Alberta en route to fall staging areas in central Saskatchewan (Fig. 6D). Cranes breeding west of Hudson Bay in Nunavut flew southwest across northwestern Manitoba en route to staging areas. Three of 12 (25%) cranes from this breeding area continued on a southwest course until they reached the Quill Lakes area of Saskatchewan, whereas the remaining 9 (75%) birds crossed into Saskatchewan stopping only briefly before moving on to fall staging areas in central North Dakota. The 3 NC–N cranes from the western Hudson Bay breeding area that staged primarily in Saskatchewan migrated southeast into North Dakota, where 2 birds were known to have stopped for a short period. From North Dakota, all NC–N cranes migrated south through central South Dakota and in central Nebraska turned southwest and crossed western Kansas and the panhandle of Oklahoma en route to their wintering grounds in western Texas (Fig. 6D); NC–N cranes made no major stops between their fall staging areas and wintering grounds.

Chronology of Migration to Fall Staging Areas

We used median weekly locations to represent overall movement of individuals from each breeding affiliation. Fall migrations of WC–A and EC–M breeding affiliations began during the third and fourth weeks of August (weeks [WKs] 33 and 34; Fig. 7), with mean departure dates from breeding areas of 20 August and 30 August, respectively (Table 6). By WK 35 (27 Aug–2 Sep), WC–A and EC–M cranes had moved 1,245 km and 175 km, respectively, from sites occupied during the breeding season (Fig. 7). Cranes of WC–A affiliation migrated more rapidly than EC–M cranes and reached their fall staging areas, on average, 6 days earlier (Table 7). After EC–M cranes arrived on their fall staging areas, the center of the EC–M crane distribution gradually moved from southern Manitoba into eastern North Dakota during 10 September–21 October (WKs 37 to 42; Fig. 7). As determined by median location, WC–A and EC–M cranes traveled approximately 1,400 km and 700 km from breeding grounds to fall staging areas in central Saskatchewan and southwestern Manitoba, respectively. Distribution of WC–A cranes changed only slightly during 3 September–14 October (WKs 36–41), whereas the median location of the EC–M crane distribution moved south 93 km by 1–7 October (WK 39 to WK 40). By 15–21 October (WK 42), EC–M distribution had moved another 123 km, with cranes becoming widely dispersed in eastern and central North Dakota (Fig. 7). From median arrival to median departure on their fall staging areas in Saskatchewan and Manitoba/North Dakota, WC–A and EC–M cranes moved a weekly average of 34 km and 61 km, respectively.

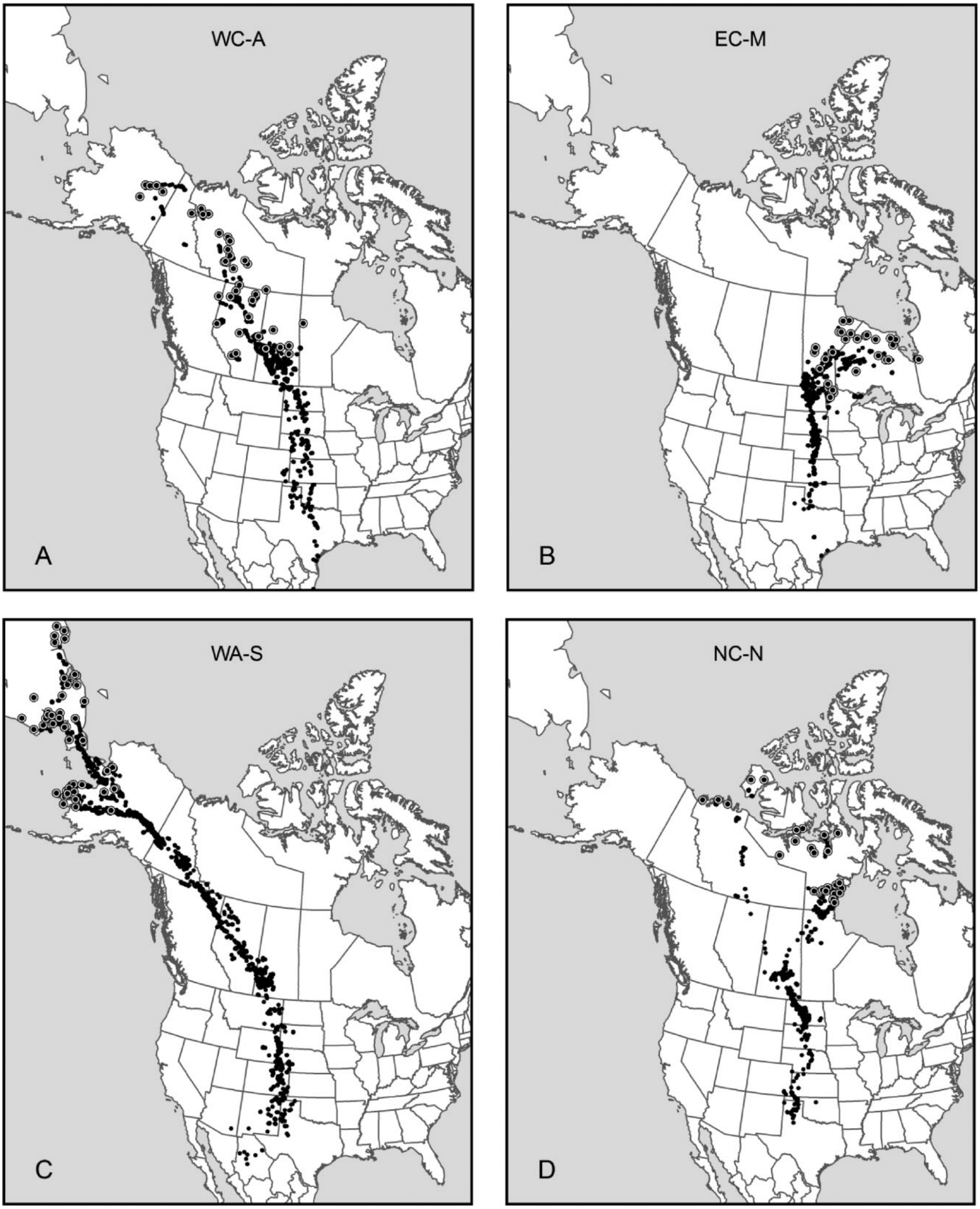

Figure 6. Fall migration routes of Platform Transmitting Terminal (PTT)-tagged MCP sandhill cranes of the 4 breeding affiliations: (A) West-central Canada–Alaska [WC–A]; (B) East-central Canada–Minnesota [EC–M]; (C) Western Alaska–Siberia [WA–S]; (D) Northern Canada–Nunavut [NC–N] based on their PTT-locations during fall 1998–2003. Closed circles with white rings represent breeding locations for cranes of each breeding affiliation.

The WA–S breeding affiliation initiated fall migration during 3–9 September (WK 36) with a mean departure date of 3 September (Table 6). During WKs 36–38, the center of the WA–S crane distribution moved 500 km, 808 km, and 2,436 km, respectively, southeast from the Chutkotka Peninsula which lies adjacent to the Bering Strait separating Alaska from Russia (Fig. 8). Cranes of WA–S affiliation staged primarily near Cabri and other areas near the South Saskatchewan River south

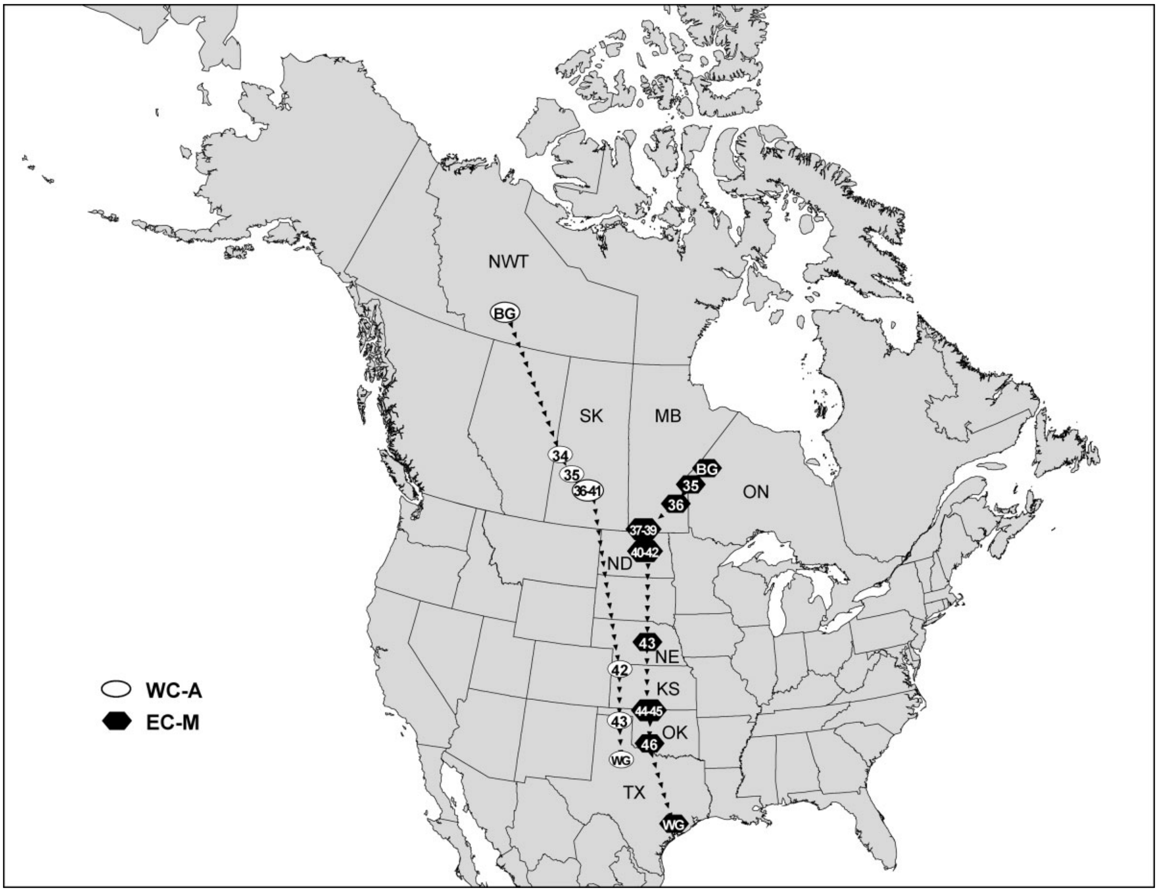

Figure 7. Median weekly locations (e.g., 1–7 Jan = week 1, etc.) of Platform Transmitting Terminal (PTT)-tagged sandhill cranes of the West-central Canada–Alaska (WC–A), and East-central Canada–Minnesota (EC–M) breeding affiliations between departure from the breeding grounds and arrival on the wintering grounds, 1998–2003. BG = breeding ground, WG = wintering ground. Numbers within symbols indicate week(s) birds were located at a site.

of Eston in western Saskatchewan during 24 September–14 October (WKs 39–41), with limited movement of cranes occurring during that period (Fig. 8).

Cranes of NC–N breeding affiliation began moving southward from their breeding grounds during 3–9 September (WK 36; Fig. 8) and moved 500 km by the end of the following week (WK 37). By 24–30 September (WK 39), PTT-tagged NC–N cranes had traveled approximately 1,900 km from their median breeding ground locations and most had reached their fall staging sites in east-central Saskatchewan and North Dakota (Fig. 8). During 24 September to 14 October (WKs 39–41), the center of fall distribution of NC–N cranes moved progressively southward across central North Dakota, averaging 119 km per week (Fig. 8). About a third (35%) of NC–N cranes headed directly to east-central Saskatchewan where they spent most of the staging period. Ten of 17 (59%) NC–N cranes continued on to North Dakota, spending less than one week in east-central Saskatchewan, whereas only 1 of 17 birds split the staging interval

Table 7. Mean arrival date, departure date, and length of stay of Platform Transmitting Terminal (PTT)-tagged sandhill cranes by breeding affiliation on fall staging areas and wintering grounds. We captured the PTT-tagged sample of sandhill cranes during springs 1998–2003 while cranes were on spring staging areas in the Central Platte River Valley and North Platte River Valley in Nebraska. We calculated dates using mid-points of appropriate previous and successive locations.

	Arrival date[a]			Departure date[a]			Length of stay (days)		
Breeding affiliation	***n***	$\bar{x}$	**SE (days)**	***n***	$\bar{x}$	**SE (days)**	***n***	$\bar{x}$	**SE**
Location									
Fall staging areas									
Western Alaska–Siberia	35	19 Sep	1.0	32	13 Oct	1.3	32	24	1.2
Northern Canada–Nunavut	18	17 Sep	1.1	17	15 Oct	2.1	17	29	2.5
West-central Canada–Alaska	35	29 Aug	2.5	31	16 Oct	0.9	31	49	3.0
East-central Canada–Minnesota	24	4 Sep	3.2	24	24 Oct	2.2	22	49	2.2
Wintering grounds									
Western Alaska–Siberia	32	17 Oct	1.3	17	6 Mar	2.1	17	140	2.5
Northern Canada–Nunavut	15	18 Oct	1.8	7	9 Mar	3.1	7	144	5.1
West-central Canada–Alaska	31	21 Oct	1.3	20	9 Mar	2.1	20	142	1.8
East-central Canada–Minnesota	25	27 Oct	1.9	19	2 Mar	2.4	19	128	3.2

[a] We did not include cranes with location intervals >10 days between previous and successive locations.

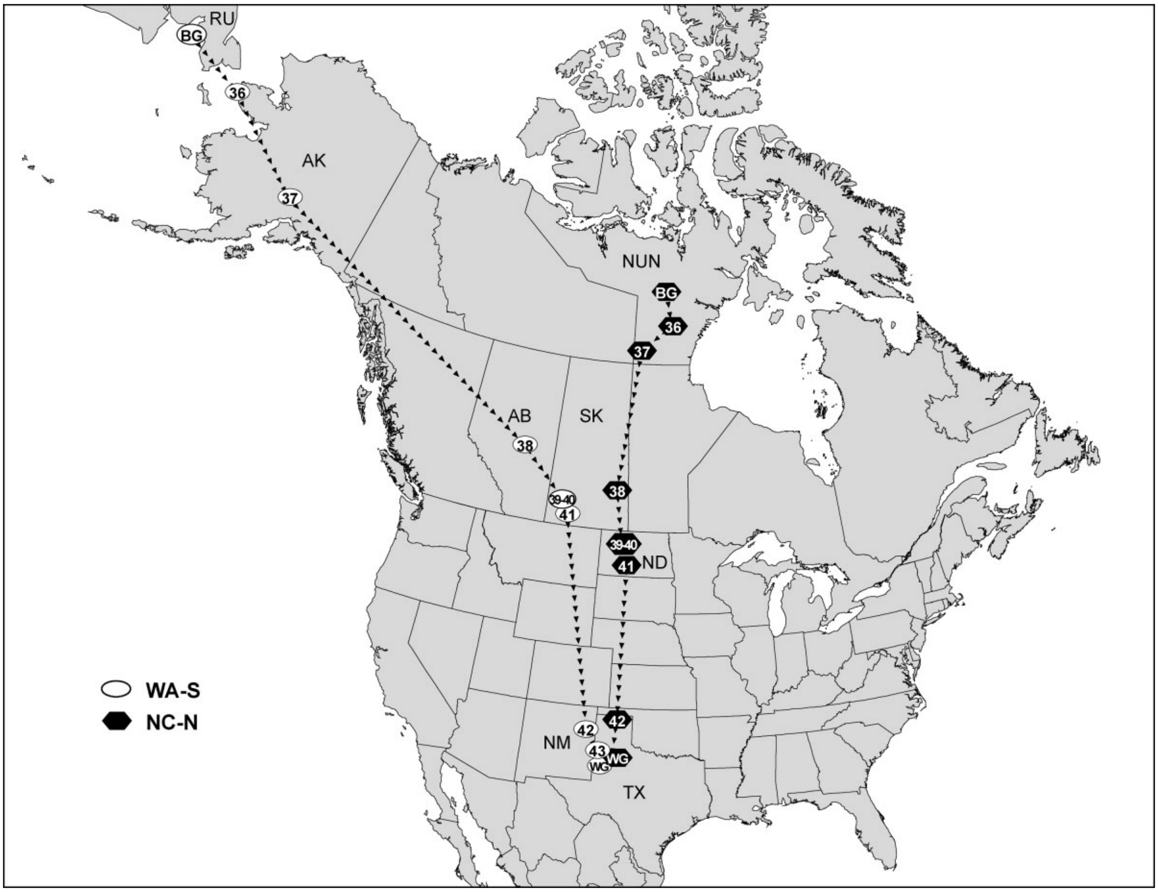

Figure 8. Median weekly locations (e.g., 1–7 Jan = week 1, etc.) of Platform Transmitting Terminal (PTT)-tagged MCP sandhill cranes of the Western Alaska–Siberia (WA–S) and Northern Canada–Nunavut (NC–N) breeding affiliations between departure from the breeding grounds and arrival on the wintering grounds, 1998–2003. BG = breeding ground, WG = wintering ground. Numbers within symbols indicate week(s) birds were located at a site.

between North Dakota and Saskatchewan. Of the 35% (6 of 17) of NC–N cranes that staged primarily in east-central Saskatchewan, the mean duration of stay was 32 days. For those birds from NC–N that stayed primarily in North Dakota, mean length of stay was 19 days. Overall, NC–N cranes spent 29 days on fall staging areas (Table 7).

