DISPERSAL AND POPULATION GENETIC STRUCTURE IN TWO FLYWAYS OF SANDHILL CRANES (*GRUS CANADENSIS*)

By

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DISPERSAL AND POPULATION GENETIC STRUCTURE IN TWO POPULATIONS OF SANDHILL CRANES (*GRUS CANADENSIS*)

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Under the supervision of Assistant Professor Mark E. Berres

At the University of Wisconsin-Madison

I studied dispersal patterns in Sandhill Cranes using distances travelled by banded and radio-tagged birds and estimates of gene flow using genetic markers. In Wisconsin, territorial Sandhill Cranes showed long-term pair bonds and strong site fidelity, however, 58% of 119 banded pairs ended due to mate switch (divorce or mate death). Territory retention was high following any mate switch. The bird leaving the territory moved (on average) 0.9 km to an adjacent territory.

Sandhill Crane chicks dissociated from their parents before fall migration (12%), over winter (79%), or following spring migration (9%). Using mark-recapture analysis, timing of separation did not affect long-term chick survival estimates (92%). Following independence, home ranges of one-year-old birds were larger than two-year-olds and three-year-olds. Females traveled further from their natal area than males, but both sexes returned near their natal area by three-years-old. Sandhill Cranes obtained breeding territories at 4.5 years-old and males nested closer (2.3 km) to their natal area than females (10.7 km).

Significant population genetic structure occurred among breeding sites in the Eastern Population. Pairwise Fst and assignment of birds to genetic clusters suggest long-distance dispersal was prevalent following the population bottleneck in the 1930's. Re-colonization in the northeastern U.S. likely resulted from eastward expansion of the EP and southern expansion of the Mid-continent Population from Hudson's Bay.

Three populations (Pacific Flyway Population, Central Valley Population, and British Columbia Coast Population) in western North America also showed significant population genetic structure. PFP Lessers and CVP Greaters each formed two genetic clusters. BCCP Canadians clustered with one CVP cluster, but on a separate topological branch. Three birds from Sauvie Island, Oregon formed a fifth genetic cluster, likely representing individuals from unrelated populations.

Population genetic structure in these study populations of Sandhill Cranes is modulated by strong natal philopatry and infrequent, but effective long-distance dispersal. This research provides a framework to study natural recolonization wild crane populations. Despite passage through population bottlenecks, remnant genetic diversity in all study populations of Sandhill Cranes is substantial. These results indicate that population bottlenecks had a greater effect on dispersal processes than loss of genetic variation during recovery.

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Table of Contents

Chapter 1

INTRODUCTION

Understanding population dynamics through time is critical for the management and conservation of species. To accurately model population size (N) through time (t), four key variables need to be quantified: rates of births (B), deaths (D), immigration (I), and emigration (E) (Caughley 1977). By combining these variables, it is possible to estimate a population size at some time in the future: $N_{t+1} = N_t + B – D + I – E$. Cormack-Jolly-Seber models (Cormack 1964, Jolly 1965, Seber 1965) were developed to estimate population size at time *t* and recruitment (unmarked individuals entering into the population) and survival (1-marked individuals leaving the population (i.e., not recaptured)). This is typically done through capturing and marking individuals and attempting to recapture them a set time after release. Without marking individuals, it can be difficult to know whether recruitment occurred through birth or immigration and egress from a population was a result of death or emigration. It is difficult to interpret estimations of movement patterns without knowledge about how individuals move among populations.

Movement patterns can be important drivers of genetic exchange among populations. The strength of natal philopatry, or the propensity to return near an individual's birth area to breed, can determine broad-scale genetic patterns of differentiation and can be mediated by habitat preference and distribution. Strong natal philopatry, combined with specific habitat requirements, can lead to distinct genetic groups among geographically stratified breeding areas creating population genetic structure. For example, both male and female Black-capped Vireos (*Vireo atricapilla*) showed strong natal philopatry and a preference for early successional habitat leading to population genetic differentiation (Barr et al. 2008). Alternatively, if all individuals are highly dispersive, with general habitat requirements, then individuals may move long distances from their natal area to breed and one panmictic population is formed. For example, a lack of genetic differentiation between highly fragmented populations of Cerulean Warblers (*Setophaga cerulean*) was likely promoted by high dispersal ability between available habitat fragments (Veit et al. 2005, Deane et al. 2013).

Monitoring dispersal processes and patterns can be challenging for species that are highly mobile (e.g., migratory birds) or cryptic and difficult to detect (e.g., nocturnal mammals). There are three main methods used to determine individual movement patterns (summarized in Webster et al. 2002). First, individuals can be captured, marked, and recaptured at a future time and place. In addition to tags or bands, transmitters (VHF or satellite) can be deployed to track individual movements. These methods provide fine-scale data and allow quantification of distances travelled and habitats utilized throughout all parts of an individual's annual cycle. Marking individuals is relatively cheap, however, there is a large cost in time and effort to detect individuals over a broad area. Application of telemetry devices can reduce time and effort and increase the scope of detection, but can cost money to purchase equipment and retrieve data and cannot be deployed on small individuals.

Second, DNA samples can be collected from body tissues of captured individuals. Some tissue collection is invasive (e.g., blood) and possibly increase stress to a captured animal, but provides high quality data to compare to other samples. Other collection is non-invasive by collecting naturally shed tissues (e.g., hair, feathers, or scales), but data quality decreases as these are dead structures with possibly low quantity of DNA present. These estimates provide insight into historic movement patterns across a broad scale. Migratory or dispersing individuals can be sampled away from natal areas and be assigned to a source population as long as there are samples from different sources to compare. Similar to method two, relative frequencies of stable isotopes can be used to determine a source of origin for sampled individuals. Samples of body tissues are collected and compared to samples of probable food items across the landscape. Relative ratios of different biochemical elements can be used to detect a probable natal area. While dispersal estimates from genetic and biochemical samples can be applied across a broad scale, they should be interpreted in the context of movement data collected from free-living individuals to verify each data set comes to the same conclusion.

To further complicate detecting highly mobile species, mobility and detectability patterns can differ depending on an individual's sex and change as an individual ages or shifts among social classes. For example, most breeding adult mammals and birds show strong site fidelity, or tenacity, as they typically return to the same breeding site each year (Greenwood 1980, Greenwood and Harvey 1982). Alternatively, independent young animals are not constrained by a breeding territory and may choose to disperse long distances from their natal area or remain philopatric to locate unutilized resources. Typically, young animals drive population genetic structure, but the amount of genetic differentiation depends on the distances that young animals travel from natal areas.

Several hypotheses have been postulated to explain philopatry differences among different age and social groups. Breeding individuals are expected to show high site tenacity because this allows these birds to defend and utilize familiar resources (Greenwood 1980). Breeding adult site tenacity is often reinforced by successful reproduction (Cuthbert 1988, Gavin and Bollinger 1988). Predictability of site tenacity by nonbreeding individuals is more challenging, but may be influenced by an individual's age, probability of obtaining a breeding site, and average reproductive success currently experienced by breeding individuals at that site (Bouliner et al. 1997, Doligez et al. 2004).

Pre-breeding dispersal patterns differ between the sexes in most species of birds (females disperse while males are philopatric) and mammals (females are philopatric while males disperse; Greenwood and Harvey 1982). In birds, one notable exception has been observed in waterfowl (Anseriformes), where males disperse and females are philopatric (Anderson et al. 1992). In these groups, philopatric individuals are expected to benefit through increased knowledge of local resources to improve mate attraction, territorial defense, and/or offspring survival which will ultimately increase that philopatric individual's reproductive fitness (Anderson et al. 1992, Greenwood 1980, Greenwood and Harvey 1982). Alternatively, there may be no difference between the sexes in natal dispersal distance for sexually monomorphic birds that show equal investment in parental care (e.g., Gratto 1988, Johns et al. 2005). Gratto (1988) suggested that, in monomorphic species, neither sex benefitted in being more philopatric because there is no sexual selection based on morphological characteristics or greater benefit for one sex than the other to be more familiar with nearby resources to successfully reproduce.

An explanation for why individuals disperse away from natal areas is less clear. Young individuals may be forced from their natal area by dominant siblings (Ellsworth and Belthoff 1999) or parents through displacement (Kamata and Tomioka 1991, Nesbitt et al. 2002) and reduced provisioning (Guo et al. 2010, Vergara et al. 2010). Dispersal patterns of young, non-breeding individuals may be influenced by spatial arrangement and allocation of available food resources in conjunction with breeding individuals' defense of these same resources.

Individuals spend more time in high quality patches if there is a long travel time (i.e., distance) to other high quality patches (see Pyke 1983). If these high quality patches are currently undefended, this could lead to settlement and defense by non-breeding individuals. While dispersers often have increased mortality compared to philopatric individuals (Greenwood 1980), dispersers have the ability to utilize currently undefended resources which could lead to higher lifetime reproductive success (Nilsson 1989, Brommer et al. 1998) or younger age at first reproduction (Steiner and Gaston 2005) compared to philopatric individuals.

Lastly, young individuals may disperse from natal areas to avoid or reduce the risk of inbreeding (Greenwood 1983). This argument has been used to support observed differences in dispersal distances between the sexes and individuals in different social classes (e.g., Szulkin and Sheldon 2008). Empirical evidence for direct measures of inbreeding avoidance is minimal and experiments are difficult to design (Moore and Ali 1984). While inbreeding avoidance may be cited as the cause for sex-biased dispersal in birds (e.g., Daniels and Walters 2000) and mammals (e.g., Sterck et al. 2005), an equally plausible alternative may be the result of resource competition. Shields (1982, 1983) argued that there is an optimal level of inbreeding that can be experienced by populations to adapt to local environs and maximize resource utilization while reducing the effects of outbreeding with populations that are not as optimally adapted.

My study utilizes movement data from banded and radio-tagged Sandhill Cranes (*Grus canadensis*) at a long-term study site in south-central Wisconsin to compare to estimates of gene flow generated from blood samples collected from color-banded cranes sampled throughout the Midwest and northeastern U.S. and Canada from the entire Eastern Population of Sandhill Cranes. This population suffered a known population bottleneck in the early 1900's (Henika 1936, Walkinshaw 1949), but has recovered and is re-colonizing extirpated areas. Lastly, I compare population genetic parameters in the Eastern Population to populations on the west coast of North America which also suffered bottlenecks at approximately the same time, yet have shown different capabilities in recovering from a population bottleneck.

It was important to combine direct and indirect approaches because I could compare fine-scale and broad-scale movements made by individuals to better understand dispersal. By closely following banded and radio-tagged individuals at a primary study site, I could understand the dispersal process from family dissociation, through the non-territorial years, and then settlement on a breeding territory. It would have been logistically and financially impractical to expend this same amount of effort across an entire population. However, I could color-band and collect blood samples across the population to estimate gene flow and determine rates of exchange among breeding sites. Since each individual was also color-marked, I could also receive re-sightings of banded birds throughout the migratory flyway to increase the understanding of dispersal.

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Chapter 2

TERRITORY AVAILABILITY BEST EXPLAINS FIDELITY IN SANDHILL CRANES

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ABSTRACT

We investigated dynamics of mate and site fidelity among color-banded Sandhill Cranes (*Grus canadensis*). Over 23 years, 81 permanent mate switches (68%) occurred in 119 pairs: 23 switches (28%) were divorces and the rest occurred following mate disappearance. The asynchronous migration, incompatibility, and better option hypotheses did not explain divorces in this population well. Reproductive success of divorced pairs prior to separation was lower than non-divorced pairs, but divorcing did not improve individual reproductive success and reproductive success of divorced pairs following separation was lower than non-divorced pairs. Following divorce or mate disappearance, territory retention was high (divorce = 100%, mate loss = 83%) while males and females did not differ in original territory retention. Long-term territory retention led to higher lifetime reproductive success and divorcing prolonged territory retention, especially for pair bonds that may have been unstable. Divorcing birds typically paired with experienced territory holders, although invasion into a pair bond by a non-territorial bird occurred. Post-divorce, relocating birds moved to adjacent territories with a vacancy rather than re-distribute to random territories. Average breeding dispersal distance for 15 birds (12 females, 3 males) was 0.9 km (range 0.2-2.2 km). Because territories in this population are limited, an opening on a proximate territory offers a potential advantage: a bird can stay with a current mate and territory, even if reproductive history is poor, or it can seek a new but familiar mate on an adjacent territory to potentially improve reproductive success in an unknown future. Pairing with familiar birds may minimize the risk of losing a territory altogether. Divorces are best explained by a new “territory limited” hypothesis rather than existing hypotheses.

INTRODUCTION

While monogamy is the most widespread breeding system among avian species (Lack 1968, Gowaty and Mock 1985), extensive inter-specific differences in pair bond duration exist (Black 1996). A short-term pair bond in birds may only last until the female produces fertile eggs. A long-term pair bond may persist for decades, but no bird species consistently “mates for life”. Severing of a pair bond can be the result of both passive and active factors (reviewed in Ens et al. 1996). While the death of a mate passively severs a pair bond, pair members may also separate while both members are still alive (i.e. divorce). Several hypotheses have been postulated to explain divorce in birds (summarized in Choudhury 1995). In migratory species with long-term pair bonds, passive pre-emption of a pair re-uniting may occur where female A is unable to re-pair with male A because he has formed a pair bond with female B who arrived on the breeding grounds first (Johnston and Ryder 1987, Fairweather and Coulson 1995, Gonzalez-Solis et al. 1999, Handel and Gill 2000). Establishment of the new pair bond in the “asynchronous arrival” hypothesis is often viewed as acceptance that a former mate will not return. Low probability of between-year nest site occurrence may cause pair members to disperse to new areas and this can passively affect mate fidelity depending on direction of travel (Cuthbert 1985). Forced divorce, or invasion into a pair bond by a third bird (Nesbitt and Wenner 1987, Williams and McKinney 1996, Sundar 2005), may be passive or active, depending on whether there is a choice of accepting an intruder as a new mate.