Use of Fall Staging Areas

Fall staging was centered at traditionally used sites in central and western Saskatchewan (69%); northwestern, central, and eastern North Dakota (16%); southwestern Manitoba (10%); and northwestern Minnesota (3%). Among WA–S and WC–A cranes, 97% of use occurred in Saskatchewan (Table 8; Fig. 9). Cranes of WC–A affiliation were distributed across 2 major areas in Saskatchewan, that is, from the Quill Lakes region, through the Quill plains and Kutawagan basin south to Last Mountain Lake, and adjacent to the South Saskatchewan River from Luck Lake to Saskatoon (Fig. 10). Comparatively, 47% and 52% of fall staging use by NC–N cranes was in North Dakota and Saskatchewan, respectively (Table 8). Sites most used by NC–N cranes in Saskatchewan were near the South Saskatchewan River in the Outlook and the Quill-Kutawagan-Last Mountain Lake areas (Fig. 10). The 16% of MCP fall use that occurred in North Dakota was split between EC–M (49%), NC–N (47%), and WC–A (4%; Table 8) affiliations, with NC–N use centered in Burke, Ward, Kidder, and Emmons counties. Of the 10% of MCP use occurring in Manitoba and the 3% of MCP use occurring in Minnesota during fall staging, all but one crane

Table 8. Distribution of known hunting-exposure days for Platform Transmitting Terminal (PTT)-tagged sandhill cranes from the Mid-continent Population in each state and province by breeding affiliation during fall staging in the northern plains, 1998–2003.

		No. of exposure days by state and province													
Breeding affiliation	***n***	**ND**	**%**	**MN**	**%**	**SD**	**%**	**SK**	**%**	**MB**	**%**	**AB**	**%**	**MT**	**%**
Western Alaska–Siberia	31							622	96.7			18	2.8	3	0.5
Northern Canada–Nunavut	16	176	47.4			3	0.8	192	51.8						
West-central Canada–Alaska	29	27	2.0					1,287	96.5	3	0.2	16	1.2		
East-central Canada–Minnesota	24	408	38.3	154	14.4	20	1.9	1	0.1	483	45.3				
Totals[a]		495	16.3	92	3.0	16	0.5	2,099	69.2	290	9.6	37	1.2	4	0.1

[a] MCP representative sample: Adjusted to represent correct breeding affiliation proportions.

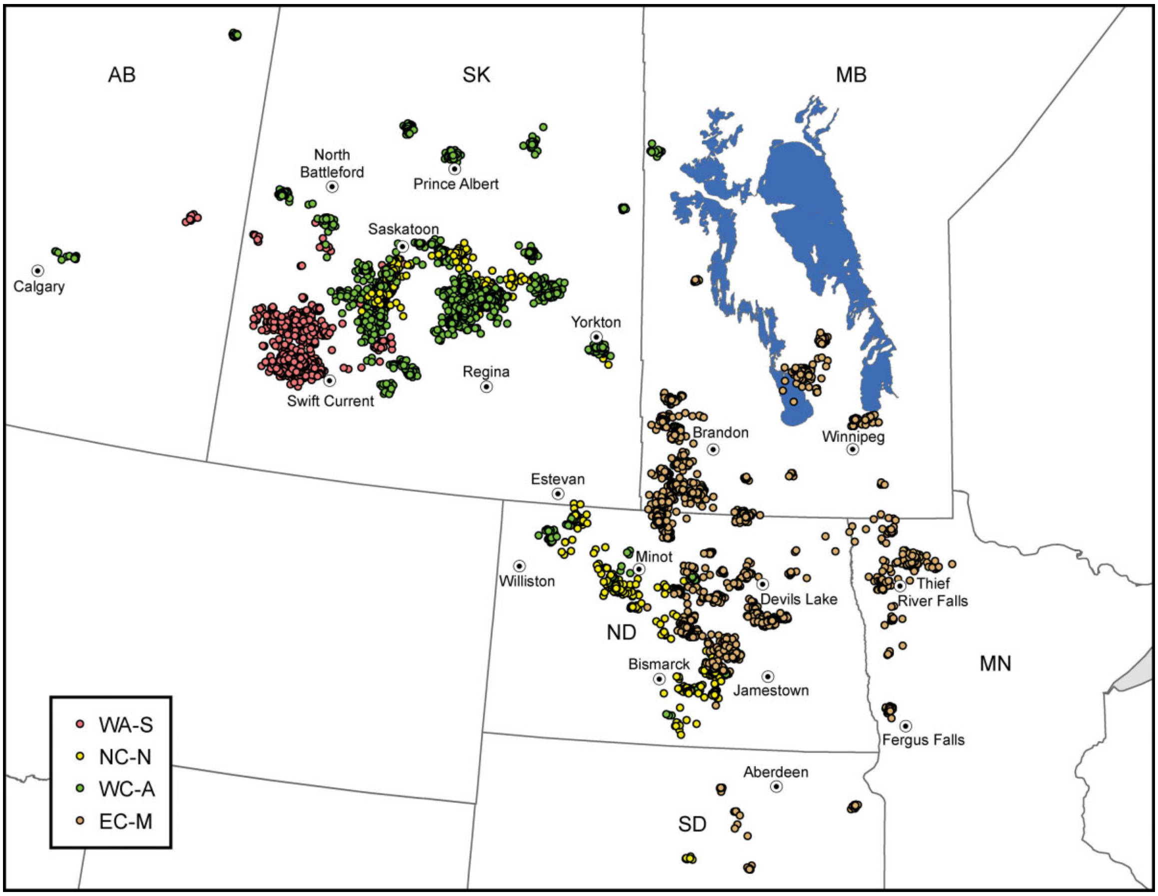

Figure 9. Distributions of Platform Transmitting Terminal (PTT)-tagged sandhill cranes of the Mid-continent Population by breeding affiliation (Western Alaska–Siberia [WA–S], Northern Canada–Nunavut [NC–N], West-central Canada–Alaska [WC–A], and East-central Canada–Minnesota [EC–M]) during fall staging in south-central Canada and the north-central United States, 1998–2003. We color-coded PTT-locations by breeding affiliation.

(a WC–A greater sandhill crane) were of the EC–M breeding affiliation (Fig. 5). Overall, about 38% and 45% of fall locations of EC–M cranes were in North Dakota and Manitoba, respectively (Table 8). Major staging locations of EC–M cranes in North Dakota included Bottineau, Eddy, Sheridan, Stutsman, Wells, and Kidder counties and in Manitoba, the Whitewater–Oak Lake area and Souris River Valley.

During their fall stay in the northern plains EC–M cranes occurred over the largest area of the 4 breeding affiliations (Table 9); no overlap occurred with WA–S cranes and minimal overlap occurred with WC–A cranes (Table 10). Overlap between EC–M and NC–N cranes was limited to North Dakota, mostly in Kidder County (Fig. 10); overlap of 95% KDEs in the state accounted for <3% of their combined use areas, and probability of an individual from one breeding affiliation occurring in the other's area of use was ≤ 0.07 (Table 10).

Cranes of WA–S affiliation staged over the smallest area of the 4 breeding affiliations (Table 9). Overlap with NC–N and WC–A affiliations occurred only in west-central Saskatchewan (Fig. 10). Probability of an individual from WA–S affiliation occurring in the fall use area of NC–N cranes was extremely low ($\mathrm{PHR}_{\mathrm{NC-N,WA-S}} = 0.07$). Cranes of WC–A and WA–S breeding affiliations overlapped approximately 5% of their combined 95% KDEs, with probability of a crane of the WA–S breeding affiliation occurring in a WC–A crane fall use area being less than the opposite ($\mathrm{PHR}_{\mathrm{WC-A,WA-S}} = 0.09$ vs. $\mathrm{PHR}_{\mathrm{WA-S,WC-A}} = 0.16$) reflecting WA–S cranes having a smaller fall use area centered more to the west (Table 9; Fig. 10). Cranes of NC–N and WC–A affiliations overlapped broadly in east-central and central

Table 9. Areas (km^2) occupied by Platform Transmitting Terminal (PTT)-tagged sandhill cranes of the 4 breeding affiliations during fall staging in the northern plains and during winter in Texas, 1998–2004.

	Kernel-density estimate of use area (km^2)							
	Fall staging				Winter			
Breeding affiliation	**95%**	**75%**	**50%**	***n***	**95%**	**75%**	**50%**	***n***
Western Alaska–Siberia	9,306	3,483	1,158	34	19,255	7,999	2,138	24
Northern Canada–Nunavut	14,820	6,637	1,601	17	25,397	11,932	3,631	16
West-central Canada–Alaska	16,788	4,844	1,499	34	33,424	11,535	3,601	28
East-central Canada–Minnesota	24,002	9,034	2,498	25	22,497	6,532	2,184	22

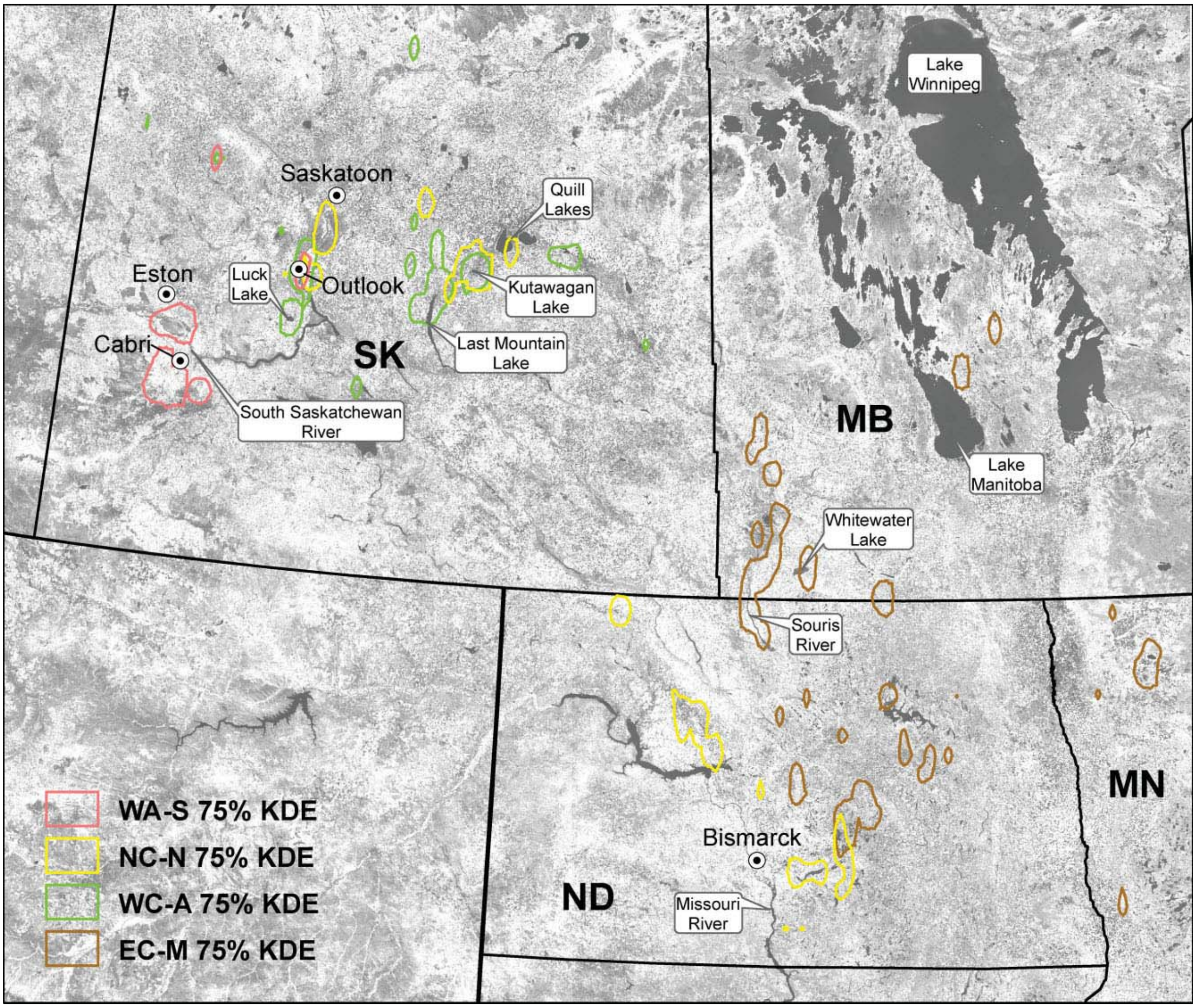

Figure 10. Spatial relationships among MCP sandhill cranes from the 4 breeding affiliations (Western Alaska–Siberia [WA–S], Northern Canada–Nunavut (NC–N], West-central Canada–Alaska [WC–A], and East-central Canada–Minnesota [EC–M]), while on fall staging areas in the northern plains, 1998–2003. We based spatial relationships among the 4 breeding affiliations on 75% kernel density estimates (KDE).

Table 10. Measures of magnitude of overlap in areas occupied by sandhill cranes of the 4 breeding affiliations during fall staging in the northern plains and during winter in Texas 1998–2004.

	Fall staging						Winter					
	KDE overlap[b]			Home range overlap[c]			KDE overlap[b]			Home range overlap[c]		
Breeding affiliations[a]	95%	75%	50%	$\mathrm{PHR}_{i,j}$	$\mathrm{PHR}_{j,i}$	UDOI	95%	75%	50%	$\mathrm{PHR}_{i,j}$	$\mathrm{PHR}_{j,i}$	UDOI
WA–S:NC–N	3.1	0.8	0.0	0.13	0.07	0.01	23.3	20.8	14.7	0.42	0.71	0.55
WA–S:WC–A	5.1	3.9	0.6	0.16	0.09	0.02	11.1	4.5	<0.1	0.19	0.49	0.08
WA–S:EC–M	0.0	0.0	0.0	0.00	0.00	0.00	1.0	0.0	0.0	0.02	0.03	0.00
NC–N:WC–A	9.5	8.6	8.0	0.24	0.32	0.10	20.7	14.5	6.2	0.38	0.54	0.22
NC–N:EC–M	2.9	2.0	<0.1	0.05	0.07	0.00	3.2	0.9	0.0	0.04	0.06	0.00
WC–A:EC–M	0.2	0.0	0.0	0.01	0.00	0.00	10.0	4.8	0.2	0.21	0.30	0.06

[a] WA–S = Western Alaska–Siberia, NC–N = Northern Canada–Nunavut, WC–A = West-central Canada–Alaska, EC–M = East-central Canada–Minnesota.

[b] Percentage of overlap area divided by combined kernel-density estimate (KDE) areas.

[c] $\mathrm{PHR}_{i,j}$ = Probability of finding a crane from breeding affiliation *j* in breeding affiliation *i*'s home range. $\mathrm{PHR}_{j,i}$ = Probability of finding a crane from breeding affiliation *i* in breeding affiliation *j*'s home range. UDOI = Space-use sharing index (0 = no overlap, ≥1 = complete overlap) for 2 home ranges (Fieberg and Kochanny 2005).

Table 11. Distance (in km) between centers of fall staging areas in the northern plains and wintering grounds in Texas by the 4 breeding affiliations based on distribution of PTT locations 1998–2004. Center of use represents the arithmetic mean of all locations for a breeding affiliation.

Breeding affiliation comparison[a]	Fall staging areas	Texas wintering grounds
WA–S:NC–N	604	79
WA–S:WC–A	313	240
WA–S:EC–M	1,022	626
NC–N:WC–A	324	167
NC–N:EC–M	418	552
WC–A:EC–M	731	386

[a] WA–S = Western Alaska–Siberia, NC–N = Northern Canada–Nunavut, WC–A = West-central Canada–Alaska, EC–M = East-central Canada–Minnesota.

Saskatchewan (Fig. 10) with each affiliation occurring in similar proportions over each other's range (Table 10).

Distances between arithmetic mean locations of each of the 4 breeding affiliations while on fall staging areas in the northern plains ranged from 313 km between WA–S and WC–A affiliations to 1,022 km between WA–S and EC–M affiliations (Table 11). Distances separating WA–S from NC–N affiliations (604 km) was nearly twice the distance separating WA–S from WC–A affiliations (313 km). Cranes of WC–A and EC–M affiliations ranked second highest in distance separation (731 km) associated with WC–A cranes staging largely in Saskatchewan and EC–M cranes staging only in Manitoba, Minnesota, and North Dakota (Fig. 9).

The space-use sharing indices for the 4 breeding affiliations on fall staging areas indicated patterns similar to other measurements of overlap. Indices of space-use sharing among breeding affiliations showed no overlap between WA–S and EC–M affiliations, WC–A and EC–M affiliations, or NC–N and EC–M affiliations and only minimal sharing between WA–S and NC–N or WC–A affiliations. Except for NC–N and WC–A affiliations, probability of finding a crane from one breeding affiliation within the home range of a crane from another breeding affiliation was extremely low ($P = 0$–0.16) during fall staging (Table 10).

Chronology of Migration From Fall Staging Areas to Wintering Grounds

Length of stay in the northern plains by cranes from WA–S and NC–N and from EC–M and WC–A averaged about 4 weeks and 7 weeks, respectively, with WC–A and EC–M affiliations spending 25 days and 20 days longer than WA–S and NC–N affiliations, respectively (Table 7). Cranes in all 4 breeding affiliations moved quickly to their wintering grounds, averaging ≤5 days en route (Table 7).

Cranes of WC–A affiliation began their migration to wintering grounds in WK 42, when their median location was centered in northwestern Kansas, about 1,304 km southeast of their median location the previous week (Fig. 7). They arrived on their wintering grounds in western Texas in WK 43 (Fig. 7). Cranes of EC–M affiliation departed fall staging areas centered in North Dakota on 24 October and arrived on wintering grounds on 27 October. However, EC–M and WC–A cranes together spent an average of 10.9 days and 14.0 days in Kansas and Oklahoma (considered part of their winter range), respectively, before continuing on to wintering grounds in Texas. During 22 October–11 November (WKs 43, 44, and 45), weekly median locations of EC–M cranes moved 626 km, 486 km, and 68 km as the center of their distribution moved through Nebraska, to southern Kansas, to northern Oklahoma, respectively (Fig. 7). These movements indicated a slowing of migration as some birds stopped in areas such as the Cheyenne Bottoms Wildlife Management Area (WMA), Quivira NWR, and near the Red River along the border of Texas and Oklahoma. On average, WC–A and EC–M cranes flew 1,986 km and 2,025 km from their primary fall staging areas to arrival at wintering areas.

Cranes of WA–S affiliation departed their staging areas, on average, by 13 October (Table 7) and by 15–21 October (WK 42); their median distribution was centered in eastern New Mexico (Fig. 8). For NC–N cranes, the median weekly location moved slowly southward from 17 September to 13 October remaining in the northern plains (WKs 38–41; Fig. 8). When departing from Saskatchewan for wintering grounds, some NC–N cranes stopped briefly in North Dakota, whereas others continued to the wintering grounds. Cranes of NC–N affiliation began migrating from fall staging areas on 15 October and moved quickly, averaging ≤3 days to areas defined as wintering grounds

Table 12. Distribution of known hunting-exposure days for Platform Transmitting Terminal (PTT)-tagged sandhill cranes from the Mid-continent Population by breeding affiliation while settled on the wintering grounds in each state in south-central and southwestern United States and Mexico, 1998–2004. We calculated exposure days only from tagged birds that we monitored from arrival at the wintering grounds through departure on spring migration after their first winter following tagging.

		Exposure days by state (U.S. and Mexico)															
Breeding affiliation	*n*	TX	%	NM	%	OK	%	KS	%	AZ	%	COA	%	CHH	%	TAM	%
Western Alaska–Siberia	20	1,894	72.5	28	1.1					111	4.2	86	3.3	493	18.9		
Northern Canada–Nunavut	11	1,444	9.9			1	<0.1	1	<0.1								
West-central Canada–Alaska	24	2,830	88.6	1	<0.1	101	3.2	57	1.8			108	3.4			96	3.0
East-central Canada–Minnesota	21	1,808	73.8			325	13.3	268	10.9							48	1.9
Totals[a]		8,087	82.3	45	0.5	242	2.5	181	1.8	178	1.8	215	2.2	789	8.0	93	0.9

[a] Projected MCP exposure: Sample adjusted to represent correct breeding affiliation proportions.

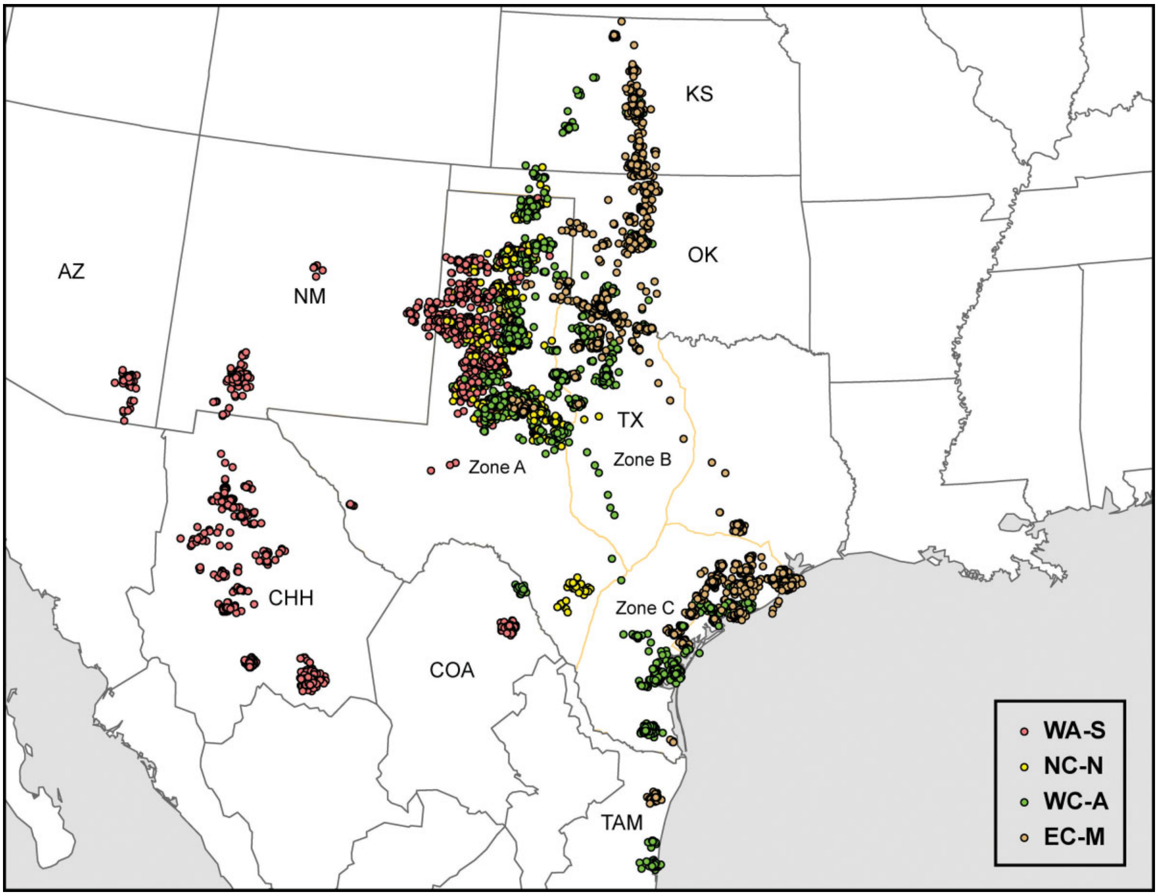

Figure 11. Distribution of Platform Transmitting Terminal (PTT)-tagged sandhill cranes of the Mid-continent Population by breeding affiliation (Western Alaska–Siberia [WA–S], Northern Canada–Nunavut [NC–N], West-central Canada–Alaska [WC–A], and East-central Canada–Minnesota [EC–M]) while on wintering grounds in the south-central and southwestern United States and northern Mexico, 1998–2004. Boundaries of Hunting Zones A, B, and C are included for Texas. We color-coded PTT-locations by breeding affiliation.

in western Texas (Table 7). Cranes of WA–S and NC–N affiliations flew 1,900 km and 1,460 km, respectively, from their last median locations on fall staging areas to arrival on or near their wintering areas.

Use of Wintering Grounds

We estimated that 82% of crane winter use occurred in Texas and remaining use was split between Oklahoma, Kansas, eastern and west-central New Mexico, southeastern Arizona, and the states of Chihuahua, Coahuila, and Tamaulipas in northern Mexico (Table 12; Fig. 11). Cranes of NC–N, WA–S, WC–A, and EC–M affiliations spent 99%, 73%, 64%, and 7%, respectively, of winter in western Texas in Hunting Zone A (Table 13; see Texas Parks and Wildlife Department Program [2010] for locations of sandhill crane hunting zones in TX). Cranes from WC–A wintered mostly in Texas (89%; Table 12) with 81% of use occurring in Hunting Zones A and B (Table 13). Remaining use was in Zone C (18%) and the area closed to hunting (<1%). Cranes from EC–M wintered primarily in Texas (74%), followed by Oklahoma (13%), Kansas (11%), and Tamaulipas (2%; Table 12). Within Texas, EC–M crane use occurred primarily along the Gulf Coast in Zone C (68%), and the Texas High Plains and Rolling Plains in Zones A and B (17%); remaining use occurred in the area closed to hunting (14%; Table 13).

Table 13. Distribution of hunting-exposure days for Platform Transmitting Terminal (PTT)-tagged sandhill cranes of the 4 breeding affiliations by hunting zone in Texas through 10 March, 1998–2004. We include only birds monitored from arrival on wintering grounds through spring departure.

	Hunting zone[a]							
Breeding affiliation	**A**	**%[b]**	**B**	**%[b]**	**C**	**%[b]**	**Closed**	**%[b]**
Western Alaska–Siberia	2,082	67.5	0		0		0	
Northern Canada–Nunavut	1,414	69.7	1	100	0		0	
West-central Canada–Alaska	2,053	69.6	266	69.5	527	21.4	11	0
East-central Canada–Minnesota	162	61.1	148	20.9	1,224	27.2	259	0

[a] Zone A = western Texas panhandle region, zone B = central Texas region, zone C = southeastern Texas, coastal region, Closed = northeastern Texas closed region and small coastal portion of zone C. See Texas Parks and Wildlife Department Program (2010) for more detailed information.

[b] Percentage of stay that birds were susceptible to harvest.

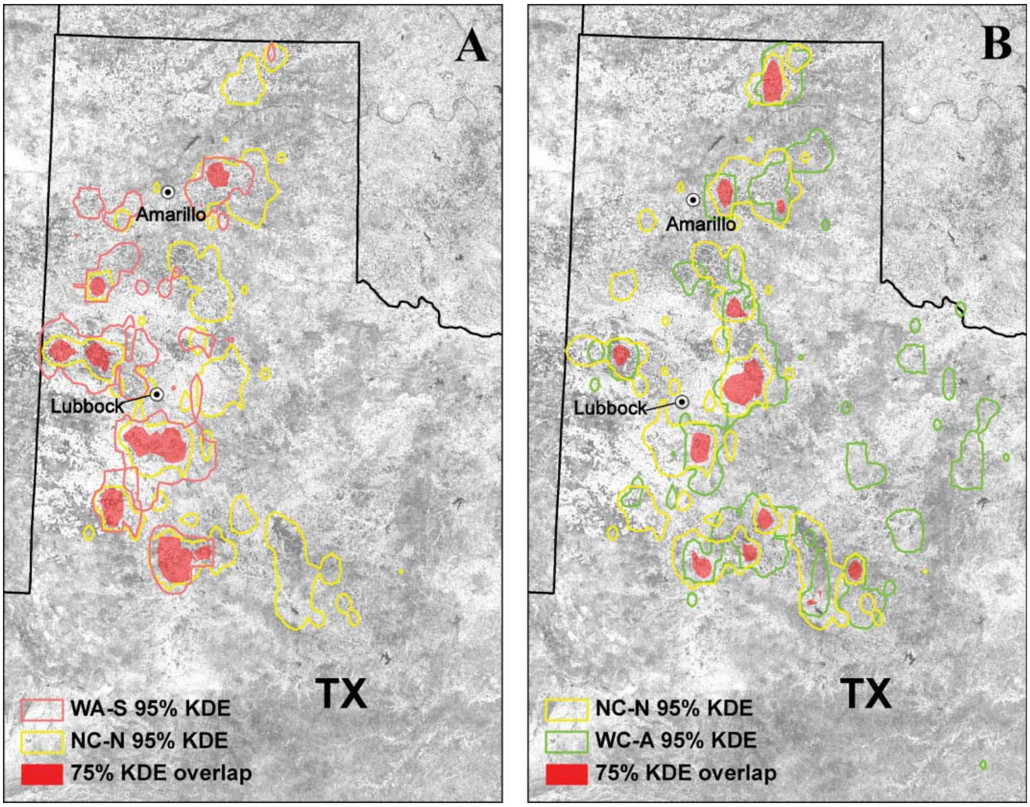

Figure 12. Spatial relationships between (A) sandhill cranes from Northern Canada–Nunavut (NC–N) and Western Alaska–Siberia (WA–S) breeding affiliations while on wintering grounds in Hunting Zone A in Western Texas and (B) sandhill cranes from NC–N and West-central Canada–Alaska (WC–A) breeding affiliations while on wintering grounds in Hunting Zones A and B in Western Texas, 1998–2004. Contour lines represent 95% kernel density estimates (KDE) and shaded areas represent areas where 75% KDEs of breeding affiliations intersect each other.

Mean distances between centers of distribution of each of the 4 breeding affiliations on Texas wintering grounds varied widely, reflecting differing degrees of spatial separation among breeding affiliations (Table 11). Distribution of the WA–S affiliation was centered farthest west of the 4 breeding affiliations in Hunting Zone A in western Texas (Fig. 12A). Overlap of NC–N and WA–S affiliations (75% KDE) was centered in the west-central part of Hunting Zone A (Fig. 12A) and declined eastward where NC–N and WC–A affiliations overlapped broadly (Fig. 12B). In Zone B, few WA–S and NC–N cranes occurred, with overlap restricted to WC–A and EC–M affiliations (Table 13). In Texas, WC–A cranes occupied the largest area; NC–N, WA–S, and EC–M cranes ranged over 24%, 42%, and 33% less area than did WC–A (Table 9). The greatest overlap in area of use occurred between the NC–N and WC–A affiliations ($12{,}199\ \mathrm{km}^2$), but the greatest percentage of overlap was between WA–S and NC–N affiliations (Table 10). The difference between overlap of use areas versus magnitude of geographic overlap is better illustrated by the space-use sharing index, which indicated that NC–N and WA–S affiliations had an overlap value >2 times that of NC–N and WC–A affiliations (Table 10). Probability of finding an individual from the NC–N breeding affiliation in WA–S crane home range was nearly equivalent to the probability of finding the bird in WC–A crane home range ($\mathrm{PHR}_{\mathrm{WA-S,NC-N}} = 0.42$ vs. $\mathrm{PHR}_{\mathrm{WC-A,NC-N}} = 0.54$), whereas probability of an individual WA–S crane occurring in the home range of the NC–N affiliation was 1.9 times greater than a WC–A crane occurring there ($\mathrm{PHR}_{\mathrm{NC-N,WA-S}} = 0.71$ vs. $\mathrm{PHR}_{\mathrm{NC-N,WC-A}} = 0.38$; Table 10).