Most hypotheses regarding active means of pair bond separation have a redundant theme of viewing divorce as an ultimate strategy to increase individual reproductive fitness. The proximate trigger for this behavior, however, can be variable. If a pair is incompatible, then low reproductive success prior to divorce may cause a pair to mutually separate (Coulson 1972, Rowley 1983). This “incompatibility” hypothesis suggests the choice to divorce is based on past reproductive history and predicts both members should increase reproductive success following divorce (Harris et al. 1985, Bradley et al. 1990, Dubois and Cezilly 2002).

Alternatively, the “better option” hypothesis suggests that divorce in birds may be unequal with one individual (i.e. a “chooser”) initiating the divorce to improve reproductive fitness by increasing the quality of their mate, territory, or both while the remaining bird (i.e. a “victim”) is negatively affected by the change (Davies 1989, Ens et al. 1993). Here, there is high variability in mate or territory quality among individuals and the chooser uses past experience to choose a new mate and predict future reproductive success. Whether the initiator disperses from or retains a breeding territory may depend upon mate quality or territory quality (see Ens et al. 1996). An individual may prefer a mate that has previously held a territory or has previous breeding experience (Coulson 1966, Black et al. 1996, Williams and McKinney 1996, Jouventin et al. 1999). In dense breeding populations, however, a lone territorial bird may risk losing its territory to an intruding pair if it does not re-pair quickly. The cues used in mate assessment can differ depending on the amount of time available for mate choice (Sullivan 1994). Females are often viewed as the “choosers” of the better option as most leave their mate and territory to pair with an available male on his breeding territory (Savard 1985, Gauthier 1987, Port 1998, Smith et al. 2000).

Because both the incompatibility and better option hypotheses focus on the interaction between divorce and reproductive success, they are not mutually exclusive. The primary difference between the two hypotheses lies in whether divorce is initiated by one or both members of a pair and how those individuals respond to the divorce event. In species where not all sexually mature adults can obtain territories and breed, however, territoriality can limit both the incompatibility and better option hypotheses because the ultimate driver affecting mate choice may be measured primarily by obtaining and maintaining a territory/nest site, and thus having any breeding potential, regardless of past reproductive performance. Where excess sexually mature birds vie for breeding territories, territorial pairs may remain together through times of low reproductive success, rather than switching mates, so that they retain the possibility that environmental conditions will change to allow higher future reproduction. This fourth, "territory limited" hypothesis has not been documented and is testable across multiple species that exhibit territoriality, are long-lived, and have a sexually mature portion of the population that are unable to breed due to lack of territory. This hypothesis may also apply to colonially-nesting species because pairs defend nesting sites as a small territory (Burger 1984, Massey 1974). The territory limited hypothesis would be evidenced by persistence of low reproductive success prior to a switch in the portion of a population that switches mates, unproductive pairs that continue to remain together, mate switches that minimize the risk of losing territorial status, an ability to assess the quality and availability of a mate/territory, and more frequent divorces when there is high probability of obtaining new mates.

Sandhill Cranes (*Grus canadensis*) are long-lived, highly territorial, and form long-term pair bonds (Walkinshaw 1973). A portion of the population is comprised of birds that are sexually mature but unable to occupy breeding territories (Hayes and Barzen 2006). After reaching independence, young, sexually-immature birds join non-breeding flocks composed of other sexually-immature birds and sexually-mature birds that do not defend a territory. Pair bonds in non-breeding flocks are often short-term and birds may gather extensive information about territorial and non-territorial birds as potential mates during this life stage (Bishop and Blankinship 1984, Stehn 1997). Individuals may pair and attempt to establish a territory as a pair or wait for openings in territories to occur where they can enter into the breeding population quickly by filling vacancies in a pair caused by mortality or divorce (Hayes and Barzen 2006). Acquisition of a breeding territory typically occurs at four to five-years-old or later (Tacha et al. 1989, Nesbitt 1992, ICF unpublished data) and pair members share equally in parental duties (Walkinshaw 1973). Since a pair can only fledge 0, 1, or 2 chicks in any given year, a pair's investment in a relatively small number of chicks can be significant (Miller 1973, Walkinshaw 1973). Finally, our study population, along with other populations of Sandhill Cranes, are migratory with scattered wintering areas (Meine and Archibald 1996). All of the above characteristics make the Sandhill Crane an ideal species to test the "asynchronous arrival", "incompatibility", "better option", and "territory limited" hypotheses. In this study, we use marked individuals, studied over two decades, to investigate changes in reproductive success from birds that switch mates and territories.

METHODS

Sandhill Cranes were captured, color-banded, and monitored near Briggsville, Wisconsin (N Lat. 43° 36', W Long. 89° 36'). This site contains a mixture of agriculture and wetland systems with limited residential or commercial development (Su 2003). Our study population supports a large population of breeding pairs (Su 2003) and non-breeding birds (Hayes and Barzen 2006).

Sandhill Crane pairs were color-banded using three techniques from 1991–2013. Territorial adult pairs with any accompanying fledged hatch year chicks (older than 90 days) were captured using an oral sedative, alpha-chloralose as a group (Wildlife Services, USDA, Waupun, WI; Hayes et al. 2003) or individually with toe snares (Hereford et al. 2001) from August through October. Flightless chicks (age 35 to 70 days) were chased on foot until they hid and could be captured during June and July (Hoffman 1985). Once captured, each crane was marked with a three-inch plastic band engraved with a unique three-digit number that was placed above the tarsal joint of one leg and with two or three one-inch colored plastic leg bands, in a unique color combination for each bird, that were placed above the same joint on the opposite leg. A U. S. Geological Survey aluminum rivet band (with an engraved unique nine-digit number) was added below the tarsal joint on one of the legs to serve as permanent identification. Redundant identification systems were used on each bird to allow the recording of more bird observations by an audience with varied training (see www.bandedcranes.org).

Age (adult or chick) of captured birds was determined through presence/absence of red skin on the bird's head (Lewis 1979). Blood samples were collected from most birds (n = 115) captured after 1995 and sex was determined through genetic analysis (Griffiths et al. 1998, Duan and Fuerst 2001). For other birds (n = 66), posture and vocalization during an antiphonal duet (unison call; Archibald 1976) observed subsequent to banding and relative size within a pair (males are typically larger than their mates; Nesbitt et al. 1992, ICF unpublished data) was used to determine sex of individuals.

Pairs were observed annually while on the breeding grounds (March-November; see Su 2003). We tested our assumption of consistent re-sighting of breeding adults across all years using AICc comparison of survival and encounter models in program MARK (White and Burnham 1999). Only observations from known breeding pairs with both members color-banded were used in divorce and reproductive success analysis. Divorce was defined as a mate switch where at least one pair member bred with a new mate (during at least one breeding season) while the previous mate was observed alive. If a crane paired with an adult different from its previous mate following nesting, but returned to its former mate before nesting again, the divorce was considered temporary. Temporary divorces were not included in analyses of permanently divorced birds.

Mate loss resulted from the death or long-term absence of one pair member. Few mate losses were confirmed through locating a carcass or band recovery (Hayes et al. 2003). We considered a banded, breeding adult crane as “missing” if it was not observed on its breeding territory at the start of the breeding season in March and its mate was observed alone (aside from the normal nesting period when pair members alternate incubation) or paired with a new individual. The missing status was upgraded to “likely dead” if the missing bird was not observed anywhere in the study area during the breeding season and through the start of fall migration. Aggregation of local birds prior to fall migration allowed us to identify banded birds which were absent from the study area during summer but remained in the general region. Bird status was verified through multiple years of observation when possible. Only 5.3% of breeding adult cranes classified as “likely dead” during 22 years of observation have been re-sighted following disappearance (ICF, unpublished data). All banded breeding adult cranes were included in determining mortality trends. The time frame for annual mortality rates ran from March of a given year to February of the following year which coincided with the annual cycle of Sandhill Cranes' return to the breeding grounds at this latitude (ICF unpublished data). If mortality of breeding adults created openings on territories, then mortality rates were hypothesized to be the primary predictor of mate switches.

Individual breeding birds were considered experienced if they were originally banded as a member of a breeding pair and were captured on territory. Birds were considered Inexperienced when they first obtained a breeding territory. Inexperienced birds were identified because they were banded as chicks on known breeding territories with color-marked parents and then, as adults, obtained a breeding territory through the course of this study. Territoriality was defined through observation of territory defense, nesting behavior, or hatching and raising chicks.

Annual reproductive success (Murray 2000) was based on chicks fledged from territories occupied by two color-banded adults that survived through the initiation of fall migration. The number of chicks (0, 1, or 2) produced for a banded pair in a given year were tallied and an average reproductive success for each pair was calculated by taking the sum of the number of chicks observed divided by the number of years that pair was observed breeding together. Few banded chicks (7%) observed alive up to their first fall migration were not observed in subsequent years (Hayes and Barzen 2006), suggesting low mortality during the first winter and spring migration for this population. Overall, there was a marked decrease in reproductive success of banded Sandhill Crane pairs over the study period, but no relationship for number of observed divorces per year over the same study period (ICF unpublished data).

Statistical analyses

Data sets were tested for normality prior to statistical analysis with a Shapiro-Wilk test (Shapiro and Wilk 1965) and significance was set at $p \leq 0.05$. A deviation from normality was verified using a Q-Q plot in R. Non-parametric tests were used to compare data sets that were not normally distributed. Fisher's exact test (Sokal and Rohlf 2001) was used to examine if either sex or territory retention after a mate switch (divorce or mate loss) was related to individual reproductive success. The same test examined the difference between male and female preference for experienced birds following divorce or mate loss. We used multiple univariate comparisons of means rather than a unified multi-way ANOVA or Kruskall-Wallis test because of the high correlation between experience, age, and reproductive success among these birds lives. For example, after a pair divorces, each individual will experience independent post-divorce reproductive success. If each divorced bird re-pairs, but then one bird consequently loses its new mate, its post-divorce reproductive success would equal its pre-loss reproductive success.

We used Mann-Whitney U tests (Sokal and Rohlf 2001) to evaluate responses due to mate switches in a variety of ways. First, we tested if there was a difference in lengths of time without fledging a chick between divorced (pre and post-divorce) and non-divorced pairs. Second, we determined if there was a difference in post-divorce reproductive success between "choosers" (birds that left the territory) and "victims" (birds that retained the territory). Third, we compared experienced and inexperienced birds in the number of years spent on territory and in annual reproductive success. Finally, we tested differences in average annual reproductive success between pairs that switched mates and non-switching pairs.

A t-test compared differences in mortality based on sex and location (on breeding grounds vs. off breeding grounds). A Wilcoxon signed-rank test (Sokal and Rohlf 2001) was used to compare average annual reproductive success pre- and post-mate switch for individuals (males and females) from pairs that switched mates.

A Kruskal-Wallis test (Sokal and Rohlf 2001) was used to determine relationships between number of divorces in a year and number of pairs observed that year, whether reproductive success varied by year, and if number of divorces in a year related to reproductive success observed for that year. This test was also used calculate relationships between divorce rate in one year and mortality rate in that same year as well as mortality rate from the previous year. We correlated the length of time a bird spent on the same breeding territory to the length of time of a bird on any breeding territory and evaluated how either of these variables affected lifetime reproductive success with a Kruskal-Wallis test as well.

We evaluated whether birds used reproductive success of a nearby territory as a proximate cue for switching to that territory if an opening occurred. For example, in Figure 2.1, we recorded the number of chicks fledged to migration per year on Territory A prior to divorce. Then, after Male 1A moved to his subsequent territory (Territory B in Figure 2.1), we compared the number of chicks fledged to migration per year for Territory B *before* Male 1A moved there. Reproductive success from both territories was measured for the same number of years to ensure unbiased observation of chick fledging. We then averaged reproductive success data for all prior territories and compared them to average reproductive success data for all subsequent territories using Wilcoxon signed-rank test. Territories in these comparisons had at least one banded individual on each of the territories measured.

For spatial analysis, we tested patterns of movement where mate switches occurred. Breeding territories were mapped using observations of banded birds collected over multiple years and territory polygons were constructed in ArcMap 10 (ESRI). We focused on only the upland portion (e.g., crop field, pasture, grassland, etc.) of territories because visual observations in wetland portions of a territory were difficult due to tall vegetation (Miller 2002). Territory boundaries in uplands were demarcated using observed territorial encounters occurring before, during, or after incubation and while chicks were flightless (<70 days old). Adjustments to territory size and shape were made annually to reflect habitat and behavioral changes in extant pairs. Overall, however, territorial boundaries were typically static from year to year as long as the same pair remained on the territory. In the cases where a new pair obtained the territories, changes in territory shape and size sometimes occurred.

Breeding dispersal distance following divorce was calculated by measuring straight-line distance between the center of a bird's initial territory and the center of its subsequent territory. When a bird had multiple divorces and left its territory each time, the initial territory was the one preceding each divorce. Even though dispersal events were likely more complicated, we assumed straight-line movement between initial and new territories to estimate minimum distances. Our goal in this spatial analysis was to test whether mate switches occurred more frequently among adjacent pairs who were likely to be more familiar to the switching birds than were birds on more distant territories. For comparison, distances were measured between the center of a bird's home territory and the center of 25 previously mapped (in ArcMap) territories chosen at random in Microsoft Excel. We used 25 random territories because the average (±SE) increased from five to 10 to 25 random samples, but the average did not change between 25, 50, or 100 random samples (data not shown). A χ^2 analysis (Sokal and Rohlf 2001) was used to compare observed breeding dispersal distances to an average of 25 replicate computer-generated random movements for each bird. All statistical analyses were conducted in Microsoft Excel and R (R Foundation for Statistical Computing, Vienna, Austria).Statistical significance for all tests was set at $P \leq 0.05$. Average values are $\pm$SE.

RESULTS

We observed 179 individually marked birds in 119 pairs (with both members banded) across 67 distinct territories over 23 years. Of 179 birds, 89 (50%) switched mates at least once. Mean pair bond length of all pairs (including currently existing pairs) was 4.1 ± 0.4 years (range = 1-21 years), while mean length of pairs with a known start and end date was 3.6 ± 0.7 years (range = 1-11 years, n = 23 pairs); this difference was not significant (Mann-Whitney U = 1453.5, p = 0.63). On average, the probability of pair bond retention from one year to the next was $80 \pm 0.02\%$ (range = 64-95%). Observation effort was consistent among years (Program MARK Encounter Rate (ρ) for breeding adults 1993-2013 avg. = $94.8 \pm 1.3\%$, range = 79.0%-100.0%). Over 23 years, average reproductive success for pairs where both members were banded was 0.41 ± 0.05 chicks fledged/territory/year (range = 0.09-1.00 chicks fledged/territory/year).