Distribution of the EC–M breeding affiliation overlapped least with the other 3 breeding affiliations in Texas (Table 10) primarily because most EC–M cranes wintered along the Gulf Coast where few NC–N and WA–S cranes occurred (Fig. 11). The EC–M crane distribution during winter was concentrated along the upper Texas Gulf Coast, whereas WC–A cranes occurred primarily along the lower Texas Gulf Coast (Fig. 11). In Hunting Zone B, WC–A and EC–M cranes accounted for 64% and 36% of use, respectively (Table 13). Outside of Texas, there was little overlap among breeding affiliations on wintering grounds as WA–S cranes accounted for nearly all exposure days in New Mexico, Arizona, Chihuahua (Table 12), and presumably other states in Mexico where some MCP lesser sandhill cranes occur (Durango and Zacatecas; Tacha et al. 1994) but no tagged birds settled. Cranes of EC–M affiliation accounted for most winter locations in Oklahoma and Kansas (Table 12).

Seasonal Exchange Between Gulf Coast and Western Subpopulations

The MCP was managed as 2 subpopulations, that is, the Gulf Coast Subpopulation and the Western Subpopulation, with each having ranges as defined by Tacha et al. (1994:85; Fig. 13). Seventy-one and 100% of tagged NC–N migrated from breeding grounds of the Gulf Coast Subpopulation to fall staging areas (central ND and Saskatchewan) and wintering grounds (western TX) of the Western Subpopulation (Table 14), respectively. For EC–M, 18% and 21% migrated from breeding grounds of the Gulf Coast Subpopulation to fall staging areas (central ND) and

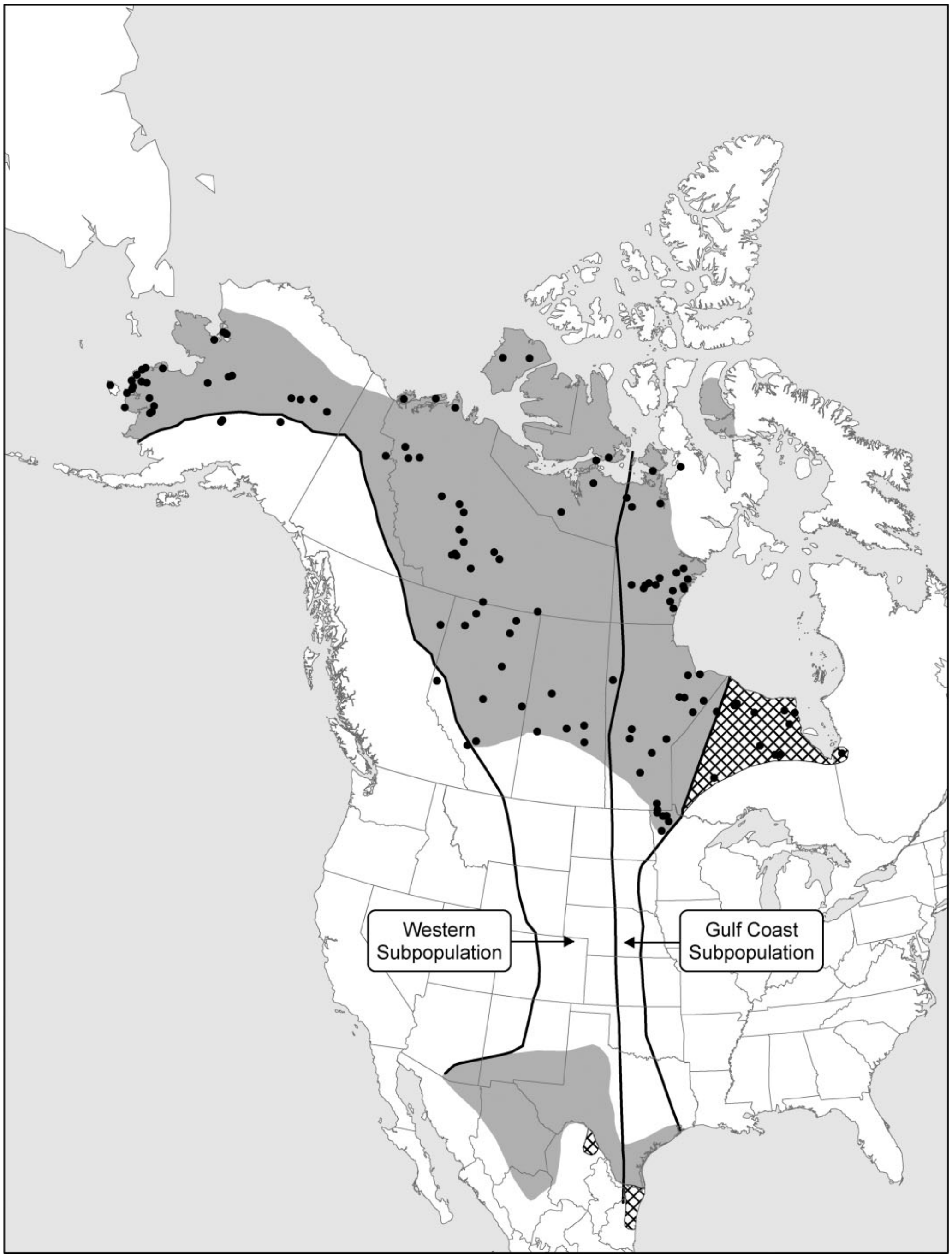

Figure 13. Breeding and wintering ranges of the Mid-continent Population of sandhill cranes in North America as estimated by Tacha et al. (1994:85) and our results. Areas showing cross-hatching represent parts of the range where the known distribution expanded as a result of monitoring settling patterns of Platform Transmitting Terminal (PTT)-tagged birds during 1998–2004. We adapted breeding and wintering ranges depicted by gray shading from Tacha et al. (1994) as the black lines that identify the estimated boundaries of the breeding and wintering ranges of the Western Subpopulation and the Gulf Coast Subpopulation.

wintering grounds (western TX) of the Western Subpopulation, respectively.

Tagged cranes from the Western Subpopulation were less prone to move between subpopulation ranges (Table 14). No WA–S cranes switched to fall staging areas or wintering grounds of the Gulf Coast Population as they migrated through Montana, Wyoming, and Colorado (Fig. 6C), states that lie to the west of the fall staging areas and wintering grounds of the Gulf Coast Subpopulation. In winter, WA–S cranes stayed in western Texas, New Mexico, Arizona, and Mexico (Fig. 11). Of WC–A cranes, 29% moved onto the winter range of the Gulf Coast Subpopulation on the Texas Gulf Coast (Table 14).

Exposure to Hunting Seasons

Tagged sandhill cranes from WA–S, NC–N, WC–A, and EC–M breeding affiliations occurred in zones open to hunting during an estimated 68%, 69%, 68%, and 44%, respectively, of the fall migration and winter period. Most exposure to hunting seasons occurred in Texas (54%) and Saskatchewan (23%), with North Dakota, Chihuahua, and Manitoba combining for an additional

Table 14. Use of Gulf Coast and Western fall staging and wintering grounds (Tacha and Vohs 1984) by Platform Transmitting Terminal (PTT)-tagged sandhill cranes of the 4 breeding affiliations, 1998–2004.

	% of use									
	Fall staging areas					Wintering grounds				
Breeding affiliation[a]	*n*	Gulf Coast range[b]	Nos. of sandhill cranes contributing locations to each estimate of % of use	Western range[b]	Nos. of sandhill cranes contributing locations to each estimate of % of use	*n*	Gulf Coast range[b]	Nos. of sandhill cranes contributing locations to each estimate of % of use	Western range[b]	Nos. of sandhill cranes contributing locations to each estimate of % of use
Subpopulation[c]										
Gulf Coast										
EC–M	26	82%	25	18%	12	25	79%	24	21%	12
NC–N	15	29%	8	71%	13	13	0%	0	100%	13
Total	41	72%	33	28%	25	38	58%	24	42%	25
Western										
WC–A	37	1%	2	99%	37	33	29%	13	71%	27
WA–S	36	0%	0	100%	36	33	0%	0	100%	33
NC–N	4	5%	1	95%	4	4	0%	0	100%	4
Total	77	1%	3	99%	77	70	14%	13	86%	64

[a] WA–S = Western Alaska–Siberia, NC–N = Northern Canada–Nunavut, WC–A = West-central Canada–Alaska, EC–M = East-central Canada–Minnesota.

[b] As defined by subpopulation distribution delineated by Tacha and Vohs (1984).

[c] As defined by breeding distribution of subpopulations delineated by Tacha and Vohs (1984) and where our PTT-tagged cranes settled for the breeding season.

14% (Table 15). Tagged cranes during fall stopovers in Manitoba, Saskatchewan, Alaska, Colorado, Montana, North Dakota, South Dakota, and Chihuahua occurred mostly within areas open to hunting but length of crane stay varied widely (Table 15). Closed areas existed in several states that have sandhill crane hunting seasons (CO, KS, ND, NM, SD, TX, and WY) but with the exception of closed areas in Texas, received limited use.

Sport hunting of the MCP in subarctic and arctic regions was limited to Alaska. All WA–S cranes migrated across Alaska (Fig. 6C) during the hunting season and all crane use occurred in areas open to hunting (Table 16), but access to the birds was limited by a restricted network of roads. We surveyed the agricultural area near Delta Junction, one of the primary WA–S hunting areas in Alaska, in early September 2007 and found <500 cranes using agricultural lands (G. Krapu, unpublished data). Only

Table 15. Relative exposure of Platform Transmitting Terminal (PTT)-tagged MCP sandhill cranes to sport hunting during fall and winter by state and province of the Central Flyway.[a] We present data as mean number of days and % of exposure to hunting and non-hunting by state and province from 1 September through 10 March during 1998–2003 (*n* = no. of PTT-tagged sandhill crane migrations in sample).

	Mean exposure (days ± SD)							
	Hunt			Non-hunt			Percent of total exposure	
State or province	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	Hunt	Non-hunt
Alberta	0.0	0.0	0	3.4	4.7	39	0.0	2.9
Alaska	7.5	6.0	38	0.0	0.0	0	3.3	0.0
Arizona	9.0	8.5	2	60.5	50.2	2	0.2	2.6
British Columbia	0.0	0.0	0	1.3	0.7	15	0.0	0.4
Chihuahua	70.8	45.8	6	12.8	12.0	9	4.9	2.5
Colorado	1.5	1.5	23	1.0	0.0	1	0.4	<0.1
Coahuila	0.0	0.0	0	87.0	11.3	2	0.0	3.8
Kansas	12.9	12.2	10	2.6	2.6	38	1.5	2.1
Manitoba	29.9	16.2	13	3.1	3.5	10	4.5	0.7
Minnesota	0.0	0.0	0	25.0	23.9	4	0.0	2.2
Montana	1.1	0.5	15	1.5	0.7	2	0.2	0.1
North Dakota	9.2	10.6	43	3.9	6.6	8	4.5	0.7
Nebraska	0.0	0.0	0	2.1	2.5	40	0.0	1.8
New Mexico	4.6	5.4	5	7.2	17.2	16	0.3	2.5
Nunavut	0.0	0.0	0	9.5	5.4	17	0.0	3.5
Northwest Territories	0.0	0.0	0	4.1	4.3	9	0.0	0.8
Oklahoma	19.3	24.0	12	5.3	7.8	22	2.7	2.6
Ontario	0.0	0.0	0	9.8	7.5	4	0.0	0.9
South Dakota	1.5	1.0	31	1.3	0.6	3	0.5	0.1
Siberia	0.0	0.0	0	5.7	5.2	27	0.0	3.3
Saskatchewan	24.3	17.5	82	1.3	0.5	4	23.0	0.1
Tamaulipas	0.0	0.0	0	96.0	0.0	1	0.0	2.1
Texas	66.9	33.0	70	38.1	27.9	76	53.9	63.4
Wyoming	1.3	0.5	10	1.0	0.0	1	0.1	<0.1
Yukon Territory	0.0	0.0	0	1.3	0.7	27	0.0	0.8

[a] Only birds from representative sample (birds marked in 2003 excluded).

Table 16. Mean number of days (and %) exposure of Platform Transmitting Terminal (PTT)-tagged sandhill cranes[a] to hunting and non-hunting by breeding affiliation and hunting unit in states (U.S., Mexico) and provinces (Canada) where hunting seasons took place, from 1 September through 10 March, 1998–2004.

			Hunting			Non-hunting			Combined	
State or province	**Hunting unit**	**Breeding affiliation**[b]	***n***[c]	**Mean exposure days**	**%**	***n***	**Mean exposure days**	**%**	***n***	**Total exposure days**
Alaska	All Units	WA–S	36	7.6	100	0	0.0	0.0	36	272
		WC–A	2	6.0	100	0	0.0	0.0	2	12
Arizona	Units 30A, 30B, 31, 32	WA–S	2	9.0	12.9	2	60.5	87.1	2	139
Chihuahua[d]		WA–S	6	70.8	78.7	9	12.8	21.3	9	540
Colorado	Central Flyway Area	WA–S	20	1.6	97.0	1	1.0	3.0	20	33
		NC–N	1	1.0	100	0	0.0	0.0	1	1
		WC–A	2	1.0	100	0	0.0	0.0	2	2
Kansas	Closed Area	EC–M	0	0.0	0.0	1	2.0	100	1	2
	W. of I-35, I-135, US-81	WA–S	0	0.0	0.0	6	1.0	100	6	6
		NC–N	1	4.0	22.2	8	1.8	77.8	8	18
		WC–A	2	19.0	51.4	15	2.4	48.6	15	74
		EC–M	13	13.8	56.5	19	7.3	43.5	21	317
Manitoba	Closed Area	NC–N	0	0.0	0.0	8	2.4	100	8	19
		EC–M	0	0.0	0.0	4	4.0	100	4	16
	GBHZ 3 & 4, GHZ 6 & 6A	EC–M	20	24.6	100	0	0.0	0.0	20	491
Montana	Montana 1	WA–S	14	1.1	100	0	0.0	0.0	14	16
		WC–A	1	1.0	100	0	0.0	0.0	1	1
	Montana 2 (Sheridan Co.)	WC–A	0	0.0	0.0	2	1.5	100	2	3
New Mexico	Closed Area	WA–S	0	0.0	0.0	7	1.9	100	7	13
		NC–N	0	0.0	0.0	1	1.0	100	1	1
	Eastern	WA–S	3	6.7	50.0	9	2.2	50.0	10	40
		WC–A	1	1.0	100	0	0.0	0.0	1	1
	EV[e]	WA–S	0	0.0	0.0	2	1.5	100	2	3
	MRGV[e]	WA–S	0	0.0	0.0	1	16.0	100	1	16
	SW[e]	WA–S	1	2.0	3.1	1	62.0	96.9	1	64
North Dakota	Closed Area[f]	NC–N	0	0.0	0.0	1	2.0	100	1	2
	Zone 1 (W of US-281)	NC–N	17	13.8	98.3	2	2.0	1.7	17	239
		WC–A	19	2.2	100	0	0.0	0.0	19	41
		EC–M	20	13.7	89.3	5	6.6	10.7	20	307
	Zone 2 (E of US-281)	EC–M	3	4.0	10.0	6	18.0	90.0	8	120
Oklahoma	W of I-35	WA–S	1	1.0	25.0	3	1.0	75.0	4	4
		NC–N	0	0.0	0.0	3	1.0	100	3	3
		WC–A	4	20.8	70.3	9	3.9	29.7	12	118
		EC–M	18	13.2	63.9	16	8.4	36.1	23	371
Saskatchewan	N & S Game Bird Districts	WA–S	38	19.2	100	0	0.0	0.0	38	729
		NC–N	15	14.0	98.1	3	1.3	1.9	15	214
		WC–A	38	37.1	100	0	0.0	0.0	38	1,408
		EC–M	0	0.0	0.0	1	1.0	100	1	1
South Dakota	Closed Area	EC–M	0	0.0	0.0	5	2.0	100	5	10
	W of US-281	WA–S	8	1.0	100	0	0.0	0.0	8	8
		NC–N	7	1.3	100	0	0.0	0.0	7	9
		WC–A	12	1.4	100	0	0.0	0.0	12	17
		EC–M	12	2.3	100	0	0.0	0.0	12	28
Texas	Closed Area	WC–A	0	0.0	0.0	3	3.7	100	3	11
		EC–M	0	0.0	0.0	7	37.0	100	7	259
	Zone A	WA–S	21	80.4	68.9	26	29.3	31.1	28	2,451
		NC–N	16	79.0	70.2	15	35.8	29.8	17	1,801
		WC–A	22	69.3	69.3	26	26.0	30.7	26	2,201
		EC–M	6	17.7	61.6	3	22.0	38.4	7	172
	Zone B	NC–N	1	1.0	100	0	0.0	0.0	1	1
		WC–A	6	36.0	70.1	15	6.1	29.9	17	308
		EC–M	5	19.8	43.6	15	8.5	56.4	17	227
	Zone C	WC–A	6	25.2	24.4	8	58.5	75.6	8	619
		EC–M	13	25.6	27.1	16	56.1	72.9	16	1,230
Wyoming	Closed Area	WA–S	0	0.0	0.0	1	1.0	100	1	1
	Central Flyway (Area 7)	WA–S	10	1.3	100	0	0.0	0.0	10	13

[a] Includes cranes tagged in all years (1998–2003) for better comparison within breeding affiliations.