Sandhill Crane Autecology

Thirteen pairs (11%) temporarily switched mates and reunited before the subsequent breeding season. Temporary divorces detected in post-nesting season were due to either: 1) asynchronous capture or release prior to fall migration (5 of 13 pairs, 38.5%), or 2) pairs that had failed in their nesting attempt for that season (2 pairs, 15.4%). Temporary divorces prior to the nesting season (6 pairs, 46.2%) were caused by pair members returning asynchronously from spring migration (see below).

Of 119 banded pairs, 81 ended due to a permanent mate switch (on-line supplementary material). Of 81 switches, 23 banded pairs permanently divorced (28%) at a mean annual divorce rate of 5.0±1.3% (Table 2.1). Number of divorces in a year did not vary by number of pairs observed in that year (slope = -0.029, p = 0.69) nor was there a pattern of divorces among years (slope = 0.043, p = 0.54, Figure 2.3). Reproductive success of banded pairs significantly declined during the 21 years of observation (slope = -0.019, p < 0.001, $R^2 = 0.45$; Figure 2.4a). Too few pairs were marked in 1991 and 1992 to be included in reproductive success estimates. The number of divorces, however, did not change over the same study period (slope = -0.13, p = 0.77, $R^2 = 0.01$; Figure 2.4b).

The remaining 71% of 81 mate switches were the result of known or probable mate death and these switches occurred in 58 of 119 pairs (48%). There were 31 males and 26 females that were “widowed” during the observation period: 12 banded pairs ended due to known mortality and 45 pairs ended because a mate was likely dead. Average annual adult mortality was 8.3±1.2% (Table 2.1) and this was consistent with annual survival estimates (Program MARK survival parameter estimate (ϕ) for adults captured 1993-2013 = 91.6±0.8%). Mortality rates from 1993-2013 did not differ ($t = 0.96$, $P = 0.34$) when we compared those that occurred on breeding areas (4.4±0.7%, range = 0-11.3%) to those that occurred off breeding areas (4.7±1.0%, range = 0-8.7%). Similarly, annual mortality rates for males (9.2±1.2%, range = 0-20.7%) and females (7.3±1.2%, range = 0-18.2%) did not differ ($t = 1.10$, p = 0.28) for the same time period. There was a trend that divorce rate was inversely related to current year mortality rate (slope = -0.42, p = 0.06; Figure 2.5), but the amount of variation explained by the model (R^2 = 0.18) was low. No relationship existed between the previous year mortality rate and current year divorce rate (R^2 = 0.026, slope = 0.22, p = 0.51).

Asynchronous migration hypothesis

With asynchronous arrival by pair members, divorces should occur more often because a new mate is procured before the previous mate arrives. Further, for the hypothesis to explain permanent mate switches, divorces arising from asynchronous arrival of mates should be permanent even if the original mate reappeared at a later date.

We followed 85 banded pairs that bred together at least one spring following capture for a total of 403 pair-years. For 48% of the observations (192 pair-years), we did not observe pair members arriving before nest initiation, so they could not be included in this analysis. Of the remaining 211 pair-years, 84% of pair members were observed together before nesting started. For the remaining 16% of observations (33 pair-years), one pair member was observed without the other member prior to nesting. Though alone, mates were obtained only eight times and these pair bonds lasted only until the original mate re-appeared and thus were temporary. Only once (0.5%, n = 211 pair-years) did a potential permanent divorce occur on breeding grounds by before nesting. In this case, it was difficult to determine the cause of the divorce because the banded female was observed associating with an unbanded male before her banded mate returned from spring migration. The original banded pair then reunited for 11 days after which they divorced permanently. In this permanent divorce, the female retained the territory with an unbanded male, and the banded male moved to the adjacent territory with a widowed banded female.

Did we simply miss most of the divorces arising from asynchronous migration? Of all 24 permanent divorces we recorded in this study, 14 (58%) occurred on breeding areas which left a maximum of 10 divorces that occurred away from breeding areas. Even if all of these off-breeding area divorces are the result of asynchronous arriving mates that we missed and added to the original 33 times when one pair member arrived without the other, this would only have occurred in 23% (*n* = 43 pair-years) of the times when pair members arrived separately. The asynchronous migration hypothesis is marginally supported by these data.

Incompatibility hypothesis

Incompatible pairs may mutually choose to separate and find more compatibile mates. A pair's incompatibility should be detected shortly after a pair bond has formed (i.e., within 1-2 breeding attempts) to avoid too many lost breeding opportunities. If incompatibility is a cause of divorce in Sandhill Cranes, we expected lower reproductive success for pairs leading up to divorce and higher reproductive success on average following divorce for both individuals after re-pairing.

Prior to separating, 16 of 23 divorced pairs (67%) had never fledged a chick, a significantly higher rate compared with 40 of 95 non-divorcing pairs (42%; Fisher's exact test = 3.71, p = 0.04). Divorced pairs also had significantly lower overall reproductive success before divorcing (average = 0.20±0.07 chicks/year over 68 pair-years) compared to pairs that never divorced (average = 0.42±0.06 chicks/year over 301 pair-years; Mann-Whitney U = 1074, p = 0.05). The length of time that a pair had not fledged a chick did not differ between non-divorced pairs (*n* = 95, average 2.5±0.2 years, range = 0-12 years) and divorced pairs (before divorcing; n = 23, average = 1.9±0.4 years, range = 0-7 years; Mann-Whitney U = 1314.5, p = 0.15).

Following divorce, however, reproductive success improved for both original pair members in only three of 23 divorced pairs (13.0%). On average, these six birds took 2.5±1.3 years (range = 0-8 years) until they successfully fledged a chick. In nine pairs (37.5%), reproductive success improved for one original pair member and decreased or remained unchanged for their former mate. On average, these nine birds took 1.9±0.6 years (range = 0-5 years) to successfully fledge a chick. In 11 pairs (48%), both members either decreased in reproductive success or remained unchanged. With these data, we rejected the incompatibility hypothesis. Twelve birds (three “one bird improved” and nine “neither bird improved”) that had never fledged a chick post-divorce are still alive and paired on territory. Post-divorce reproductive success results, therefore, could change as these birds remain on a breeding territory (see inclusive reproductive success analyses below).

Better option hypothesis

The “better option” hypothesis has similar predictions to the incompatability hypothesis except that only one member of the divorcing pair needs to improve its reproductive output through switching mates. As stated above, 48% of divorced pairs showed at least one individual improving its reproductive success following separation. Divorcing, however, did not change individual reproductive success for divorced birds (pre-divorce average = 0.20±0.05 chicks/year, post-divorce average = 0.18±0.05 chicks/year, Wilcoxon signed-rank test = 193.5, p = 0.92). This is likely because the birds that decreased in reproductive success declined enough to offset those that increased their individual reproductive success. There was no change for males (pre-divorce average = 0.20±0.07 chicks/year, post-divorce average = 0.11±0.04 chicks/year, Wilcoxon signed-rank test = 56, p = 0.48) or females (pre-divorce average = 0.20±0.07 chicks/year, post-divorce average = 0.26±0.10 chicks/year, Wilcoxon signed-rank test = 45, p = 0.66) following divorce.

Similar to the incompatibilty hypothesis above, where pre-divorce rates were compared to non-divorce rates, post-divorce reproductive success (average = 0.18±0.05 chicks/year) was signficantly lower than pairs that had never divorced (average = 0.42±0.06 chicks/year; Mann-Whitney U = 22219, p = 0.003). Of 48 divorced birds, only nine females and six males were able to fledge chicks to migration following divorce. Males and females did not differ in the time taken to produce, fledge, or migrate with a chick after re-pairing following divorce (Table 2.2). Overall fledging success declined through the course of this study independently of number of divorces (Figure 2.4) but there was no trend in frequency of divorce across years (Figure 2.3).

Individual reproductive success declined significantly following the known and likely death of a mate (pre-loss average = 0.50±0.07 chicks/year, post-loss average = 0.24±0.04 chicks/year, *n* = 54, Wilcoxon signed-rank test = 764.5, p < 0.001). When this was restricted to birds with ≥ three years of observation before and after mate loss (i.e. past the initial adjustment period for new pairs, Table 2.2, n = 21), there was a trend that individual reproductive success declined after losing a mate (pre-loss average = 0.42±0.07 chicks/year, post-loss average = 0.28±0.07 chicks/year, n = 21, Wilcoxon signed-rank test = 142, p = 0.06). Males and females did not differ in the time taken to produce, fledge, or migrate with a chick after re-pairing following the death of a mate (Table 2.2).

With the better option hypothesis, we also predicted divorced birds would choose experienced individuals as new mates as this would likely increase the probability of maintaining or increasing reproductive success. Experienced birds were preferred as new mates following divorce. In 10 cases, the new mate was banded prior to forming a pair bond and all 10 birds previously held breeding territories and were experienced. Most males (66%, n = 3) that paired with experienced females moved to their territories, but only 33% of these females were previously successful at fledging chicks to their first migration. Similarly, most females paired with experienced males and moved to their territories (86%, n = 7), but only 57% of males were previously successful. This difference between males and females was not significant (Fisher's exact test = 0, p = 1.00).

Experienced birds were also preferred as new mates following mate death. Of new mates, 12 previously banded birds were chosen: nine (75%) were known to be previous territory holders and were experienced, while three (25%) were from the non-territorial flock and had not yet obtained a territory. All three non-territorial cranes previously had unbanded mates and likely divorced to pair with the banded bird. We did not include these likely divorces in our analyses above because the birds were not of breeding status and because the fate of their original unbanded mates could not be determined. Males tended to choose experienced females (88%, n = 8) while female choices were split between experienced (50%, n = 4) and inexperienced males. Similar to divorced birds, there was no difference in males and females in choice of experienced birds (Fisher's exact test = 0.5, p = 0.24).

Is experience advantageous for a bird seeking a new mate in terms of reproductive fitness? Average reproductive success for experienced birds (n = 126; mean = 0.34±0.03

chicks/year) and inexperienced birds (n = 26; mean = 0.30±0.07 chicks/year) did not differ (Mann-Whitney U = 1821.5, p = 0.37) for birds observed at least three years. Additionally, lifetime reproductive success was not predicted by the number of divorces that occurred for an individual bird (Figure 2.6). Experienced birds, however, were observed defending a breeding territory for a longer period of time (mean = 8.6±0.4 years) than inexperienced birds (mean = 5.5±0.5 years; Mann-Whitney U = 2229.5, p = 0.004). These data suggest that while experience may be important, the better option hypothesis, as measured by reproductive success, is not supported as the best reason Sandhill Cranes in this population are choosing to divorce.

"Territory limited" hypothesis

We predicted that birds in this highly dense breeding area would retain their breeding mate or territory, regardless of past reproductive performance, until a new mate/territory becomes available. High site fidelity to a specific breeding territory is key to the territory limited hypothesis and is based not only on philopatry but on individuals obtaining knowledge about the area surrounding the territory they occupy. Therefore, if a bird remains on its established breeding territory, regardless of the number of times it pairs, it should have higher lifetime reproductive success than those that switch. If a bird chooses, or is forced, to move from its current breeding territory, it will attempt to secure a territory near its former breeding location where it has a higher likelihood of retaining its breeding status because prior experience allows it to know the territory or mate to which it is switching.

In our study, one bird (either male or female) retained the territory 100% of the time following a divorce with males (n = 14) retaining the territory more often than females (n = 7; Fisher's exact test = 3.43, p = 0.06). Three females and one males experienced multiple divorces. After removing these birds, no difference in territory retention between males (n = 10) and females (n = 7; Fisher's exact test = 1.71, p = 0.18) occurred. Retaining the territory did not change post-divorce reproductive success (up, down, or unchanged; Fisher's exact test = 2.00, p = 0.42).

Similar to divorces, territory retention was also high following mate loss (86%, n = 59). Males (97%, n = 30) retained the territory following mate loss more often than females (75%, n = 28; Fisher's exact test = 4.24, p = 0.02). Similar to divorces, retaining the territory post mate loss did not change reproductive success (up, down, unchanged; Fisher's exact test = 3.64, p = 0.22).

The longer an individual could maintain its breeding status, the more chicks were raised to their first fall migration over its lifetime (Figure 2.7, slope p < 0.001). Also shown in Figure 2.7 are data showing the longest time a bird spent on the same (as opposed to any) territory versus lifetime reproductive success. As expected, these data are correlated (*r* = 0.97, p < 0.001).

After divorcing, 20 of 23 (87%) individuals known to have left the territory re-paired. We were able to measure dispersal distance for 15 of these individuals, only 3 of which were males. With males and females combined, the average breeding dispersal distance a bird moved post-divorce was 0.9±0.2 km (range = 0.2-2.2 km, n = 15). Breeding adults stayed closer to their previous territory after dispersing post-divorce than expected (average random dispersal distance average = 5.1 ± 0.3 km, range = 4.0-7.5 km; $\chi^2 = 51.7$, p < 0.001).

Similar trends were observed with birds that suffered mate loss. Two males and three females that left their territories paired with mates on adjacent territories (0.4-0.8 km) while the fourth female paired with a male four territories away (2.3 km). The remaining three females were observed in non-breeding flocks before disappearing and have not been observed again.

Does an individual crane use recent reproductive success information from adjacent breeding territories to determine their potential as an alternative breeding site if a vacancy occurs? For this analysis, 13 of the 22 subsequent territories had sufficient reproductive success information available prior to an opening occurring (Figure 2.1). While average pre-divorce reproductive success on a previous territory (0.12 ± 0.02 chicks/year over 24 pair-years) appeared nearly three times lower than average reproductive success for the subsequent territory during the same time period (0.35 ± 0.04 chicks/year over 24 pair-years), there was no statistically significant difference between these two groups (Wilcoxon signed-rank test = 63.5, p = 0.17).