[b] WA–S = Western Alaska–Siberia, NC–N = Northern Canada–Nunavut, WC–A = West-central Canada–Alaska, EC–M = East-central Canada–Minnesota.

[c] *n* = no. of PTT-tagged sandhill crane migrations in sample.

[d] Data was not available on recent hunting history and season dates for Coahuila and Tamaulipas.

[e] Estancia Valley (EV), Middle Rio Grande Valley (MRGV), Southwest NM (SW), all primarily RMP hunting areas.

[f] North Dakota east of U.S. 281 was closed prior to 2001.

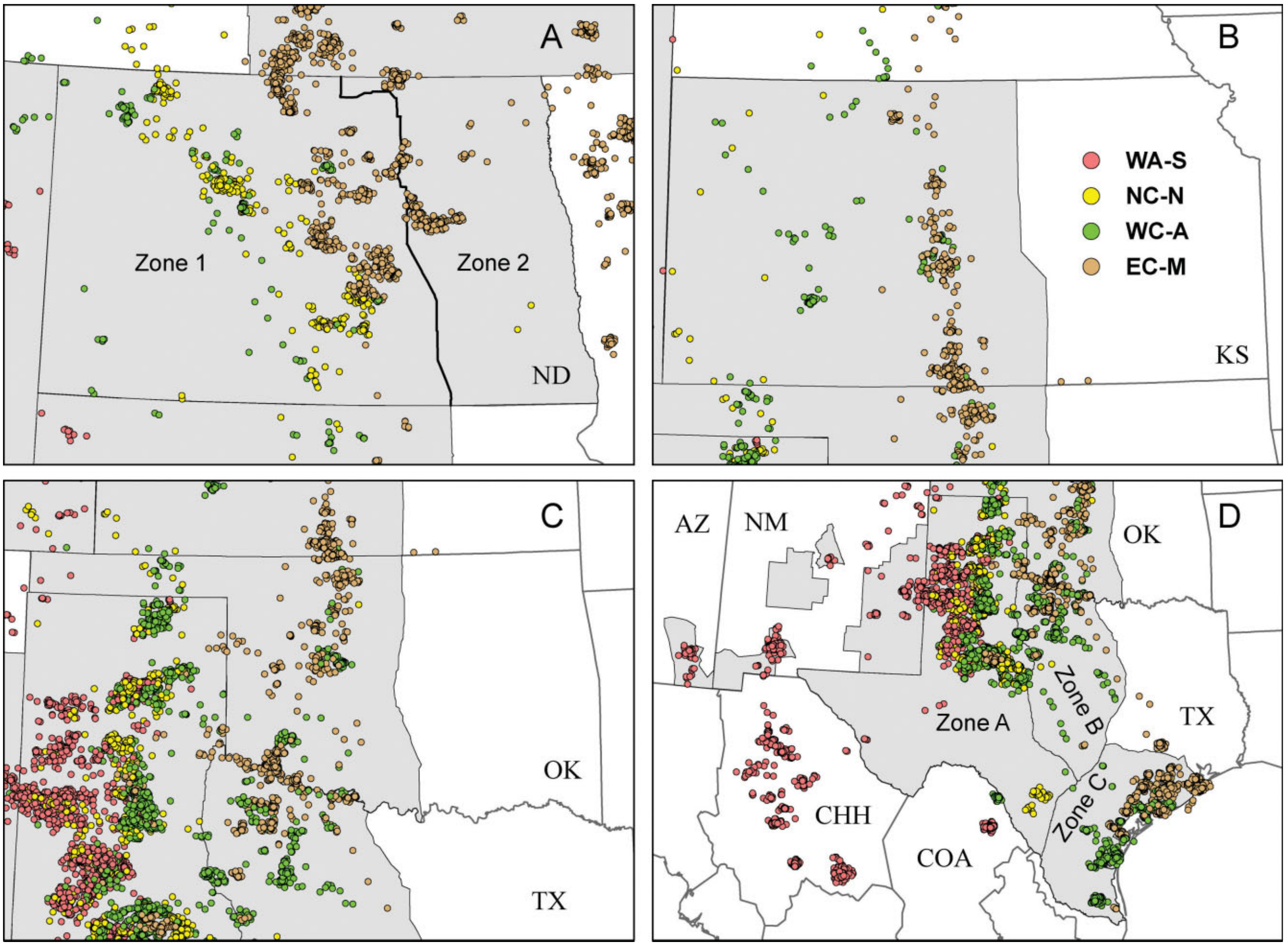

Figure 14. Distribution of Platform Transmitting Terminal (PTT)-locations of tagged MCP sandhill cranes of the Mid-continent Population of sandhill cranes by hunting unit and zone during stopovers in: (A) North Dakota; (B) Kansas; (C) Oklahoma; and (D) Texas, 1998–2004. We color-coded PTT-locations by breeding affiliation. Shaded areas identify parts of states where sport hunting is allowed.

about 2,025 ha of the agricultural area remained in grain production in 2007; most of the rest was in the Conservation Reserve Program, abandoned, or being used for hay production (C. Hadley, U.S. Department of Agriculture, personal communication). None of our tagged cranes stopped in the Delta Junction area during fall migration. Length of stay in Alaska by tagged cranes during the hunting season averaged about a week (Table 15), with cranes generally departing the state by mid-September.

During fall staging, most tagged cranes were exposed to hunting seasons throughout most or all of their stay (Table 15) except in Minnesota. In Manitoba, EC–M crane use occurred primarily in areas open to hunting during the hunting period (MB Units 3 and 4; Table 16). The lack of exposure of tagged NC–N cranes in Manitoba to hunting seasons reflects that the birds flew over the northwestern part of the province (Fig. 6B), which is closed to sport hunting of cranes. In Saskatchewan, where virtually the entire province is open to crane hunting, NC–N, WA–S, and WC–A breeding affiliations were exposed to hunting seasons almost 100% of their stay (Table 16). In North Dakota, NC–N cranes occurred only in Zone 1, whereas about 28% of EC–M crane use occurred in Zone 2 (Table 16, Fig. 14). Hunting Zone 1 included all lands in the state located west of U.S. Highway 281 and Hunting Zone 2 encompassed the rest of the state. Cranes of EC–M affiliation were exposed to hunting seasons 89% of their stay in Zone 1 and 10% of their stay in Zone 2; NC–N cranes were exposed to hunting seasons about 98% of their stay in North Dakota. After departing fall staging areas, WA–S and NC–N crane affiliations encountered limited exposure to hunting en route to the wintering grounds due to their rapid migration. In Kansas and Oklahoma, WC–A and EC–M affiliations accounted for 94% and 99% of all crane use with 56% and 54% occurring during hunting periods. In Oklahoma, WC–A and EC–M affiliations were located in the hunted area (Fig. 14) 70% and 64% of the hunting period, respectively (Table 16).

Level of exposure of MCP cranes to hunting seasons varied widely across their winter range. In Texas, the 4 breeding affiliations were exposed to hunting seasons 62–70% of their stay while in Hunting Zone A (Table 16). In Hunting Zone B, EC–M and WC–A cranes were exposed to hunting seasons 44% and 70% of their stay (Table 16). In Hunting Zone C, 24% and 27% of use by WC–A and EC–M cranes occurred during the hunting period (Table 16). In New Mexico, WA–S was the primary MCP breeding affiliation (Fig. 11), with minimal use occurring in the closed areas (i.e., an average of 1.9 days; Table 16). Most use by WA–S cranes in New Mexico occurred in areas also occupied by the RMP and overall, average WA–S crane exposure was 5.5 days and 7.6 days during the MCP and RMP hunting and non-hunting periods, respectively (Table 16, Appendix B). In Arizona, WA–S crane use occurred primarily during the non-hunting period and within areas also occupied by the RMP

Table 17. Estimated composition of sandhill crane harvest (1998–2003) by breeding affiliation and by state and province of the Central Flyway. Harvest estimates by breeding affiliation assume that composition of the harvest in each state and hunting zone is proportional to the spatial and temporal distribution of exposure by breeding affiliation during the respective state or provincial season. Harvest estimates for MCP sandhill cranes by state and province during 1998–2003 are from Kruse et al. (2008).

		Estimated % harvest by breeding affiliation[a]			
Location	**1998–2003 mean harvest**	**WA–S**	**NC–N**	**WC–A**	**EC–M**
Alaska	830	96.0	0	4.0	0
Colorado	211	91.4	2.9	5.7	0
Kansas	1,075	0	3.1	21.7	75.2
Montana	29	94.1	0	5.9	0
New Mexico	358	95.2	0	4.8	0
North Dakota	5,231	0	48.7	6.3	45.0
Oklahoma	580	0.4	0	30.3	69.3
South Dakota	303	17.8	20.0	33.3	28.9
Texas	8,688	30.6	22.9	31.1	15.4
Wyoming	11	100	0	0	0
Saskatchewan	7,783	24.3	13.4	62.3	0
Manitoba	1,166	0	0	0	100
Mexico[b]	2,638	100	0	0	0
Arizona$_{\text{(RMP)}}$[c]	146	100	0	0	0
New Mexico$_{\text{(RMP)}}$[c]	103	100	0	0	0
Total %		30.4	19.5	29.0	21.1
Total harvest	29,149	8,852	5,681	8,459	6,158

[a] WA–S = Western Alaska–Siberia, NC–N = Northern Canada–Nunavut, WC–A = West-central Canada–Alaska, EC–M = East-central Canada–Minnesota.

[b] Unknown harvests (Mexico) were assumed to be 10% of harvests in the U.S. and Canada.

[c] Hunting areas established for harvest of the Rocky Mountain Population of sandhill cranes.

(Table 16). Use by WA–S cranes in Mexico was highest in Chihuahua (Table 12; Fig. 14) and occurred primarily during the hunting season (Table 16, Appendix B).

MCP Harvest by Breeding Affiliation

Sport harvest of MCP cranes during 1998–2003 was concentrated in Texas, Saskatchewan, and North Dakota (Table 17). We estimate that WA–S, NC–N, WC–A, and EC–M affiliations accounted for 30%, 20%, 29%, and 21% of the harvest, respectively (Table 17), indicating harvest of WC–A and EC–M affiliations were disproportionately high to their percentages in the MCP (Table 4). For WA–S cranes, sport harvest was concentrated in Saskatchewan, Texas, and possibly Chihuahua, but detailed information is lacking on size of harvest in Mexico (Table 17). For WC–A cranes, Saskatchewan accounted for an estimated 57% of the harvest, followed by Texas at 32%. We estimate Hunting Zone A in Texas accounted for about 20% of total MCP crane harvest, and 20%, 3%, and 5% of the MCP harvest of the WC–A affiliation occurred in Hunting Zones A, B, and C, respectively. In Saskatchewan, harvest of WC–A cranes was centered near the South Saskatchewan River by Outlook, and in the Quill Lakes, Kutawagan Lake, and Last Mountain Lake areas (Fig. 10). For the EC–M breeding affiliation, we estimated that North Dakota, Texas, Manitoba, and Kansas accounted for an estimated 38%, 22%, 19%, and 13% of the harvest, respectively. In North Dakota, approximately 89% of the estimated EC–M crane harvest occurred in Hunting Zone 1 (Fig. 14A), along with an estimated 100% of the harvest of NC–N cranes. Harvest composition in Hunting Zone 1 was estimated to be: NC–N cranes (60%), EC–M cranes (34%), and WC–A cranes (6%). In Texas, we estimated about 89% and 16% of EC–M and WC–A crane harvest occurred in Hunting Zone C, respectively.

In Canada, we estimated 87% of the MCP harvest occurred in Saskatchewan, with the remaining 13% in Manitoba (Table 17). In Saskatchewan, 62% of harvest was of WC–A cranes (Table 17), whereas all harvest in Manitoba was composed of EC–M cranes (Table 17). In Saskatchewan, harvest was highest in the eastern region (56%), followed by the western region (20%) and the central region (17%); harvest of WC–A cranes was disproportionately high to their percentage in the MCP population.

DISCUSSION

Extent of Breeding Distribution

Geographic distribution of our tagged sample of MCP sandhill cranes on the breeding grounds compared favorably with the distribution as previously reported (Walkinshaw 1949, Johnsgard 1983, Tacha et al. 1994), suggesting our sample was representative of the geographic distribution of the MCP. Our tagged sandhill cranes occupied all previously described major breeding grounds of the MCP in North America and extended the breeding range of the MCP in east-central Canada and the Canadian sandhill crane morph in northwestern Canada and Alaska. Settling patterns indicated relative abundance of tagged cranes followed expected patterns for the MCP across the breeding range in Canada and Alaska, based on previous work. The Yukon Delta, for example, has long been recognized as the most important crane breeding ground in Alaska and contains the highest density of breeding pairs reported for the MCP (Conant et al. 1985, Melvin et al. 1990), traits also corroborated by settling patterns of our tagged sample. The lack of exchange of cranes between breeding affiliations from 1 yr to the next and the exceptional level of philopatry to sites used the previous year suggests that our tagged sample were virtually all breeders or were approaching breeding age.

The size of the known breeding range of the MCP increased by about 322,000 km^2 in east-central Canada after accounting for settling patterns of our tagged sample of cranes (Fig. 13). Much of the documented range increase came in the Hudson Bay Lowlands of northern Ontario, a region where cranes had been known to breed since the 18th century (Williams and Glover 1969) but previously was thought to be part of the breeding range of the Eastern Population (EP; Tacha et al. 1994). The large number of tagged cranes that settled in the Hudson Bay Lowlands during springs 1998–2003 (Fig. 5) indicates this region is a major breeding ground of the MCP, with most cranes being of the Canadian morph. In northwestern Canada, Canadian sandhill cranes previously were reported nesting in the southern Mackenzie District of the Northwest Territories (Walkinshaw 1965, Johnsgard 1983); our results indicate Canadian sandhill cranes now occur northward in the Great Slave Plains (Fig. 5) to within approximately 350 km of the Arctic Ocean. In Alaska, Canadian sandhill cranes settled in the forested interior of the state where lesser sandhill cranes also were present.

We detected no major differences in breeding distribution of lesser sandhill cranes across arctic North America when we compared settling patterns of our 87 tagged lesser sandhill cranes to the distribution reported by Walkinshaw (1981). Tagged lesser sandhill cranes settled on all major arctic river deltas, along the arctic mainland coast, the Canadian Archipelago, and along the northwest side of Hudson Bay. Lesser sandhill cranes occurred widely but at low breeding densities in the Canadian Archipelago during the mid-20th century (Parmalee and MacDonald, 1960, Manning and MacPherson 1961), a pattern also suggested from our data. An exception is Banks Island, Northwest Territories, where pair densities were high (i.e., 17 pairs/100 km^2; Walkinshaw 1965). Two of 4 tagged cranes that settled in the Canadian Archipelago were on Banks Island.

Factors Influencing Breeding Distribution and Abundance

Distributions of WA–S and NC–N cranes were centered on productive river deltas and other sites made fertile by nutrient transport and deposition. The many tagged cranes breeding in western Alaska is linked to the vast size and high productivity of the Yukon Delta. This area had the highest crane nest densities reported for the MCP (0.54 nests/km^2 in 1975 and 0.78 nests/km^2 in 1976; Boise 1977). In northern Canada, the largest concentration of tagged lesser sandhill cranes occurred along the northwest coast of Hudson Bay within areas where marine sediments were deposited early in the postglacial period (Lumsden 1971). Distributions of tagged Canadian sandhill cranes were centered in the fertile wetland habitats of the Hudson Bay Lowlands, Interlake area of Manitoba, the western boreal forest, Great Slave Lake Plains, and Yukon Flats.

The distribution of our tagged sample of cranes during the breeding season indicates a vast area of central Canada where few cranes settled extending from near Great Bear Lake in the Northwest Territories to southwestern Nunavut, across northern Saskatchewan, northern and southeastern Manitoba, western Ontario, and northeastern Minnesota (Fig. 5). The geologic land form of this region, the Laurentian Shield, covers an estimated 3.3 million km^2 (Fig. 5) and has long functioned as a vast natural barrier separating breeding ranges of Canadian sandhill cranes and lesser sandhill cranes in subarctic and arctic Canada. Repeated continental glaciations over the past 2.5 million years left landscapes of the Laurentian Shield with a thin soil interspersed with rocky outcrops, resulting in lands not capable of supporting sandhill cranes except in isolated areas where nutrient transport and deposition produced fertile sites.

Tagged individuals that settled in the central Arctic of Canada were all lesser sandhill cranes. However, in northwestern Canada and interior Alaska where natural barriers comparable to the Laurentian Shield do not exist, the Canadian sandhill crane morph breeds near lesser sandhill crane, indicating that gene flow between greater sandhill crane and lesser sandhill crane has occurred in this region (Jones et al. 2005). In northern Ontario, Lumsden (1971:289) noted "Almost all the summer records [Canadian sandhill crane] come from the area of post-glacial marine submergence or from post-glacial lake beds" whereas lesser sandhill crane migrate over the Laurentian Shield without stopping to breed. The exceptional philopatry to breeding sites in the MCP likely has contributed to keeping Canadian sandhill crane separated from lesser sandhill crane in the central Arctic where vast areas of unsuitable habitat separate these subspecies. Gene exchange also likely is impeded because spring stopovers of EC–M and NC–N breeding affiliations in the northern plains are widely spaced, as are migration corridors from their staging areas to breeding grounds (G. Krapu, unpublished data).

MCP sandhill cranes were extirpated from most of their breeding range in temperate mid-continent North America in the late 19th and early 20th centuries due to habitat loss and uncontrolled hunting (Walkinshaw 1949, Littlefield and Ryder 1968, Drewien and Bizeau 1974, Johnson 1976). The area formerly occupied included virtually all of the Prairie Pothole Region (PPR), a vast glaciated region within the northern plains containing millions of fertile basin wetlands of widely varying size. The PPR extends across most of North Dakota and South Dakota east of the Missouri River, southern Saskatchewan, and southwestern Manitoba. Failure of tagged cranes to settle across most of the PPR during the breeding season reflects the general absence of breeding by sandhill cranes in most of the region. The scarcity of recent nesting records by sandhill cranes in most of the PPR suggests a general lack of pioneering or high mortality of cranes that attempt to breed in the region, as wetland habitat suitable for sandhill crane breeding remains widely available. High philopatry to breeding sites that we documented across the current MCP breeding range suggests pioneering is limited to young birds that have not nested.

Failure of the MCP to re-occupy most of its former breeding range in the PPR also may have been influenced by a harvest through sport hunting of WC–A and EC–M cranes disproportionate to their numbers in the population. The disproportionate harvest of WC–A and EC–M cranes in the northern plains during 1998–2003 (Table 17) occurred in association with an early start of the sandhill crane hunting seasons (i.e., 1 Sep in Saskatchewan and Manitoba and 1–3 weeks later in ND; Kruse et al. 2008). With most WC–A and EC–M cranes arriving on fall staging areas before or soon after the start of the fall hunting seasons (Table 7), WC–A and EC–M affiliations receive higher exposure to hunting than do NC–N and WA–S affiliations, which arrive approximately 2 weeks and 3 weeks later, respectively. Early onset of the fall hunting seasons in the northern plains also may be removing cranes that successfully pioneered into the PPR but become vulnerable to hunting early in the hunting season before joining larger groups of cranes.

Harvest of EC–M and WC–A cranes on fall staging areas likely has been disproportionately high to their numbers in the MCP for several decades, as fall hunting seasons began in early September starting in Saskatchewan and Manitoba in 1964 (Central Flyway Webless Migratory Game Bird Technical Committee 2006), but significance has grown over time as number of crane hunters and harvest have increased. Melvin and Temple (1983) reported that 93% and 62% of VHF radio-tagged sandhill cranes (EC–M) breeding in the Interlake area of Manitoba arrived in North Dakota prior to or during the 1978 and 1979 hunting seasons, respectively, which began on 7–11 September. Results of Melvin and Temple (1983) indicated a first-year hunting mortality rate in North Dakota of 14%, which exceeds the percentage of fledged young (12%) in the Last Mountain Lake, Kutawagan Lake, and Quill Lakes region of Saskatchewan (Buller 1979). After NC–N cranes (virtually all lesser sandhill crane) arrive in North Dakota during fall, they become the principal subspecies harvested in areas where they occur (Kendall et al. 1997), reflecting that composition of the harvest is linked to exposure to hunting. However, because of their shorter stay in North Dakota and Saskatchewan, NC–N cranes accounted for a disproportionately smaller take than EC–M and WC–A cranes.

Sport hunting of sandhill cranes in Minnesota was prohibited in 1918 with the enactment of the Migratory Treaty Act and did not re-open until fall 2010. EC–M cranes produced in Minnesota largely bypass fall staging areas in Manitoba and North Dakota so experience a lower annual exposure to hunting and harvest than those that fall stage in Manitoba and North Dakota. This lower exposure probably has contributed to a higher breeding density of EC–M cranes in Minnesota than in Manitoba and only occasional breeding records in North Dakota (Fields et al. 1974).

Factors Influencing Fall Staging Distribution

Cranes stage in the northern plains in landscapes containing cropland where birds can acquire their energy needs primarily from waste cereal grains (Madsen 1967, Tacha et al. 1985) and protein and calcium needs by foraging on soil macro-invertebrates in pastures and hayland (Reinecke and Krapu 1986, Krapu and Johnson 1990). Stable and plentiful supplies of high-energy waste grain in cropland, particularly over the past half century, likely have allowed cranes to develop stronger staging traditions to specific sites and to stage in larger numbers than in the past. Prior to agriculture, cranes probably had to be more opportunistic in their fall staging patterns and winter distribution given wide annual fluctuations in food resources in natural prairie ecosystems.

Sandhill cranes are selective in their choice of nocturnal roost sites, limiting the distribution of fall staging across the northern plains. Birds roost primarily in association with shallow lakes, mostly saline, and less frequently in wide, braided river channels where available (e.g., the Souris River in southwestern Manitoba and South Saskatchewan River in central Saskatchewan). Cranes roosting in shallow lakes seek those with sparse vegetation and open water at some distance from a bare shore, allowing high visibility (Soine 1982).

Inundation of Missouri River bottomlands in North Dakota and South Dakota following construction of major dams in the 1960s eliminated several important fall staging areas of sandhill cranes (Johnson 1963). Crane displacement from some of these areas was documented by the U.S. Fish and Wildlife Service during aerial surveys of sandhill crane distribution upstream of Big Bend and Oahe dams before and during the period the reservoirs were filling with water (Buller and Boeker 1965). From fall 1963 to fall 1964 in Hughes County of central South Dakota upstream from Big Bend Reservoir, the number of roosting sandhill cranes declined from 3,500 to 9 as waters inundated roosting areas. Upstream from Oahe Dam in the Pollock-Mobridge area, aerial surveys revealed $\leq$18,000 cranes roosted in the shallow braided channels of the Missouri River prior to inundation of their roosts. Northward in south-central North Dakota, 5,000 cranes roosted on the river in fall 1964 on river bottomlands that thereafter became part of Oahe Reservoir. No tagged cranes used the Missouri River Valley of North Dakota and South Dakota during our study, reflecting avoidance by sandhill cranes of the river in its altered state. The long-term reduction of hunting opportunities from loss of the Missouri River roosts is apparent in South Dakota, where currently only limited use occurred during fall migration based on information from tagged cranes during 1998–2003.

Cranes move to other areas when traditionally used wetland roosts in the northern plains are temporarily made unsuitable for use because of drought or high water levels. In western Saskatchewan, where most WA–S cranes stage during spring in association with saline lakes, tagged cranes during springs 2001 and 2002 returned to find most of their traditionally used lakes to be dry. Many cranes moved as far as 250 km northwest into Alberta where they remained for the staging period (Krapu and Brandt 2008). When suitable habitat conditions re-appeared in western Saskatchewan staging areas after the drought ended, most cranes returned to stage there in spring.

Factors Influencing Winter Distribution

Most tagged cranes wintered in parts of the southern and southwestern United States and northern Mexico previously identified as important wintering sites for the MCP (Drewien and Bizeau 1974, Buller 1982, Drewien et al. 1996, Schmitt and Hale 1997, Chavez-Ramirez 2005). However, a few tagged cranes, mostly from the EC–M affiliation, wintered in central Kansas and in Oklahoma (Table 12, Fig. 11) at sites located north of the traditional winter range of the MCP (Tacha et al. 1994).

Crane distribution across the winter range occurs near shallow, mostly saline, water bodies with high visibility for roosting and near cropland with high-energy waste grains. Wintering habitats of tagged cranes along the Texas Gulf Coast from near Houston to the Mexican border typically were large and inaccessible bodies of water located in broad tracts of native vegetation adjacent to cropland (Aldrich 1979). Along the middle and lower Texas Gulf Coast, sorghum (*Sorghum bicolor*) and rice (*Oryza sativa*) are the dominant agricultural foods taken (Ballard and Thompson 2000). In western Texas, cranes roost largely on saline pluvial lakes. Magnitude of crane use of lakes is correlated with amount of sorghum stubble surrounding the lakes (Iverson et al. 1985) reflecting that plentiful supplies of high-energy foods are needed to attract many cranes to a site for an extended period.

Loss of most high-energy agricultural food on a major wintering ground can dramatically reduce use. The few winter PTT-locations from eastern New Mexico during 1998–2003 reflects limited use of this region in marked contrast to 1960–1976, when concentrations of up to 340,000 cranes moved between eastern New Mexico and western Texas during winter (Buller 1979). Distributions of PTT-locations indicate MCP cranes now stay mostly in western Texas where sorghum remains widely available from crane arrival to departure. At Bitter Lake NWR in eastern New Mexico, peak crane numbers during winter fell from 67,000 in 1970 to 5,400 in 1987 concomitant with >90% decreases in cropland area planted to sorghum, with most being replaced with alfalfa (Montgomery 1997).

The widespread distribution of WA–S cranes in the arid southwest, including the Chihuahuan Desert in north-central Mexico, indicates that these birds have adapted for survival in highly arid environments where saline wetlands, often reduced to freshwater springs and salt flats during drought, provide adequate roosts. Energy needs are supplied from waste grain in cropland and from grama grasses (*Bouteloua* spp.) in native grasslands (R. Drewien, Hornocker Wildlife Institute [Retired], personal communication).

MCP Use of the Gulf Coast Management Unit

Detailed knowledge of numbers and subspecies composition of sandhill cranes occupying the Gulf Coast Management Unit (GCMU) in Texas during late fall and winter is needed to facilitate sandhill crane management (Ballard et al. 1999). Satellite telemetry provided a new approach for estimating number and subspecies composition of cranes present. Our estimated 600,000 cranes in the MCP in spring, assuming a 12% annual recruitment rate (Buller 1979), would produce a fall population of 672,000 cranes. We based our spring estimate of 600,000 cranes in the MCP on an estimated average of 510,000 cranes in the CPRV on the fourth Tuesday of March 2000–2003, when numbers of cranes on nocturnal roosts were surveyed at the peak of spring migration using aerial infrared videography (Kinzel et al. 2006) and from an average ocular estimate of 93,227 MCP cranes in the NPRV during aerial surveys conducted on the fourth Tuesday of March 2005 and 2006 by the U.S. Fish and Wildlife Service and the Nebraska Game and Parks Commission (J. Solberg, U.S. Fish and Wildlife Service, personal communication; M. Vrtiska, Nebraska Game and Parks Commission, personal communication). With 17.4% of our random tagged sample of the MCP wintering within the GCMU, we estimated an average of 116,928 cranes present during 1998–2002. Our estimate is nearly 4 times larger than the ≥30,000 sandhill cranes estimated by Tacha et al. (1994) and approaches the 121,057 ± 31,521 (±SD) estimate made by Ballard et al. (1999) for the 1997–1998 winter. Our finding that the breeding area supplying cranes to the GCMU is much larger than previously thought (includes the Hudson Bay Lowlands of Ontario and western Quebec and the entire WC–A breeding grounds) helps explain the many cranes wintering in the GCMU.

Our information showing that cranes using the GCMU are primarily Canadian sandhill crane and greater sandhill crane is supported by results from previous studies (Ballard et al. 1999). Basing subspecies composition of the Gulf Coast Subpopulation on morphometry of collected birds, Ballard et al. (1999) estimated 62–68% Canadian sandhill crane, 28–32% greater sandhill crane, and 4–8% lesser sandhill crane. In comparison, we had 77% Canadian sandhill crane, 23% greater sandhill crane, and no lesser sandhill crane. The lack of lesser sandhill cranes in our tagged sample from within the winter range of the Gulf Coast subpopulation probably reflects lesser sandhill crane occurred in numbers too small to be represented in our sample.

The GCMU represented the southern terminus of fall migration for 23% and 77% of WC–A and EC–M cranes, respectively. Relative proportions of each breeding affiliation found in the GCMU differed markedly, with EC–M cranes in the GCMU representing 83% of all wintering EC–M cranes and with WC–A cranes accounting for 15% of all wintering WC–A cranes. Evidence of an increase in numbers of sandhill cranes wintering along the Gulf Coast over the past 4 decades (see Guthery and Lewis 1979) likely reflects both population growth and improvements in census techniques.

Range Overlap With Other Crane Populations

Distribution of EC–M cranes on their breeding grounds in Minnesota approaches and possibly overlaps with the EP. Greater sandhill crane from the MCP breed widely across northwestern parts of Minnesota based on distribution of our tagged sample, whereas greater sandhill cranes from the EP breed across central Minnesota (Henderson 1978, Toepfer and Crete 1979). Tacha et al. (1994) included most of Ontario in the breeding range of the EP, which, if accurate, would indicate broad overlap in distribution with the MCP across the central and northern parts of the province based on our tagged sample. More likely, cranes in the Hudson Bay Lowlands are mostly or all from the MCP, a conclusion supported by the observation that most cranes from this region have morphological measurements indicative of Canadian sandhill cranes (Lumsden 1971, our study). The northern limits of breeding of the EP in Ontario, Quebec, and, to a lesser extent, Minnesota remain poorly defined and need further study.

Occasional gene flow occurs between the EC–M affiliation and EP based on results from microsatellite studies (Jones et al. 2005), although no tagged cranes moved into the known range of the EP during our study. Gene flow likely will increase between the EP and MCP in the future if breeding ranges and wintering grounds of both populations continue to expand, resulting in greater overlap in area occupied and likely pairing between cranes of the 2 populations. Some MCP Canadian sandhill cranes and greater sandhill cranes (from EC–M) winter in central Louisiana (S. King, USGS Louisiana Cooperative Fish and Wildlife Research Unit, unpublished data).