DISCUSSION

Permanent mate switches occurred in most pairs in this dense breeding population of Sandhill Cranes over the 22-year study period. More individuals switched mates following the confirmed and suspected death of a mate than switched while their mate was still alive. With an average pair bond lasting just four years, pair-bond length was relatively short compared to the average lifespan of this species and it took nearly five years for the average pair to produce two chicks and replace themselves in the population. The monogamous mating system utilized by cranes, therefore, is much more complicated than previously described (Walkinshaw 1973).

In this study, pair bond longevity was over a year shorter than previous estimates for this population of Sandhill Cranes (Nesbitt and Tacha 1997) while the divorce rate was similar.

In non-migratory populations in Florida, the response to losing a mate (either via death or divorce) was sex-biased, whereas there was no such trend in this study. In Florida, males could more easily gain a mate and retain the breeding territory whereas females returned to non-breeding flocks (Nesbitt 1989, Nesbitt and Tacha 1997, Nesbitt and Wenner 1987, Nesbitt et al. 2001). The opposite trend was observed in Mississippi with a female-dominant response (L. Billodeaux, U.S. Fish and Wildlife Service, pers. comm.). It's probable that these trends may be related to a skewed sex ratio in each of these populations where there is a surplus of females in the Florida population (Nesbitt et al. 2001) and a surplus of males in Mississippi (L. Billodeaux, pers. comm). Sex ratio for the population in this study is unknown. It is also plausible there is a difference in food or habitat quality between migratory and non-migratory populations as there was no such bias in this study or in Sandhill Cranes breeding in Gray's Lake, ID (see Nesbitt and Wenner 1987), but more research on both migratory and non-migratory populations would help confirm this.

While asynchronous migration often led to temporary divorces, it was not a determinant of permanent divorce in this population of Sandhill Cranes. Temporary divorces could have been opportunistic or to hedge against the possibility of a previous mate not returning. Asynchronous migration is a primary cause of divorce in colonial avian species (Fairweather and Coulson 1995, Johnston and Ryder 1987, Gonzalez-Solis et al. 1999), but also in one territorial species, the Black Turnstone (*Arenaria melanocephala*) which nests in arctic and sub-arctic areas (Handel and Gill 2000). Nesting in arctic areas leaves little time between arrival and nest initiation. In Wisconsin, cranes typically arrive at least one month before nest initiation (unpublished data), allowing mates that may arrive asynchronously time to re-form pair bonds prior to nest initiation. Asynchronous arrival could be a larger factor in permanent divorce in arctic-nesting Sandhill Cranes due to reduced time allotted between arrival and nest initiation (Boise 1979, Reed 1988), but the extent of mate switching in these populations is unknown.

Reproductive performance for pairs that permanently divorced was lower prior to divorce compared to the reproductive performance of pairs that did not divorce. Yet, though low reproduction by a pair may stimulate divorce, there was no increase in reproductive success following divorce for either member of the original pair. Additionally, decreasing reproductive success over time did not affect divorce rate in our study population. The incompatibility hypothesis was not supported as a major driver of divorce and mate fidelity in this study. In non-migratory populations in Florida (Nesbitt 1989, Nesbitt and Tacha 1997) and Mississippi (S. Hereford, pers. comm), low reproductive success is a proximate driver of divorce. Whether these splits improved reproductive success for original pair members is unknown.

The better option hypothesis was also not strongly supported by our data. Although some individuals increased reproductive performance following divorce, divorcing did not ultimately improve reproductive success, on average, for either pair member following divorce, regardless of sex or territory retention. Additionally, reproductive success is declining in our population over time, yet divorces were not linked to declining reproductive success. Instead, pairs in this study separated in response to openings on nearby territories, as seen in Blue Ducks (Williams and McKinney 1996), Magpies (Baeyens 1981), and Oystercatchers (Ens et al. 1993). How individuals, especially females are evaluating a territory to make the choice to move to that territory is unclear. It is possible that these birds are seizing open opportunities when they arise. However, these birds interact daily with their neighboring territorial pairs during territorial disputes, feeding, etc. These birds are also choosing to move to neighboring territories rather than territories further from their established territory. High site fidelity suggests birds want to remain in an area with known available resources.

If reproductive success is not an ultimate driver of divorce, the choice may be driven by mate or habitat quality. Distinguishing between territory and mate quality is difficult due to high site fidelity of breeding Sandhill Cranes. While many territories are consistently more productive than others (see on-line supplementary material), reproductive success has declined in our study population over time. Therefore, variation in environmental factors may be driving successful reproduction in a given year as seen in Willow Ptarmigan (*Lagopus lagopus*; Schieck and Hannon 1992). Our study area experiences high amounts of land-use change in the upland areas on an annual basis due to agricultural activity. Crop type planted can affect a pair's annual reproductive success (Donald et al. 2002). These land-use changes can also occur over a longer time frame when a land-owner discontinues cultivation of a field or plows, grazes, or mows a grassland area that was previously left fallow. All of these unpredictable possibilities could potentially affect chick survival (Baines 1996).

The largest proximal cause for a mate switch to occur was a vacancy on a breeding site. This is an important limitation for both the incompatibility and better option hypotheses because both posit that an individual should not move from a breeding site unless there is an alternative opening to consider. Ens et al. (1993) recognized that Oystercatchers were moving to adjacent territories and Ens et al. (1996) mentioned that mate fidelity may be enforced by low mate availability. Oystercatchers responded to a vacancy on a nearby territory and this was considered by the better option hypothesis (Ens et al. 1993). In terms of reproductive success, it was not a “better” option for a Sandhill Crane to move to a different territory because this did not guarantee increased reproductive success. Other variables, such as available food resources, decreased risk of predation, etc., may also affect a bird’s evaluation of a “better” option.

The most important factor leading to higher lifetime reproductive success was constancy on a breeding territory. The longer an individual was on any territory, the higher lifetime reproductive success it experienced. These data support the territory limited hypothesis and suggest that territory maintenance is more important than mate fidelity in determining reproductive fitness in this population of Sandhill Cranes. Mate fidelity, however, is not solely a by-product of site fidelity. In non-migratory populations in Florida, partnerships are maintained year-round (Nesbitt and Tacha 1997). In migratory populations, pair members are often observed together or apart off breeding areas (D. Aborn, University of Tennessee-Chattanooga, pers. comm., G. L. Ivey, ICF, pers. comm) and 10 of our observed divorces occurred outside the summer period when no territory could be evaluated. Prolonged associations seem to assist in mate familiarity and synchronization which likely builds a stronger pair bond.

Experienced birds were preferred as new mates following divorce and mate loss. Similar results have been observed in other long-lived, avian species (Black et al. 1996, Rees et al. 1996, Jouventin et al. 1999). Specifically, Sandhill Cranes chose a mate that resided on a nearby, if not adjacent, territory. It is possible that neighboring pairs may use territorial encounters and previous reproductive success as a way to evaluate the quality of a territory or the current territory holder as a future mate (as postulated by Ens et al. 1996). The short amount of time between when a divorce took place and when a new mate was acquired support this assertion as well as the fact that maintaining a territory is critical for reproductive success. Similar results were found with Florida Scrub Jays (*Aphelocoma coerulescens*, Marzluff et al. 1989) and Australian Ravens (*Corvus coronoides*, Rowley 1983). Repeated encounters and signs of successful reproduction may be used as mate assessment signals to make a quick decision if territorial birds are suddenly found without a mate (Sullivan 1994). This is also evidenced by short average breeding dispersal distances of less than one km. The high number of non-breeding, yet sexually mature, cranes in our study population (Hayes and Barzen 2006) confound this significance because non-breeding birds are also vying for a breeding territory and are sometimes chosen as a new mate. This tended to happen when a switch occurred off the breeding grounds and there was possibly more time to evaluate this inexperienced bird as a quality mate.

So, why would Sandhill Cranes divorce and move territories? That this was an expensive decision for Sandhill Cranes to make was apparent from the two to three year time lag in reproductive success following re-pairing, as seen in other species (Coulson 1972, Black et al. 1996, Rees et al. 1996, Nilsson and Persson 2001). Also, the longer an individual was a resident on a breeding territory, reproductive success increased and moving did not improve reproductive success unless it prevented territory loss.

Hypothetically, Sandhill Cranes in this population should only move when there is an opening for them to consider and this is especially true when there is a vacancy on a nearby/adjacent territory (Figure 2.8). Moving to an adjacent territory has the added benefit of knowing the prospective territory and potential new mates available due to the close proximity to their previous territory. This supports the territory limited hypothesis. It is possible a pair could divorce due to instability in the pair bond and an opening allows a bird to make a choice to try a new territory and mate. Past reproductive experience or evaluation of neighboring birds during territorial encounters could also help a bird evaluate whether changing mates and territories would be worth the risk of leaving a territory altogether but more data are needed to confirm this trend as our results were insignificant, perhaps due to small sample size. Once a bird loses its breeding territory and cannot find another, it must return to the non-breeding portion of the population where its chance of reproducing while in the non-breeding flock is zero. Once in the non-breeding population, it is difficult to obtain a new breeding territory because of the high density of breeding pairs. This includes four males, forced off their territory by a usurper, who were unable to re-gain a new mate and territory. Sandhill Cranes in this population, therefore, should maximize their probability of retaining any breeding territory including trying to force unstable pairs apart or conduct extra-pair copulations with a breeding bird (Hayes 2007).

The territory limited hypothesis best explains divorces observed in this population of Sandhill Cranes. High territory retention, regardless of pre- or post-divorce reproductive success, supports our contention that the most important factor for successful reproduction is to maintain a breeding territory. This explains the significance of experienced birds being preferred as new mates because birds chose to move to territories only when there was an opening. This was especially true for openings on neighboring territories.

We offer the territory limited hypothesis as an alternative explanation for mate and site fidelity and switching in Sandhill Cranes. Territories are limited in this population and not all adult birds have the chance to breed in their lifetime (Hayes and Barzen 2006). Therefore, limited territory openings may be forcing Sandhill Crane pairs to remain together regardless of past reproductive success. This would explain why, as with some of our pairs, mates may remain together on a territory for decades even when they do not fledge young (e.g. the “Anacker” pair occupied the same territory from 1996-2012 without fledging a single chick; see online supplementary material). Similar results were obtained from other avian species as a result of limited food availability (Freed 1987, Morton et al. 2000) and limited mate availability (Port 1998, Smith et al. 2000).

The territory limited hypothesis may apply to other long-lived avian species that defend nesting sites, whether those species are territorial (Jenkins and Jackman 1993, Rees et al. 1996) or colonial (Johnston and Ryder 1987, Fairweather and Coulson 1995, Black et al. 1996). We expect the territory limited hypothesis to be testable in species that have: (1) highly dense breeding populations, (2) a portion of the summering population that is sexually mature but is prevented from breeding because territories are limiting, and (3) are long-lived. With many species showing a preference for experienced birds following divorce (Ens et al. 1993, Black et al. 1996, Jouventin et al. 1999), species fitting these three criteria can be tested for the territory limited hypothesis. If the available nesting sites are full, then individuals should only move among sites when an opening occurs, through death or divorce. If a bird leaves its nesting territory, but does not have another site to use, it loses breeding opportunities. This is especially true for long-lived species with long-term pair bonds and high site fidelity and is critical in explaining the ultimate reason for divorce even when no gain in reproductive success occurs as a result.

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Table 2.1. Annual divorce and mortality rates for banded breeding Sandhill Crane adults in south-central Wisconsin.

Year[a]	No. Pairs Divorced	No. Pairs Observed	Annual Divorce Rate[b]	Breeding Adults Removed[c]	Breeding Adults Observed	Annual Breeding Mortality Rate[d]
Aug-Nov 1991	0	4	0.0	2	9	22.2
1993-94	0	11	0.0	2	23	8.7
1994-95	2	14	14.3	1	31	3.2
1995-96	1	14	7.1	4	35	11.4
1996-97	3	17	17.6	3	43	7.0
1997-98	2	23	8.7	1	54	1.9
1998-99	0	25	0.0	7	61	11.5
1999-00	1	29	3.4	5	65	7.7
2000-01	1	27	3.7	7	73	9.6
2001-02	1	28	3.6	6	78	7.7
2002-03	0	23	0.0	12	62	19.4
2003-04	0	22	0.0	2	69	2.9
2004-05	0	20	0.0	5	68	7.4
2005-06	0	20	0.0	9	68	13.2
2006-07	3	19	15.8	4	68	5.9
2007-08	4	24	16.7	5	80	6.3

Table 2.1 (cont.)

2008-09	1	23	4.3	5	83	6.0
2009-10	1	27	3.6	12	92	13.0
2010-11	2	28	7.4	12	92	13.0
2011-12	1	29	3.4	6	92	6.5
2012-13	0	33	0.0	7	91	7.7
2013-2014	0	30	0.0	2	103	1.9
Total	23	460	5.0	117	1440	8.8

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[a] Aside from 1991, observations occurred from March to November each year.

[b] Annual divorce rate calculated by dividing number of divorces in a year divided by the number of banded pairs observed in that year.

[c] Includes adults confirmed dead through band recovery and adults not observed on breeding territory or elsewhere throughout multiple years of observation.

[d] Annual mortality rate calculated by dividing number of adult breeding birds that died or disappeared in a given year (March of year t through February year t+1; see Methods) divided by the total number of breeding adults observed in that same year.

Table 2.2. Differences in number of years taken to hatch, fledge, or have a chick survive to its first migration following the end of the pair bond between divorced and surviving widowed male and female Sandhill Cranes.

		Produce chicks		Fledge chicks		Migrate chicks	
		Females	Males	Females	Males	Females	Males
Divorce	Avg.	1.00	2.4	1.90	2.5	1.22	2.43
	SE	0.50	0.77	0.98	0.99	0.43	1.17
	N	11	10	10	8	9	7
	Mann-Whitney U	30.5		30		24	
	p-value	0.08		0.38		0.44	
Mate Loss/ Disappearance	Avg.	1.43	1.24	1.53	1.88	1.53	1.63
	SE	0.34	0.32	0.36	0.60	0.36	0.45
	N	21	21	17	17	17	16
	Mann-Whitney U	233		142.5		137	
	p-value	0.75		0.96		0.99	

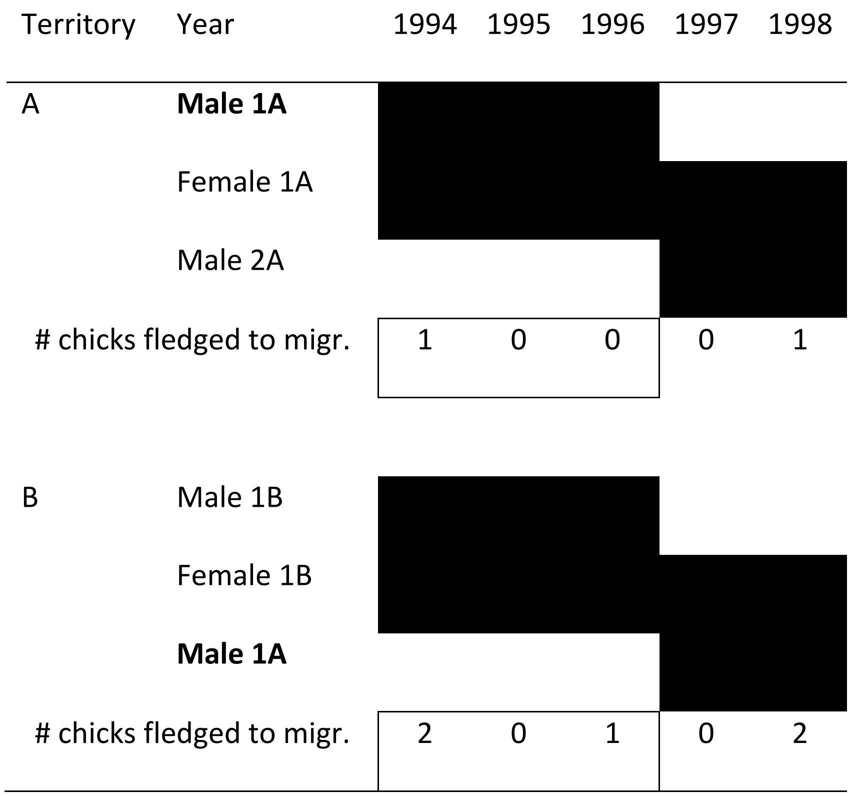


Figure 2.1. Time graph showing how reproductive success was compared between previous and subsequent territories. Black lines indicate presence on a territory. Male 1A was paired with Female 1A and then moved to pair with Female 1B after Male 1B died. The average reproductive success for each pair was compared for the same time periods (contained within the rectangles) before the divorce event occurred.

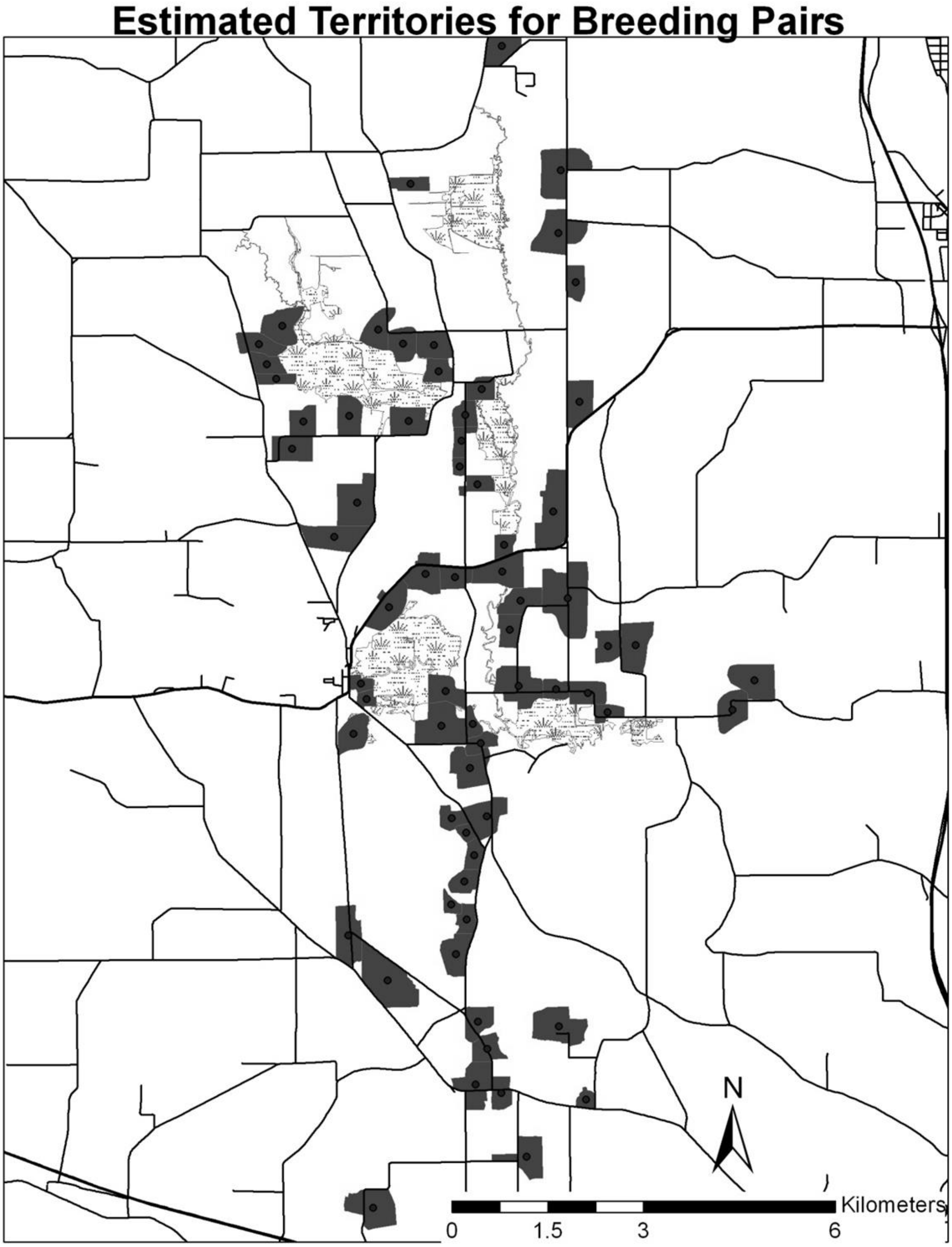


Figure 2.2. Estimated upland territories for Sandhill Cranes in south-central Wisconsin. The dots indicate the center of the territory.

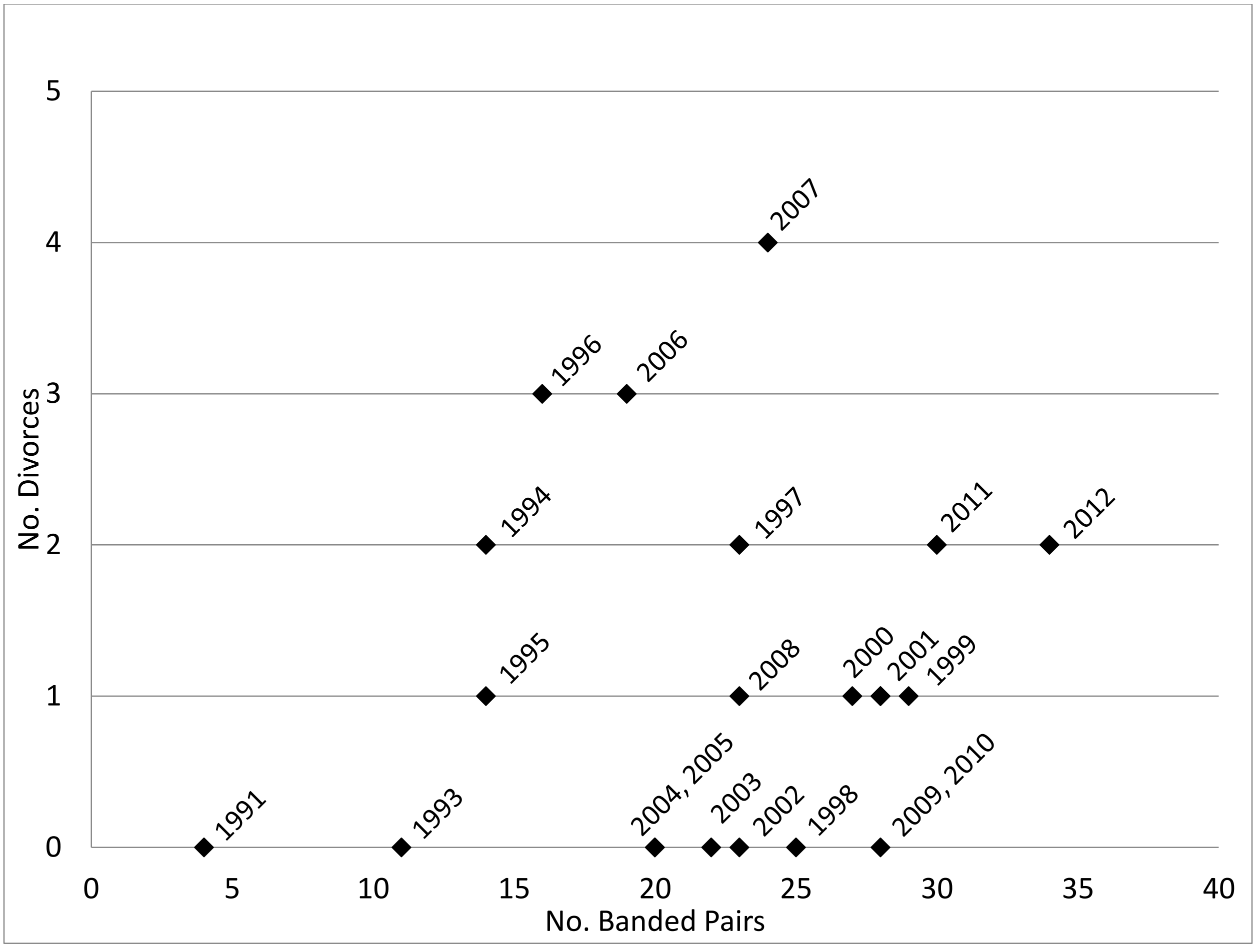
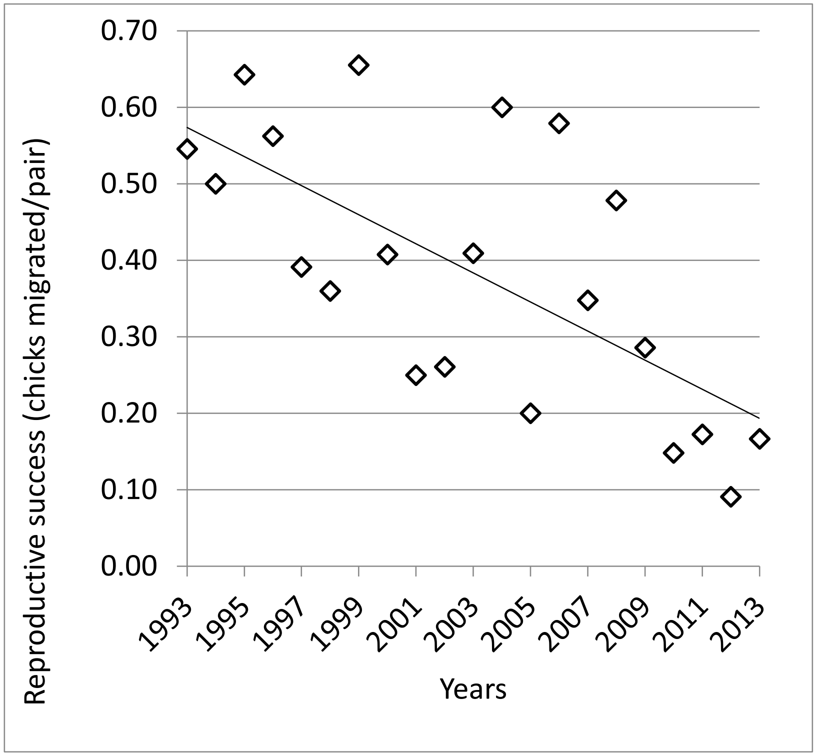


Figure 2.3. Number of divorces in relation to number of banded pairs of Sandhill Cranes observed in a given year.



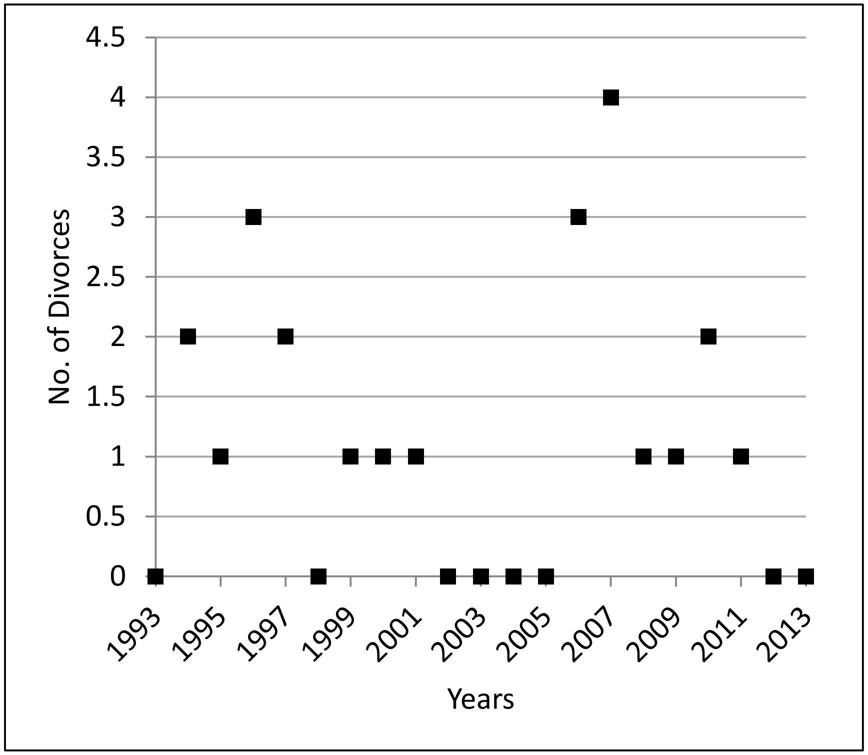


Figure 2.4a. Change in reproductive success of Sandhill Cranes near Briggsville, WI from 1993 – 2013.