The RMP breeds in Montana, Wyoming, Utah, Idaho, and Colorado (Drewien and Bizeau 1974), where we found no evidence of breeding by tagged MCP sandhill cranes. However, the winter range of MCP lesser sandhill cranes overlaps with the RMP in west-central New Mexico, southeastern Arizona, and parts of northern Mexico (Drewien and Bizeau 1974, Drewien et al. 1996, Schmitt and Hale 1997, Krapu and Brandt 2008). Most MCP lesser sandhill cranes that winter in the same areas as the RMP are in the WA–S breeding affiliation, based on winter distribution of our tagged birds (Fig. 11). Some MCP Canadian sandhill crane, presumably WC–A cranes, also winter in west-central New Mexico (Schmitt and Hale 1997) and migrate through the San Luis Valley of south-central Colorado in spring migration as do some WA–S lesser sandhill crane (Benning et al. 1997, Krapu and Brandt 2008). No records of pairing have been reported between MCP lesser sandhill crane and RMP greater sandhill crane in regions where their spring-fall migration and winter distributions overlap (R. Drewien, Hornocker Wildlife Institute [Retired], and W. Brown, U.S. Fish and Wildlife Service, unpublished data).

The PFP breeds across parts of southwestern Alaska including the lowlands of the Alaska Peninsula (Mickelson 1987, Petrula and Rothe 2005) where they occur within approximately 200 km of the nearest site used by a tagged WA–S crane during the breeding season (Fig. 13). The PFP winters primarily in the Central Valley of California (Lewis 1977, Herter 1982, Littlefield and Thompson 1982) and some may also winter near the Pacific Coast in Mexico (Lewis 1977, Herter 1982, Littlefield and Thompson 1982, Drewien et al. 1996). We found no evidence of WA–S mixing with the PFP on their wintering grounds, staging areas, or breeding grounds, but we suspect that limited mixing occasionally occurs between these populations. On the breeding grounds, occasional contact between PFP and WA–S seems plausible, most likely involving yearlings or subadults, which move more during the breeding season (Drewien et al. 1999). However, information gained from monitoring summer movements of a small sample of tagged PFP yearlings did not indicate movements into areas occupied by WA–S (Petrula and Rothe 2005).

In spring migration, WA–S breeding in western Alaska may occasionally stray from their traditional spring migration route in northeastern British Columbia and take a more direct path to their breeding grounds, leading to a potential stopover at the Copper River Delta, a major spring staging area of the PFP (Herter 1982, Mickelson 1987). Although occasional mixing between PFP and the MCP has genetic implications, it is unlikely such infrequent mixing has significance to issues pertaining to hunting.

Factors Influencing Composition of Harvest by Breeding Affiliation

Estimated flyway-wide harvest of the WC–A breeding affiliation was disproportionate to subpopulation size (29% of harvest vs. 23% of MCP) with an estimated 62% of harvest occurring in Saskatchewan being WC–A cranes. The large and disproportionate harvest of WC–A cranes in Saskatchewan is linked to an early start of the hunting season when virtually all cranes present in the province are of the WC–A affiliation. In addition, an earlier arrival and longer stay of WC–A cranes than WA–S and NC–N cranes on fall staging areas in the province, a 5-crane daily bag limit, harvest concentrations in areas where WC–A dominate, and an increasing number of sandhill crane hunters, primarily non-Canadians from the United States (D. Nieman, Canadian Wildlife Service, unpublished report) likely contribute to a disproportionate harvest of WC–A cranes. Most tagged WC–A cranes were on their fall staging areas at the onset of the hunting season, arriving an average of 17 days before NC–N cranes (257 ± 3.8 vs. 240 ± 3.0 Julian date; $\bar{x} \pm$ SD) resulting in a 2.6-fold higher mean exposure. There were approximately twice as many WC–A cranes as NC–N cranes, resulting in WC–A cranes being subject to 5 times as much exposure to hunting as were NC–N cranes.

The disproportionate take of EC–M cranes relative to subpopulation size (21% of overall harvest but composing an estimated 14% of MCP) resulted from an early onset of hunting seasons on the primary fall staging areas in southwestern Manitoba and North Dakota, a slow fall migration that increased exposure to hunting in Kansas and Oklahoma, and an extended stay on Gulf Coast wintering grounds in Texas. The disproportionate harvest of EC–M cranes in North Dakota (Table 17) also is influenced by the many crane hunters in the state (Kruse et al. 2008). The factor that likely contributed most to disproportionately fewer WA–S and NC–N cranes harvested on fall staging areas was a much shorter stay than that by WC–A and EC–M cranes. Also, WA–S cranes benefit from fall staging occurring at a more remote location than the other 3 breeding affiliations.

Major Risks to MCP From Habitat Change

Habitat loss and degradation from agricultural intensification, global climate change, and oil and mineral exploration and development pose potential significant long-term risks to the MCP. The MCP faces potential major threats from habitat loss and alteration in parts of its breeding range. Extensive energy development is underway on a major breeding ground of the WC–A affiliation in Alberta. Two of the 10 (20%) tagged cranes that settled in Alberta occurred at sites currently under lease for extraction of oil from tar sands, one each in the Athabasca Oil Sands Area and the Cold Lake Oil Sands Area. Under current plans, an estimated 3,000 km^2 of Alberta's boreal forest and associated wetlands will be strip-mined by 2030 to remove bitumen to process into oil. Development is expected to spread across a 149,000-km^2 area (equivalent in size to the state of Florida) and transform the land into an industrialized landscape fragmented by a network of steam well pads, roads, pipelines, and other infrastructure (Woynillowicz et al. 2005). This transformation could have adverse effects on the WC–A subpopulation if development continues as currently planned. Continued northward expansion of agricultural development in Canada in areas with fertile soils could cause further fragmentation of crane breeding habitats and culminate in lower EC–M and WC–A reproductive success in affected areas. Extensive logging in central Canada also poses significant threats to the WC–A and EC–M subpopulations if environmental concerns are not adequately addressed.

The primary breeding grounds of WA–S and NC–N in the Arctic have not been substantially impacted to date by large-scale energy and mineral development, in part because of the remoteness of breeding grounds and severity of the climate. In Alaska, the most important MCP breeding grounds include the Yukon Delta NWR and Yukon Flats NWR, which cover >7.3 million ha and 2.0 million ha, respectively. Strict environmental safeguards will be required to protect these and other publicly owned habitats important to sandhill cranes and other migratory birds, particularly in those parts not protected by wilderness designation and thus potentially subject to energy and mineral development.

The North Slope in Alaska has undergone extensive oil development over the past several decades but the areas most affected by development to date contained relatively few sandhill cranes before oil development (Bergman et al. 1977) and none of our tagged cranes settled there, reflecting low densities across this region.

Eastward in arctic Canada, the MacKenzie Delta-Beaufort Sea Basin contains an estimated 10.9 trillion cubic feet of discovered and 45.8 trillion cubic feet of predicted marketable natural gas deposits estimated to be worth about $115 billion (Sproule Associates Ltd., unpublished report). The MacKenzie Delta region is an important breeding area for sandhill cranes and waterfowl, so ecologically sound methods of gas extraction would be prudent if the Delta is to continue to meet the needs of cranes, waterfowl, and other migratory water birds. Most mineral development in the Northwest Territories to date has not involved major breeding areas of cranes nor has development significantly impacted crane breeding areas in the central Canadian Arctic, along the northwest side of Hudson Bay, or in the Hudson Bay Lowlands. However, because of the myriad of potential threats to wildlife populations inhabiting subarctic and Arctic regions from various forms of development, more safeguards may need to be considered to protect arctic- and subarctic-nesting cranes and other wildlife before development becomes widespread.

Competition with agriculture for fresh water on wintering grounds in the United States and Mexico is likely to intensify, emphasizing a need for effective strategies to ensure protection of groundwater hydrology responsible for maintaining freshwater springs associated with saline lakes that support the MCP on the wintering grounds. Our tagged sample relied primarily on 18 saline lakes in western Texas (Appendix C) to meet roost-site needs during winter, a number that closely follows the recommendation of Tacha et al. (1994) that conservation of <20 saline pluvial lakes with freshwater springs in western Texas is essential to provide sites for roosting and drinking water. Crane use of saline pluvial lakes in western Texas as roost sites is correlated with the number of freshwater springs present (Iverson et al. 1985), underscoring the importance of maintaining the shallow aquifers capable of supplying cranes with fresh drinking water. Key wintering areas of migratory waterfowl and sandhill cranes have been lost or degraded in northern Mexico, where competition for fresh water also is intense (Drewien et al. 2003), indicating a need for strong conservation measures to protect important existing migratory waterbird habitat. Greater insight is needed concerning the distribution of saline lakes used by the MCP across the winter range so more comprehensive and effective strategies can be developed to protect important sandhill crane wintering sites throughout the region.

Maintaining adequate supplies of high-energy food across the winter range of the MCP also is essential as reflected by the drastic decline in MCP use of eastern New Mexico over the past several decades as high-energy agricultural crops declined there. To help ensure adequate food resources remain available in the future, it is vital that a widely distributed wetland base capable of meeting roost-site needs of the MCP be maintained across the wintering grounds so cranes can continue to shift their distributions as agricultural cropping practices, drought, and other factors change.

Tagged cranes using fall staging areas in the northern plains roosted primarily on saline lakes. Expanding development of center-pivot irrigation in parts of the region where cranes stage during fall poses a potential major threat to crane habitat in the future. Pumping of ground water for irrigation, if not adequately controlled, could eliminate freshwater springs that allow saline lakes to be important roosts of cranes. With the Missouri River no longer providing extensive roosting habitat, a greater urgency exists to ensure availability of saline lakes with freshwater springs and to maintain the limited braided-river-channel habitat in the northern plains that remains suitable for roosting. In general, given the sensitivity of cranes to human disturbance in the vicinity of their roosts (Krapu et al. 1984), forms of activity that increase disturbance near nocturnal roost sites can be expected to displace cranes and alter distribution of fall staging.

The MCP stages in the CPRV for about 4 weeks during early spring and acquires a major part of fat reserves that supply energy used in migration and after arrival on the breeding grounds where foraging conditions initially are poor, particularly in arctic regions (Krapu et al. 1985). The ability of cranes to store large quantities of fat in the CPRV is being threatened by a decline in waste corn due to increased harvest efficiency (Krapu et al. 2004) and competition from snow geese (Pearse et al. 2010). Also, reduced flows in the Platte River and woody vegetation encroachment into channels have increased crowding at remaining roost sites over the past half century (Krapu et al. 1982). This change has forced the birds to roost at fewer sites and fly farther from their roosts to forage, increasing energy costs (Pearse et al. 2010). As waste corn has declined in cropland, fat storage has been reduced (G. Krapu, unpublished data). A Platte River Recovery Implementation Program has been created in a joint effort between the United States Department of Interior and the States of Nebraska, Colorado, and Wyoming to restore key habitats in the CPRV for whooping cranes (*Grus americana*) and other threatened and endangered species (Platte River Recovery Implementation Program 2010). This program, if successful, also has the potential for improving habitat conditions for sandhill cranes.

MANAGEMENT IMPLICATIONS

Detailed knowledge of breeding affiliations of sandhill cranes using fall staging areas and wintering grounds has been a long-standing information need of managers of Central Flyway sandhill cranes (Sharp and Cornely 1997). Sandhill cranes from the 4 breeding affiliations we delineated (WA–S, NC–N, WC–A, and EC–M) exhibited exceptional levels of philopatry from 1 yr to the next at sites occupied during the breeding season, and we predicted fall staging and wintering locations by breeding locations of cranes. These patterns of recurring use of fall staging areas and wintering grounds by cranes of known breeding origins during the same time intervals each year, combined with knowledge of harvest composition by breeding affiliation, provide the necessary information to target harvest as desired.

We found major exchange of birds between the ranges of the Western and Gulf Coast subpopulations, complicating efforts to effectively target harvest where most appropriate. Also, disproportionately greater harvest of temperate and subarctic breeding greater sandhill crane and Canadian sandhill crane compared to arctic-breeding lesser sandhill crane occurred on fall staging areas due to differences in fall staging distribution and chronology. Drawing upon our results, MCP sandhill crane managers have the information necessary on spatial and temporal use of fall staging areas and wintering grounds by cranes of each of the 4 breeding affiliations to update guidelines as necessary for managing MCP harvest. We suggest that, in conjunction with updating the management plan, consideration be given to managing the MCP as 4 subpopulations (WA–S, NC–N, WC–A, and EC–M) to help achieve the long-term goal of providing diverse recreational opportunities consistent with the welfare of the MCP. A key part of that goal is managing the population in ways that will maintain a sustainable harvest across subpopulations.

Evidence of a disproportionate harvest of WC–A and EC–M cranes relative to numbers of individuals in these subpopulations casts doubt on whether recent harvest levels are sustainable. Cranes from WC–A and EC–M subpopulations provide a major part of hunting opportunities in 4 states and 2 provinces that include key fall staging areas and wintering grounds, indicating the importance of taking steps necessary to ensure harvest levels are sustainable in these subpopulations. One of the most conspicuous outcomes of the high harvest rates of WC–A and EC–M cranes suggested by our results has been the failure of MCP greater sandhill cranes over time to rebuild their numbers to levels capable of re-occupying their extensive former breeding range in the PPR. This status contrasts with the EP, which has re-occupied a major part of their historic range in the Midwest including parts of Iowa, Illinois, and Indiana (Meine and Archibald 1996) despite the loss of >90% of the original wetland habitat in these states (Tiner 1984).

Targeting Harvest at Subpopulation Level

The 4 subpopulations of MCP cranes we identified are spatially separated to various degrees on their fall staging areas and wintering grounds. In 8 U.S. states, 1 Canadian province, and 1 Mexican state used by tagged cranes, one MCP subpopulation accounts for all or most use of the zones where cranes are hunted, permitting harvest to be focused largely on management needs for that subpopulation (i.e., Alaska [WA–S], Kansas [EC–M], Oklahoma [EC–M], Colorado [WA–S], Wyoming [WA–S], Montana [WA–S], New Mexico [WA–S], Arizona [WA–S], Manitoba [EC–M], and Chihuahua [WA–S]). In parts of New Mexico, Arizona, and Chihuahua, RMP cranes co-exist on the same areas as WA–S cranes (Drewien and Bizeau 1974), so RMP presence must be accounted for when setting hunting regulations. Because most WA–S cranes take less than a week to migrate from their fall staging areas in the northern plains to their wintering grounds, exposure to sport harvest is limited along the migration route and changes in hunting regulations in those states are not likely to cause major changes in WA–S harvest.

Harvest of WC–A cranes was disproportionately high to numbers present. Saskatchewan is the primary source of harvest of WC–A cranes so any steps to reduce the disproportionate harvest of birds from this breeding affiliation would need to include measures to reduce WC–A harvest in the province. Three potentially effective ways to reduce the take of WC–A in Saskatchewan would be to delay the onset of sandhill crane hunting in the province, reduce the bag limit, and establish hunting zones to allow harvest to be managed more conservatively for WC–A.

In Manitoba, and in North Dakota east of U.S. Highway 281 (Hunting Zone 2), EC–M is the only subpopulation present (Fig. 14A), so harvest can be managed independently. A later start date in North Dakota and an expanded Hunting Zone 2 (including fall staging areas where EC–M cranes dominate but now are located in Hunting Zone 1 [i.e., Bottineau, Pierce, Wells, Stutsman, and Kidder counties]), would allow harvest to be targeted at different rates for EC–M and NC–N affiliations. In Kansas and Oklahoma, harvest is about 75% EC–M cranes with most of the remainder being WC–A cranes (Table 17). If reducing harvest of EC–M or WC–A cranes (or both) was deemed necessary, changing hunting dates or bag limit would likely be most effective.