Figure 2.4b. Change in number of divorces in Sandhill Crane breeding pairs near Briggsville, WI from 1993 – 2013.

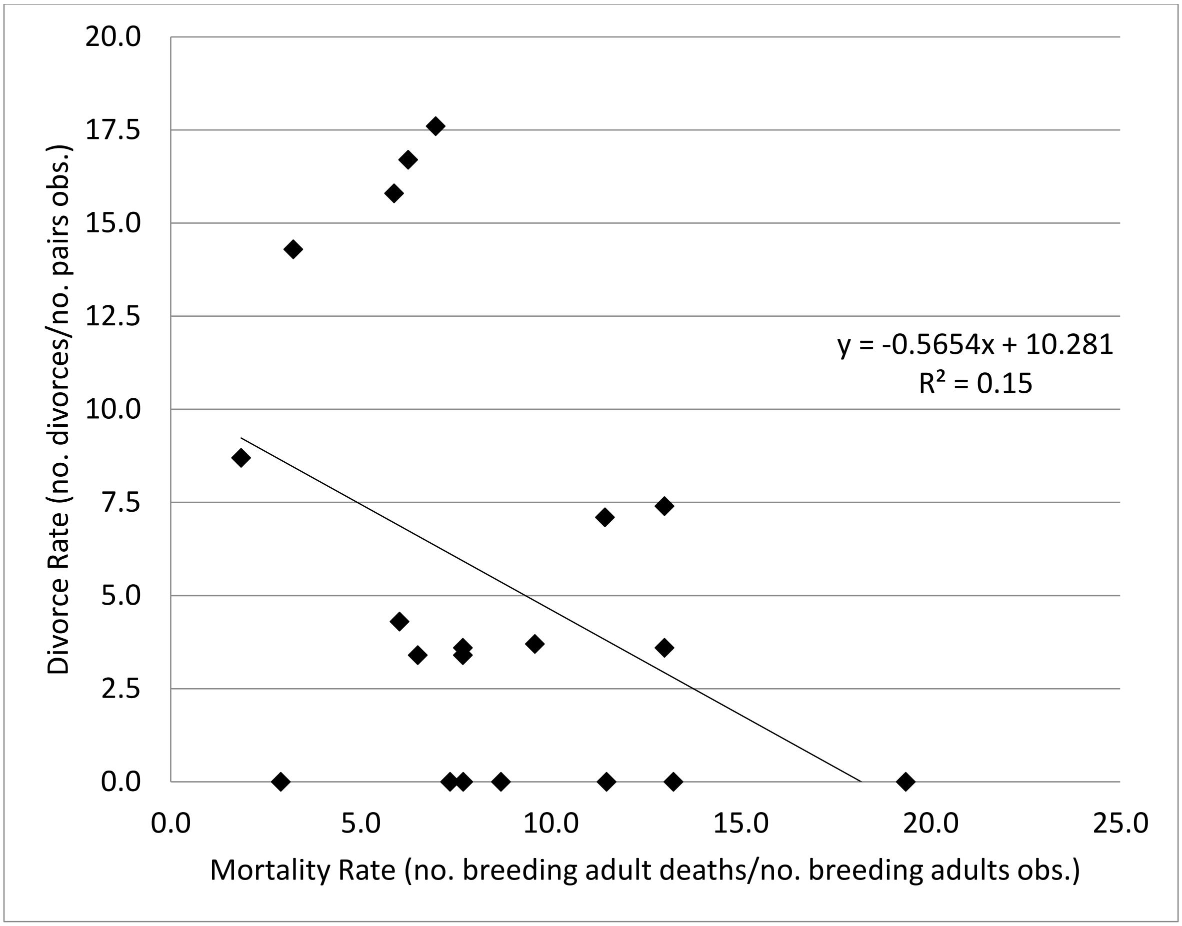


Figure 2.5. Relationship between mortality rate in a given year and divorce rate in that same year for Sandhill Cranes.

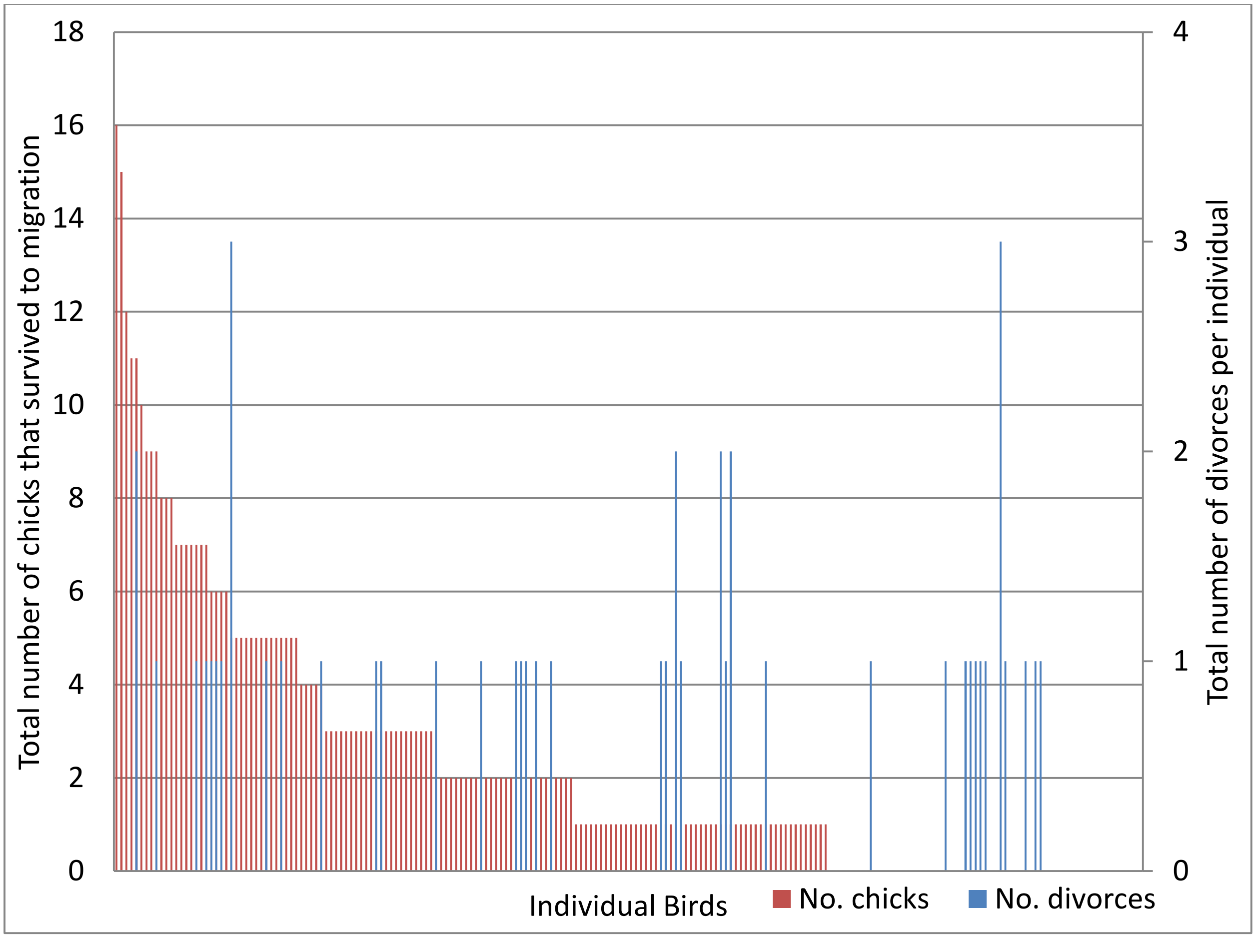


Figure 2.6. Lifetime reproductive success (red bar) paired with total numbers of divorces (blue bar) per individual Sandhill Crane.

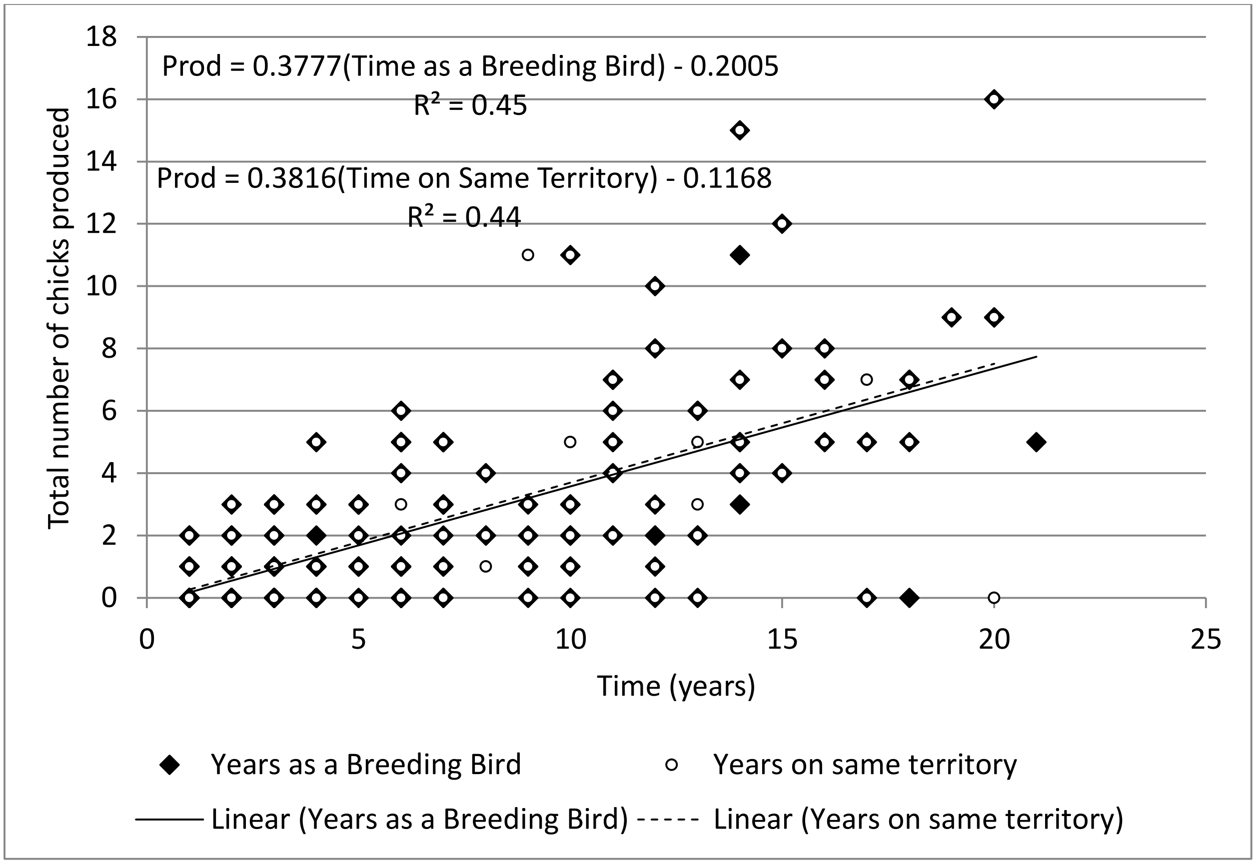


Figure 2.7. Relationship between longest time an individual spent on a breeding territory relative to the total number of chicks raised to their first fall migration by that individual.

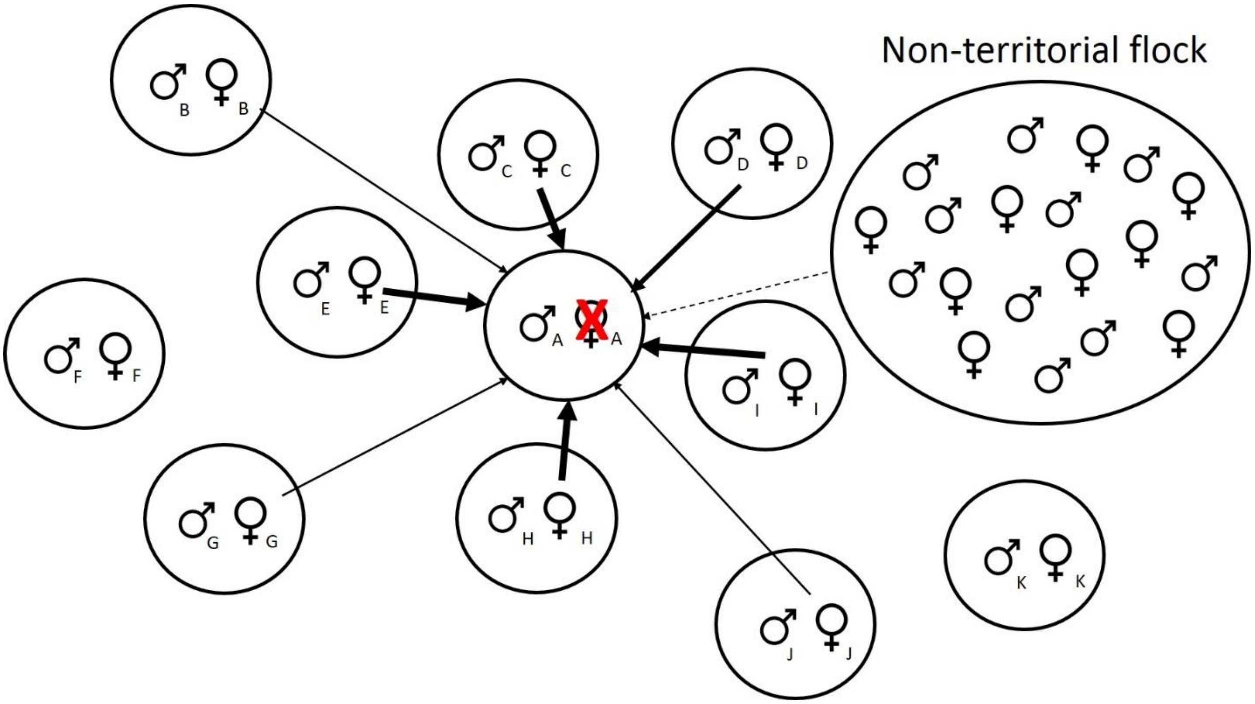


Figure 2.8a. The death of the female on territory A causes females from nearby territories to consider re-locating to this open position to pair with the male on territory A. The thickness of the arrow reflects the probability that a bird will shift territories. The dotted line from the non-territorial flock reflects the lowest probability that a non-territorial female is chosen.

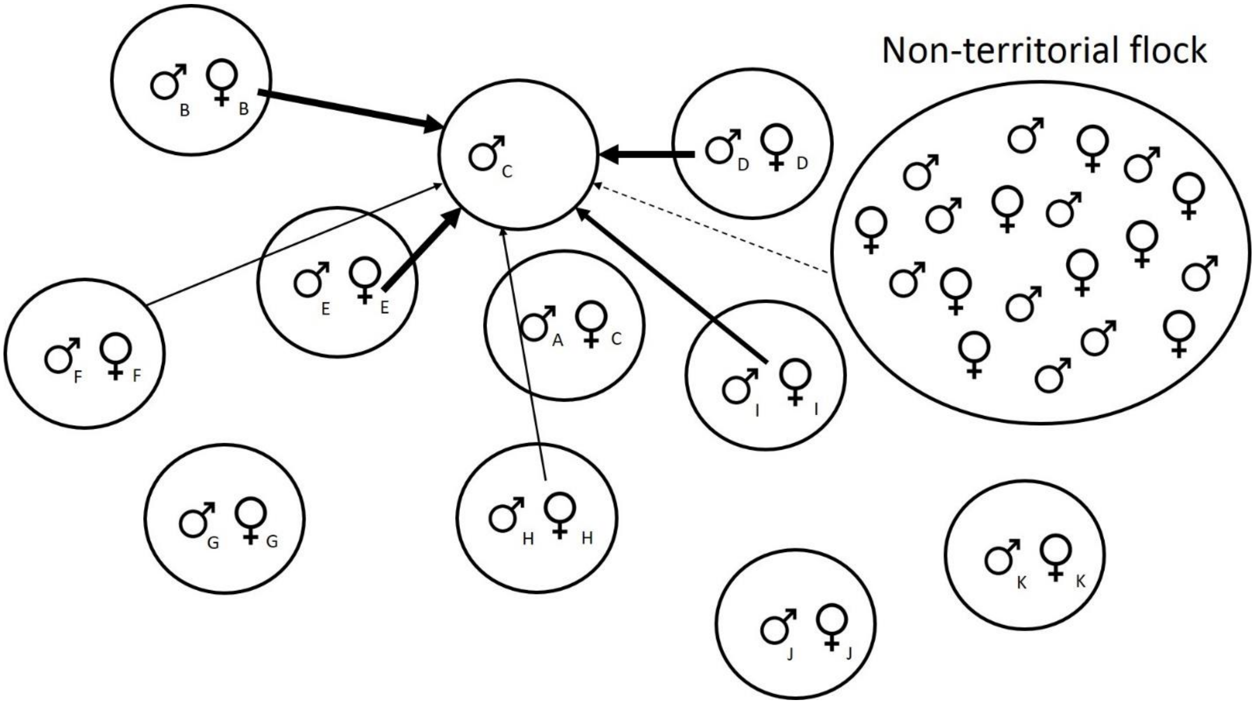


Figure 2.8b. The female from territory C chose to move to pair with the male on territory A. This leaves a vacancy on territory C. This chain reaction of openings can occur until a female from the non-territorial flock is ultimately chosen as a new mate.

Chapter 3

TIMING OF FAMILY DISSOCIATION DOES NOT AFFECT LONG-TERM SURVIVAL ESTIMATES OF SANDHILL CRANE CHICKS

ABSTRACT

Sandhill Crane chicks depend on their parents beyond the fledging period, however the timing of when chicks separate from their parents is largely unknown. I monitored color-banded and radio-tagged Sandhill Crane chicks marked on known natal territories in south-central Wisconsin. Of 96 chicks with a known timing of dissociation from their parents, 11 (12%) became independent from their parents in the fall before migration of their hatch year, 76 (79%) became independent during the winter, and nine (9%) returned from spring migration with their parents in their first year and then became independent. Average age at independence varied between 146 days (fall), 248 days (winter), and 335 days (spring). Season of chick dissociation did not affect whether a chick was philopatric or dispersive in its first year. Using mark-recapture analysis, long-term survival estimates were high (92%) and did not differ based on marking scheme (radio-tagged vs. color-banded), sex (male or female), or timing of dissociation (fall, winter, or spring). Chicks that did not migrate with their parents likely learned migratory routes and behaviors from other conspecifics. More research on interactions between parents, their offspring, and other conspecifics on wintering and migratory stopover areas could provide insight into dissociation patterns and the mechanism of separation that occurs on these areas or whether a chick returns with its parents in the spring.

INTRODUCTION

Three main phases of the dispersal process occur: departure, transience, and settlement (Bowler and Benton 2005, Clobert et al. 2008); the transience and settlement phases are discussed in Chapters 4 and 5, respectively. During the departure phase, individuals separate from their parents and begin the process of living independently. The length of time that offspring are dependent on parents can affect population change through time. While prolonged dependence increases offspring survival, it can also limit the number of breeding attempts for a breeding individual or pair in a given season (Verhulst et al. 1997).

Duration and degree of an offspring's post-fledging dependence on its parents varies widely among avian species. Post-fledging family associations persist approximately as long as the nestling period in many passerines (Skutch 1976) while long-lived avian species often require double the nestling period or longer (Jonker et al. 2011, McIntyre and Collopy 2006, Warren et al. 1993). For example, exhibiting a brief post-fledging dependence, Glaucous Gulls (*Larus hyperboreus*) take 45-50 days to fledge but dependent on their parents for only 5-10 days after fledging (Gaston et al. 2009). In contrast, Bewick's Swan (*Cygnus columbianus bewickii*) cygnets that remained near their parents during a second and third winter benefited through an advantage during aggressive interactions with other, unrelated swans (Scott 1980). Prolonged associations between parents and offspring are expected to increase offspring survival without impinging extensive cost to parents (Guo et al. 2010).

Precise stimuli for family dissociation are not well known. Departure behavior may be proximately driven by interactions among social groups as parents seek to balance fledged offspring survival with maintaining resources for the next breeding attempt. The end of the post-fledging period may also result from an offspring's innate decision to disperse (Bustamante 1994, 1995, Weise and Meyer 1979) or a response to a reduction in feeding by the parents (Guo et al. 2010, Holleback 1974, Vergara et al. 2010). Additionally, parents may actively chase offspring from their natal territory prior to the subsequent breeding season (Holleback 1974, Kamata and Tomioka 1991, Nesbitt et al. 2002).

Social hierarchies among brood mates in the same clutch may also be important drivers of departure. Dominant nest mates tend to explore away from natal locations and obtain open breeding sites while subordinate individuals remain near the natal site, losing potential breeding opportunities (Ellsworth and Belthoff 1999). Alternatively, dominant individuals may force subordinate nest mates to disperse from natal locations before they are socially or physiologically prepared (Ekman et al. 2002), thereby increasing their risk of mortality. Forced departure of subordinates by dominants has often been observed at high population densities (Chitty 1967, Krebs 1978).

Cranes (Gruidae) are long-lived avian species where family groups (a territorial breeding pair and 1 or 2 offspring produced in a given year) remain together for many months (depending on the species) after chicks fledge at 70-110 days (Walkinshaw 1973). The extensive length of the post-fledging period is thought to be the result of the prolonged learning required by juvenile cranes. While chicks learn a broad array of foraging behaviors and food preferences from their parents, provisioning to offspring by parents declines following chick fledging, but does not cease (ICF unpublished data). Chicks also learn how to avoid predators and socialize with other cranes from their parents. Most importantly, crane chicks learn migratory routes from their parents and those that are not taught these routes and habits beforehand are typically sedentary (Nesbitt and Carpenter 1993) or show sporadic, non-traditional movements that do not resemble regular migration (Nagendren 1992, but see Hayes et al. 2007).

The process of crane family group dissociation is poorly understood. Family group dissociation in non-migratory (Nesbitt et al. 2002) and migratory (Tacha 1988) Sandhill Cranes (*Grus canadensis*) occurred rapidly and parents separated from their chicks less than a month prior to nest initiation. In non-migratory Red-crowned Cranes (*Grus japonensis*; Kamata and Tomioka 1991, Kamata 1994) and in migratory Eurasian Cranes (*Grus grus*; Alonso et al. 1984, Alonso et al. 2004), familial dissociation was prolonged over a one to three month period during the winter/non-breeding season but was completed before the next breeding season. Proximate triggers of familial bond dissociation in cranes are unknown, but may result from chick voice and plumage maturation into adulthood (Klenova et al. 2010) which often coincides with seasonal hormonal changes of breeding adults in preparation for the next nesting attempt (Tacha 1988, Kamata 1994). In Red-crowned Cranes, parental behavior towards chicks changed from provisioning to displacement (by pecking and harassment) or abandonment of the young by parents on winter/non-breeding areas (Kamata and Tomioka 1991, Kamata 1994).

The goal of this study was to investigate the timing of chick dissociation from their parents in a migratory population of Sandhill Cranes breeding in south-central Wisconsin. If Sandhill Crane offspring benefit from prolonged association with their parents (e.g., learning foraging and survival skills and migratory routes), then chicks should remain with their parents until at least their first fall migration. I expected chicks that dissociated from their parents in the spring after returning from migration to show higher levels of philopatry in the first year than those that dissociated during the previous fall or winter. I hypothesized that any offspring that dissociated from their parents before fall migration would also have lower estimated survival than those that dissociated either over winter or post-migration in the spring. I did not expect any difference in estimated survival between chicks that dissociated over winter or post-spring migration because chicks in both of these age groups have learned necessary survival skills and the southward migratory route from their parents, which should equally enhance survival probability. Moreover, I expected more chicks would dissociate from their parents over winter than post-spring migration because a chick's association with its parents through the spring may increase energetic cost to the parents with minimal benefit to the chick which is nearly full grown and independent.

METHODS

Colored leg bands were deployed on Sandhill Crane chicks near Briggsville, Wisconsin (N Lat. 43^{o} 36', W Long. 89^{o} 36'). This has been the site of a long-term study on Sandhill Crane breeding ecology and habitat selection by the International Crane Foundation since 1991 (Hayes et al. 2003, Su 2003). The study area is primarily an agriculture-dominated landscape intermixed with small woodlots or forest patches, grasslands, flow-through wetlands, and dispersed human residences (see Su 2003). During summer, this study area contains a high density of territorial pairs that breed (Su et al. 2004) and flocks of non-territorial birds that do not breed (Hayes and Barzen 2006).

Capture and banding

Sandhill Cranes were captured 1991-2012 using multiple methods. Flightless chicks (35-70 days of age) were pursued on foot until they hid and could be procured (Hoffman 1985).

Volant adults and chicks (older than 70 days) were captured using 1) alpha-chloralose (Bishop 1991), an oral tranquilizer (Fisher Scientific Company, Fairlawn, New Jersey, USA and Biosynth Ag, Switzerland) using the methodology described in Hayes et al. (2003), or 2) leg snares (Hereford et al. 2001).

A captured crane was classified as a chick or adult by the absence or presence of red skin on the crown (Lewis 1979). For flightless chicks, age was further classified into the approximate number of weeks using growth criteria (Table 3.1). Blood samples were collected from 198 of 204 (97%) chicks banded 1996-2012. For birds with blood samples collected, sex was determined using molecular techniques (Griffiths et al. 1998, Duan and Fuerst 2001). For birds without blood samples, sex was determined through relative size (males are larger than females; Nesbitt et al. 1992, ICF unpublished data) or behavioral observations (males and females have different pitches to their voices and exhibit different postures during unison call; Archibald 1976) once birds had achieved adult status. Any chicks without the above elements were considered “unknown” sex.

Each crane received a size 9 rivet U.S. Geological Survey band and a unique combination of colored plastic leg bands to allow re-sightings in the field using binoculars or spotting scope (Dickerson and Hayes 2014). Additionally, some adults and chicks received leg band mounted transmitters or backpack harness transmitters to allow identification and provide location when colored leg bands could not be observed due to vegetation, topography, or flock density (see Chapter 4).

Behavioral observations

Re-sightings of colored leg bands and radio telemetry were used to determine the last date when family groups were still intact, the first date when parents were observed without their fledged offspring, and the first date when fledged offspring were observed without their parents. Hatch date was estimated in one of two ways. If a chick was banded while flightless, its hatch date was calculated by subtracting its approximate age in days at capture (Table 3.1) from the date of capture. Fledged chicks are more difficult to age (Table 3.1) because morphological growth slows near the time of fledging while weight continues to increase (Ricklefs et al. 1986). For chicks banded post-fledging (n = 67), an average hatch date was calculated from chicks caught while flightless in that same year. For post-fledged chicks with banded parents (n = 18), I then attempted to verify this average hatch date by reviewing re-sightings while the chick was still flightless. From these dates, an approximate maximum age (days) of independence for each chick was obtained by subtracting the date when the family was last observed intact from the first date when either the chick was observed independent of the parents or the parents were observed without the chick.