Management of cranes in Texas is the most complex, as all subpopulations winter in the state. Exposure of WC–A cranes to hunting in Texas was highest in Hunting Zone A, the primary wintering ground. Our results showed major overlap among WC–A and NC–N cranes in Hunting Zone A, so more conservative hunting regulations in that portion of Zone A where WC–A distribution is centered would also result in a reduced harvest of NC–N cranes (Fig. 12B). In Hunting Zone B, WC–A and EC–M cranes accounted for most use and harvest. Hunting Zone B (Fig. 14D) was the least used by tagged cranes of the 3 zones in Texas and accounted for only approximately 4% of the harvest, limiting the potential for altering overall harvest patterns through management actions undertaken in this zone. Hunting Zone C (GCMU) comprised the primary and secondary wintering grounds of the EC–M and WC–A subpopulations, respectively, with the EC–M subpopulation occurring primarily in the Upper Gulf Coast and WC–A occurring principally in the Mid- to Lower Gulf Coast. This pattern of distribution suggests that it may be feasible to manage harvest of the EC–M affiliation differently than the WC–A affiliation by splitting Zone C into 2 sub-units. However, our data suggest that both subpopulations are being taken disproportionately to their numbers on fall staging areas and during winter, so it is unclear whether managing the WC–A affiliation differently than the EC–M affiliation in Zone C will achieve desired goals under current circumstances. Any adjustments in harvest in Zone C can be expected to have a greater effect on the EC–M subpopulation, with 3 times as many EC–M cranes wintering on the Gulf Coast as WC–A cranes. Given that few NC–N and WA–S cranes winter along the Gulf Coast, crane management in Zone C can be directed exclusively on managing for the needs of the EC–M and WC–A subpopulations.

We assumed in our estimates of harvest that each subpopulation is harvested proportional to its presence (exposure) in a hunted area. In areas of major overlap of WC–A and NC–N cranes (i.e., Hunting Zone A in West Texas and east-central and central Saskatchewan), greater sandhill crane, Canadian sandhill crane, and lesser sandhill crane commonly occur in mixed flocks and under these conditions hunters may selectively or subconsciously target larger cranes (greater sandhill crane and Canadian sandhill crane). As a result, our estimates of WC–A harvest may be conservative in areas of major WC–A affiliation overlap with the NC–N affiliation.

Opportunities for Increased International Collaboration

Our results provide natural resource managers in the United States, Canada, Mexico, and Russia with new insight into where conservation, research, and management efforts involving specific subpopulations of the MCP will be most effective. The WA–S subpopulation is shared by all 4 nations; breeding grounds are exclusively in western Alaska and northeast Russia, the primary spring staging area is in Nebraska, the primary fall staging area along with a major spring staging area are in western Saskatchewan (Krapu and Brandt 2008), and wintering grounds are in Texas, New Mexico, Arizona, Chihuahua, Coahuila, Durango, and Zacatecas. With all 4 nations providing vital habitat to the WA–S breeding affiliation, close coordination and collaboration is needed among federal natural resource agencies to ensure that the habitat base that supports the WA–S throughout the annual cycle receives adequate protection. The WC–A, EC–M, and NC–N subpopulations breed primarily in Canada. All 3 subpopulations winter primarily in the southern United States, with some use occurring in northern Mexico. As a result, conservation, research, and management efforts affecting the WC–A, EC–M, and NC–N subpopulations are the responsibility of natural resource agencies and non-government organizations in the United States, Canada, and Mexico.

SUMMARY

1) We monitored a PTT-tagged random sample of the Mid-continent Population (MCP) of sandhill cranes from their arrival on the breeding grounds to the end of winter to describe chronology of use and breeding affiliation of cranes using fall staging areas and wintering grounds. Information gained on temporal and spatial separation of tagged cranes by breeding affiliation during fall and winter allowed an assessment of exposure to hunting seasons, and distribution and size of harvest by subpopulation, thereby providing guidance to Central Flyway crane managers seeking to regulate crane hunting in ways that will help ensure a sustainable harvest.
2) We noted a high rate of philopatry by tagged MCP sandhill cranes to previously used breeding sites and could predict locations of fall staging areas and wintering grounds by breeding site. These data allowed separation of the MCP into 4 geographically discrete subpopulations for management purposes linked to their breeding affiliation: Western Alaska–Siberia (WA–S), Northern Canada–Nunavut (NC–N), West-central Canada–Alaska (WC–A), and East-central Canada–Minnesota (EC–M).
3) The size of the known breeding area supplying cranes to the Gulf Coast Management Unit (GCMU) in Texas increased several-fold with information gained from tagged birds. New insight into breeding origins and numbers of cranes wintering in the GCMU together with knowledge gained on wintering distributions of EC–M and WC–A cranes within the GCMU provide managers with new insight for managing harvest in the Unit.
4) Disproportionately high harvests of WC–A and EC–M cranes relative to their estimated numbers in the MCP have resulted from high exposure of these subpopulations to hunting seasons and hunter concentrations, particularly in the northern plains. Differences in temporal and spatial use of fall staging areas and wintering grounds by the 4 subpopulations provide guidance for developing strategies to reduce take of WC–A and EC–M cranes should a reduction in their harvest become necessary.
5) The MCP currently is managed as 2 subpopulations, the Gulf Coast Subpopulation and the Western Subpopulation. Information from tagged cranes showed 71% and 100% of NC–N cranes and 18% and 21% of EC–M cranes migrated from breeding grounds of the Gulf Coast Subpopulation to fall staging areas and wintering grounds of the Western Subpopulation, respectively. This magnitude of exchange of cranes between ranges of the 2 subpopulations reduces effectiveness of current harvest management strategies. We recommend that consideration be given to managing the MCP as 4 subpopulations (WA–S, NC–N, WC–A, and EC–M) to help maintain a sustainable harvest and current recreational opportunities consistent with welfare of the MCP.
6) Texas overwinters approximately 80% of the MCP with Hunting Zone A providing wintering habitat for an estimated 99%, 74%, and 64% of NC–N, WA–S, and WC–A subpopulations, respectively. The unique role of Texas in providing wintering habitat sufficient to maintain the MCP at its current status of providing diverse recreational and other benefits emphasizes the need for a comprehensive effort to maintain habitat resources supporting the MCP in the state.
7) Environmental change, mostly associated with energy and agricultural development, pose long-term risks to the MCP at key breeding grounds, migration stopovers, and wintering areas, suggesting that conditions be monitored at identified sites and appropriate actions be undertaken where needed to minimize adverse impacts.
8) Key habitat resources supporting the MCP are located in 4 nations (United States [breeding, wintering, migration], Canada [breeding, migration], Mexico [wintering], and Russia [breeding]), indicating a need for international collaboration and a holistic approach when addressing conservation and management issues.

ACKNOWLEDGMENTS

This research was conducted by the Central Platte River Priority Ecosystem Study, Biological Resources Discipline, USGS. We thank D. Douglas for providing technical and Argos program support. We thank D. Sharp, J. Dubovsky, J. Roberson, M. O'Meilia, T. Mitchusson, J. Hansen, M. Szymanski, M. Johnson, J. Gammonley, H. Hands, S. Kohn, D. Nieman, M. Vrtiska, S. Taylor, S. Vaa, V. Bevill, R. George, L. Roberts, J. Solberg, D. Dolton, the late J. Gabig, D. Benning, R. Parker, S. Anschutz, P. Kinzel, J. Cornely, M. Forsberg, and P. Tebbel for their help in facilitating various aspects of the study. We thank the late P. Currier and F. Chavez-Ramirez, Directors of the Whooping Crane Habitat Maintenance Trust, for allowing use of their facilities near Wood River, Nebraska, when trapping and tagging sandhill cranes in the Platte River Valley and North Platte River Valley. We thank R. Kirby, J. Hestbeck, and J. Powell, Directors, and D. Jorde, Deputy

Director, at the Northern Prairie Wildlife Research Center for their support. We thank D. Fronczak, A. Olson, A. Stonsifer, J. Drahota, W. Jones, T. Buhl, F. Sargeant, J. Fiest, L. Wood, S. Hawks, D. Grandmaison, M. Westbrock, K. Seginak, B. Hanson, C. Mettenbrink, R. Knopik, C. Graue, V. Carter, B. Geaumont, J. McCabe, D. Smith, L. Potter, J. Thibault, B. Toay, M. Stoley, M. Heiser, and M. Pieron for field assistance. We are grateful for comments by R. Drewien, D. Sharp, and G. Ivey, which improved earlier drafts of this manuscript and Ingrid Barcelo, Audrey Desmarteaux-Houle, and Galina Revina for translating the abstract into Spanish, French, and Russian. We thank the many private landowners in Nebraska that allowed access to their lands to trap and tag cranes. Any mention of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This study was supported by U.S. Geological Survey, Northern Prairie Wildlife Research Center, U.S. Fish and Wildlife Service, Central Flyway Council, North Dakota Game and Fish Department, Texas Game and Parks Commission, Oklahoma Department of Wildlife Conservation, Nebraska Game and Parks Commission, Kansas Department of Wildlife and Parks, New Mexico Department of Game and Fish, South Dakota Game, Fish and Parks Department, Wyoming Game and Fish Department, Montana Department of Fish, Wildlife and Parks, Colorado Division of Wildlife, International Crane Foundation, Platte River Whooping Crane Maintenance Trust, and Playa Lakes Joint Venture. Publication costs were provided by United States Geological Survey, Science Support Program.

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Appendix A: List of acronyms and abbreviations.

Acronym	Definition
CPRV	Central Platte River Valley
DAR	Distance Angle Rate
EC–M	East-central Canada–Minnesota
EP	Eastern Population
GCMU	Gulf Coast Management Unit
JD	Julian date
KDE	Kernel Density Estimate
LC	Location
MCP	Midcontinent Population
MRD	Minimum Redundant Distance
NC–N	Northern Canada–Nunavut
NPRV	North Platte River Valley
NWR	National Wildlife Refuge
PFP	Pacific Flyway Population
PTT	Platform Transmitter Terminal
PPR	Prairie Pothole Region
RMP	Rocky Mountain Population
USGS	U.S. Geological Survey
WA–S	Western Alaska–Siberia
WC–A	West-central Canada–Alaska
WK	Week
WMA	Wildlife Management Area

Appendix B: Mean number of days (and %) exposure of Platform Transmitting Terminal (PTT)-tagged MCP sandhill cranes[a] by breeding affiliation to hunting and no-hunting periods by state (U.S., Mexico) and province (Canada) from 1 September through 10 March, 1998–2004.

		Hunting			Non-hunting			
State or province	**Breeding affiliation[b]**	***n*[c]**	**Mean exposure days**	**%**	***n***	**Mean exposure days**	**%**	**Total exposure days**
Alberta[d]	WA–S	0	0.0	0.0	29	2.1	100.0	60
	NC–N	0	0.0	0.0	1	1.0	100.0	1
	WC–A	0	0.0	0.0	9	8.0	100.0	72
Alaska	WA–S	36	7.6	100.0	0	0.0	0.0	272
	WC–A	2	6.0	100.0	0	0.0	0.0	12
Arizona	WA–S	2	9.0	12.9	2	60.5	87.1	139
British Columbia[d]	WA–S	0	0.0	0.0	15	1.3	100.0	19
Chihuahua	WA–S	6	70.8	78.7	9	12.8	21.3	540
Colorado	WA–S	20	1.6	97.0	1	1.0	3.0	33
	NC–N	1	1.0	100.0	0	0.0	0.0	1
	WC–A	2	1.0	100.0	0	0.0	0.0	2
Coahuila	WA–S	0	0.0	0.0	1	79.0	100.0	79
	WC–A	0	0.0	0.0	1	95.0	100.0	95
Kansas	WA–S	0	0.0	0.0	6	1.0	100.0	6
	NC–N	1	4.0	22.2	8	1.8	77.8	18
	WC–A	2	19.0	51.4	15	2.4	48.6	74
	EC–M	13	13.8	56.1	19	7.4	43.9	319
Manitoba	NC–N	0	0.0	0.0	8	2.4	100.0	19
	EC–M	20	24.6	96.8	4	4.0	3.2	507
Minnesota[d]	EC–M	0	0.0	0.0	8	26.6	100.0	213
Montana	WA–S	14	1.1	100.0	0	0.0	0.0	16
	WC–A	1	1.0	25.0	2	1.5	75.0	4
North Dakota	NC–N	17	13.8	97.5	3	2.0	2.5	241
	WC–A	19	2.2	100.0	0	0.0	0.0	41
	EC–M	20	14.3	67.0	11	12.8	33.0	427
Nebraska[d]	WA–S	0	0.0	0.0	11	1.7	100.0	19
	NC–N	0	0.0	0.0	7	1.0	100.0	7
	WC–A	0	0.0	0.0	20	2.4	100.0	48
	EC–M	0	0.0	0.0	15	3.0	100.0	45
New Mexico	WA–S	4	5.5	16.2	15	7.6	83.8	136
	NC–N	0	0.0	0.0	1	1.0	100.0	1
	WC–A	1	1.0	100.0	0	0.0	0.0	1
Nunavut[d]	NC–N	0	0.0	0.0	17	9.5	100.0	161
Northwest Territories	WA–S	0	0.0	0.0	1	1.0	100.0	1
	NC–N	0	0.0	0.0	4	4.5	100.0	18
	WC–A	0	0.0	0.0	4	4.5	100.0	18
Oklahoma	WA–S	1	1.0	25.0	3	1.0	75.0	4
	NC–N	0	0.0	0.0	3	1.0	100.0	3
	WC–A	4	20.8	70.3	9	3.9	29.7	118
	EC–M	18	13.2	63.9	16	8.4	36.1	371
Ontario[d]	EC–M	0	0.0	0.0	8	8.8	100.0	70
Quebec[d]	EC–M	0	0.0	0.0	1	29.0	100.0	29
South Dakota	WA–S	8	1.0	100.0	0	0.0	0.0	8
	NC–N	7	1.3	100.0	0	0.0	0.0	9
	WC–A	12	1.4	100.0	0	0.0	0.0	17
	EC–M	12	2.3	73.7	5	2.0	26.3	38
Russia[d]	WA–S	0	0.0	0.0	27	5.7	100.0	153
Saskatchewan	WA–S	38	19.2	100.0	0	0.0	0.0	729
	NC–N	15	14.0	98.1	3	1.3	1.9	214
	WC–A	38	37.1	100.0	0	0.0	0.0	1,408
	EC–M	0	0.0	0.0	1	1.0	100.0	1
Tamaulipas	WC–A	0	0.0	0.0	1	96.0	100.0	96
	EC–M	0	0.0	0.0	1	48.0	100.0	48
Texas	WA–S	21	80.4	68.9	26	29.3	31.1	2,451
	NC–N	16	79.1	70.2	15	35.8	29.8	1,802
	WC–A	28	67.6	60.3	32	39.0	40.4	3,139
	EC–M	20	26.9	28.5	20	67.5	71.5	1,888
Wyoming	WA–S	10	1.3	92.9	1	1.0	7.1	14
Yukon Territory[d]	WA–S	0	0.0	0.0	23	1.4	100.0	32
	WC–A	0	0.0	0.0	4	1.0	100.0	4

[a] Includes cranes marked in all years (1998–2003) for better comparison within breeding affiliations.

[b] WA–S = Western Alaska–Siberia, NC–N = Northern Canada–Nunavut, WC–A = West-central Canada–Alaska, EC–M = East-central Canada–Minnesota.

[c] *n* = no. of PTT-tagged sandhill crane migrations in sample.

[d] No sport hunting season in place.

Appendix C: Saline lakes and other wetlands used as nocturnal roosts by Platform Transmitting Terminal (PTT)-tagged MCP sandhill cranes in western Texas during 1998–2003 compared to wetlands in the same region identified as nocturnal roosts during January and February 1980 Iverson et al. (1985, Table 1).

Pluvial basin	**Years used during 1998–2003**
Wetlands used during 1980	
Lower Paul's Lake	2000, 2001, 2002
Mound Lake	1998, 1999, 2001, 2002
Rich Lake	1998, 2001, 2002
Skeen Lake	2001, 2002, 2003
Buffalo Lake	Not used
Bull Lake	1998, 1999, 2000, 2001, 2002
Brownfield Lake	2001, 2002 (nearby)
Silver Lake	1998, 2000, 2001, 2002
Tahoka Lake	1999, 2000, 2001, 2002
Wetlands not used during 1980	
Double Lakes	1999, 2001, 2002, 2003
Yellow Lake	1998, 2001, 2002
Monument Lake	2000, 2001, 2002
Coyote Lake	2002
Grulla NWR (NM)	2002
Saleh Lake-Gooch Lake	2001, 2002, 2003
Cedar Lake	1999, 2002
McKenzie Lake	1999, 2002
Natural Dam Lake	1998, 1999, 2000, 2001, 2002
Red Lake/Sulfur Spring Creek	1999, 2000, 2002
White Lake	2002, 2000
Goose Lake	2002, 2000