Following dispersal, all banded birds were monitored annually through re-sighting of colored leg bands or radio telemetry. While birds were on breeding areas, observations within the study area were regularly monitored from March through November annually. Outside of Wisconsin, monitoring was more sporadic in some winter locations (e.g., Georgia and Florida), but regular from other locations (e.g., Hiwassee Wildlife Refuge in Tennessee since 2000 and Jasper-Pulaski State Wildlife Area in Indiana since 2009; see Chapter 6). Re-sightings on off-breeding areas were sent to the ICF or Bird Banding Lab (U.S. Geological Survey) by the general public after observing a banded bird. All re-sighting and telemetry data were stored in a Microsoft Access or on-line Mapfeeder database at the ICF.

Statistical Analyses

All data sets were tested for normality using a Shapiro-Wilk test (Shapiro and Wilk 1965), and significance was set at $p<0.05$. A deviation from normality was verified using a Q-Q plot in R. I used non-parametric tests for statistical analyses on all data that were not normally distributed. A Mann-Whitney U test (Sokal and Rohlff 2001) was used to determine if males and females differed in the approximate ages when chicks dissociated from their parents. A Mann-Whitney U test was also used to determine if there was a difference in age for chicks that dissociated from their parents pre-migration in the fall as a result of capture compared to those that were not directly related to capture. Significance for all statistical tests was set at $p \leq 0.05$.

Observation within the study area was used to evaluate whether a chick was philopatric (observed within the study area) or dispersive (not seen in the study area or seen outside of the study area) during its first year of independence. I used the boundary of the study area to define natal philopatry for all chicks captured in the study area because this meant a chick was within the distance of 10 times the diameter of an average home range/territory (Shields 1982; Chapter 4). If, during its first year of independence, a chick was observed at least once within the study area during the pre-nesting (March 1 to May 31) or post-nesting (June 1 to August 31) timeframes (ICF unpublished data) during its first year of independence, it was classified as philopatric. If a chick was observed outside of the study area during the pre-nesting or post-nesting timeframes or only observed in the study area during the pre-fall migration timeframe (September 1 to November 30), it was classified as dispersive. Birds that breed outside the study area often congregate in the study area during fall. I evaluated radio-tagged and non-radio-tagged chicks separately and categorized philopatric and dispersive chicks based on the season they dispersed from their parents to determine if there was a difference in frequency for each monitoring method. A Fisher's exact test (Sokal and Rohlff 2001) was used to determine if there were frequency differences among groups.

For birds with a known season of dissociation from its parents, long-term (lifetime) survival (ϕ) and encounter (ρ) rates were estimated using a Cormack-Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965) open population model in Program MARK (White and Burnham 1999). Because radio-tagged birds have increased detectability, especially on monitored wintering areas, I separated radio-tagged birds ($n = 32$) from non-radio-tagged birds ($n = 57$) and ran each set separately in Program MARK. Each set of birds was further grouped based on sex or timing of familial dissociation (i.e., pre-fall migration, over winter, post-spring migration). Program MARK was run three times for both radio-tagged and non-radio-tagged groups: allowing survival and encounter rates to vary by 1) time, sex, and the interaction between time and sex, 2) time, season of familial dissociation, and the interaction between year and season, and 3) time, sex/season, and the interaction between time, sex/season. Model fit was evaluated by AICc and any model $\leq$ 2 AICc from the theoretical best model were considered valid (Burnham and Anderson 2002).

RESULTS

We banded 234 chicks (95 M: 123 F: 16 U) on 71 territories 1991-2012. Of these chicks, 90% had at least one banded parent and hatched on local territories in the study area. The remaining 10% had unbanded parents, but were banded as flightless chicks on their natal territory, so were known to be local. Of all chicks, 44 (19%) died or disappeared during their hatch year; 11 died and 18 disappeared pre-fledging while nine died and six disappeared post-fledging. Of the remaining 190 chicks that were observed alive until their first fall migration, 14 (7.9%) were never observed after their first fall migration. This left 176 chicks (75%; 70 M: 97 F: 9 U) that survived their first migration and were observed at least once after reaching independence.

Of 176 chicks that survived their first migration and then were observed at least once after reaching independence, five had unbanded parents, so timing of dissociation could not be determined. For the remaining 171 chicks with at least one banded parent, dissociation timing was unknown for 75 chicks (44%; 29 M: 41 F: 5 U). I could not determine dissociation timing for these 75 chicks because neither the chicks nor their parents were observed prior to the parents' nesting season following their hatch year.

Of 96 (56%; 39 M: 53 F: 4 U) chicks with a known timing of dissociation, 11 (12%) dissociated from their parents pre-migration in the fall. This dissociation occurred approximately three weeks after being last observed with their parents (Table 3.2). Two of these chicks had radio transmitters and were never recorded in the same vicinity as their parents following dissociation. Seven of these offspring were from two-chick broods. Chicks from two two-chick broods (1 M-M: 1 M-F) dispersed together while one chick dispersed earlier than its brood mate in the remaining three two-chick broods (2 F-F: 1 M-F). The average age of chicks that departed from their parents before fall migration was similar for males (n = 6; 143±10 days, range = 116-170 days) and females (n = 5; 150±11 days, range = 140-191 days; Mann-Whitney U = 16.5, p = 0.86). Six of the 11 pre-fall migration departures (3 M: 3 F) were likely caused by capture and subsequent asynchronous release of the family group because we never observed the chicks reunited with their parents following capture. Dissociation of families resulting from capture (average = 126±4 days, range = 116-134 days) were earlier than pre-migration dissociations that were not capture-caused (average = 157±5 days, range = 140-170; Mann-Whitney U = 25, p = 0.01).

Because this population is migratory, the age of chicks that dissociated from their parents during winter or migration was difficult to quantify. Eight chicks of 96 chicks (8.3%) were observed on wintering grounds without their parents (Table 3.2). Five of these chicks (2 M: 3 F) had radio transmitters, as did one parent of each chick, when observed apart. Each parent varied in the distance from its chick from being in different flocks (i.e., one kilometer apart) to residing in different states (i.e., hundreds of kilometers apart). An additional 68 of 96 chicks (71%) were observed with their parents before fall migration but parents and chicks were not observed together prior to the subsequent nesting season. Though these separations likely occurred during the winter, there was not confirmation from observations on wintering grounds. Twenty-three (8 Males, 15 Females) of these 68 chicks, however, had active radio transmitters when they returned the following spring and each chick’s frequency was not heard when its parents were observed in the spring, reducing the likelihood that the chick had returned with its parents and then flown outside of our range of detection.

Nine of 96 chicks (9.4%), two of which had active radio transmitters, returned to the breeding grounds with their parents the spring following their hatch year. Similar to chicks that dissociated from their parents in the fall, these chicks dissociated from their parents approximately three weeks later. Four chicks from four different two-chick broods dissociated from their parents later than their nest mates. One of these siblings was not observed after its first fall migration while another sibling was found dead south of its natal area and the other two presumably dissociated from their parents over the winter. Average chick age at familial dissociation post-migration in the spring did not differ between males (average = 334±18 days, range = 307-385 days, n = 4) and females (average = 344±14 days, range = 304-378 days; Mann-Whitney U = 10.5, p = 1.00, n = 5).

Overall, there was no effect of season of family dissociation on whether a bird was classified as philopatric or dispersive during their first year (Table 3.3). For each dissociation timing group, 50% of chicks were philopatric and 50% of chicks were dispersive in their first year.

Mark-recapture analysis was used to estimate long-term survival (ϕ) and encounter rates (ρ) for radio-tagged and non-radio-tagged birds. When sex and time were allowed to vary, four models were considered valid for radio-tagged birds and three models for non-radio-tagged birds (Tables 2.4 a, b). For both radio-tagged and non-radio-tagged birds, ϕ was consistent among data sets, even when ϕ varied by sex. Estimates of ρ were more variable and tended to be higher for radio-tagged birds compared to non-radio-tagged birds.

When the season of dissociation (fall, winter, or spring) and time were allowed to vary in the mark-recapture models, estimates of ϕ and ρ were more consistent between radio-tagged and non-radio-tagged birds (Tables 2.5 a, b). For radio-tagged birds, two models were considered valid with ρ always varying based on season of dissociation and ϕ remaining constant or varying based on season. For non-radio-tagged birds, there was one best model with both ϕ and ρ remaining constant. Estimates of ϕ and ρ were more similar between the radio-tagged and non-radio-tagged data sets compared to models allowing estimates to vary based on sex.

When radio-tagged and non-radio-tagged birds were grouped based on time and sex/season of dissociation from their parents, there was one best model for each data set (Tables 2.6 a, b). Estimates of ϕ remained constant and were identical for both data sets. Estimates of ρ were constant for radio-tagged birds, but more variable for non-radio-tagged birds, with females encountered less than males and chicks dissociating in the fall (both males and females) encountered less than chicks that dissociated during the winter or spring.

DISCUSSION

Sandhill Crane chicks dissociated from their parents and became independent at a continuum of ages, but these separations occurred at three discrete points in their life cycle: before their first fall migration, over their first winter, or after returning with their parents in the spring following their hatch year. Most chicks stayed with their parents through their first fall migration and the highest frequency of dissociations occurred over winter followed by the spring of their first year and then the fall of their hatch year. Overall survival rates of chicks were high, regardless of sex or season of dissociation from their parents. These observations show the flexibility of Sandhill Crane chicks to adapt to scenarios that diverge from the normal pattern of winter separation. There may not be an optimal time period that post-fledged Sandhill Crane chicks depend on their parents.

Season of dissociation from their parents did not affect philopatry during the first year. Chicks that dissociated from their parents in the fall were as likely to remain philopatric or disperse as those that dissociated over winter or returned with their parents in the spring. A chick’s philopatric or dispersive behavior during their first year of independence may be more reliant on social influence from conspecifics that are not their parents.

Differences in a juvenile Sandhill Crane’s season of dissociation from their parents was not related to dominance or displacement among siblings. With two-chick broods, both chicks dissociated from their parents pre-migration in the fall nearly as often as one chick dissociated early while the other did not. Caution needs taken with these results because intensive behavioral observations were not conducted for this study. However, while dominance hierarchies occur among siblings (Miller 1973, ICF unpublished data), these relationships are typically established within a few days to weeks after hatching. Comparatively, Layne (1982) noted no obvious aggression among brood mates in seven Sandhill Crane families in Florida and suggest that dominance relationships may not solely drive familial dissociations in Sandhill Cranes. Brood mates from some two-chick broods remained together during their first and second years of independence (Chapter 4).

While encounter rates were highly variable among the sexes and seasons of dissociation (likely driven by dispersal rates), lifetime survival estimates were similar between chicks that dispersed from their parents before their first fall migration and those that dispersed over winter or the following spring. If Sandhill Crane chicks in this study are capable of living independently at six months of age or earlier, why do they remain with their parents for a longer time period? Sandhill Crane chicks are likely dependent on their parents to learn migratory routes and behaviors (Nesbitt and Carpenter 1993). Because this study area is occupied by a dense breeding population of Sandhill Cranes during summer and large congregations in the fall, chicks that separated from their parents prior to their first fall migration likely joined pre-migratory aggregations and learned appropriate migration patterns and behaviors from conspecifics. For chicks from small and isolated populations (e.g., the northeastern U.S., see Chapter 6), pre-migratory aggregations are not typically observed (D. Racine, personal communication). Separation from parents (either accidental or by choice) could be detrimental to long-term chick survival because there would not be as many conspecifics nearby to learn these patterns. Familial dissociation patterns of Sandhill Cranes in the northeastern U.S. are currently unknown.

If migratory behavior was the main reason for a chick's dependence on its parents after it has already fledged, why are more chicks not remaining with their parents through the return spring migration? This behavior would reinforce migratory routes and behaviors. Familial dissociation on non-breeding areas after the first fall migration may be related to costs to parents (e.g., provisioning and defending dependent chicks that are capable of living independently) versus the benefits to offspring (e.g., provisioned food and protection leading to increased survival). For example, Alonso et al. (2004) found that Eurasian Crane families that defended winter territories had higher offspring survival than families that did not defend winter territories. These territories were costly to parents, however, because energy was used for territorial defense and offspring provisioning rather than in the pair's preparation for the next breeding attempt by building fat reserves (Krapu et al. 1985). Eurasian Crane parents balanced this increased cost by leaving winter territories for breeding grounds earlier than their offspring, which migrated later (Alonso et al. 1984, Alonso et al. 2004). Winter territoriality is known to occur in Sandhill Cranes (G. L. Ivey personal communication, ICF unpublished data), however, it is infrequent and the cause is unknown. Most Sandhill Cranes, regardless of reproductive status, form flocks during the non-breeding season (Tacha 1988, Krapu et al. 2011). While the exact cause of familial dissociation is unknown, this cost-benefit analysis could explain why Sandhill Crane parents remained with their chicks after teaching them the migratory route, but then dissociated from their chicks on wintering grounds (Kamata and Tomioka 1991, Kamata 1994) to focus on the next breeding attempt. Whether family group separation occurred through displacement behavior or a natural reduced dependence through maturation while on these areas is unknown.

More research is needed on dissociation of Sandhill Crane families in the Eastern Population, especially on non-breeding areas during the winter. For example, pair members may or may not remain in close proximity during the non-breeding season (D. Aborn, personal communication). Does the presence of a chick increase the chance that a pair will remain together during the winter? Are families that remain together throughout the non-breeding season more likely to return as a family unit in the spring? Does a chick home to its first wintering area in subsequent years? If a chick does home to a wintering area, does this affect wintering behavior and pair tenacity after it finds a mate? More intense behavioral observations during the non-breeding season would assist in addressing these questions.

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Table 3.1. Descriptive scale to age Sandhill Crane chicks based on morphological characteristics. Developed by Marianne Wellington, Crane Conservation Department, International Crane Foundation, with additions by the author.

Month	Week	Descriptive Characteristics
1	1	Downy, brown puff, very round body. Legs scales soft and flesh colored. Eye color dark brown.
	2	Legs elongated.
	3	Legs longer than body, ear tufts developing.
	4	Pin feathers more visible, tail is fluffy, skull cap developing.
2	5	Feathers erupting out of the shaft, ear tufts more visible. Wings small for body size, chick more active, running with wings out.
	6	Chick plumage becoming grayer, wings longer than at five weeks. Primary and secondary flight feathers about ½ emerged, tail feathers still fluffy, but feather shafts more visible. Leg scales still flesh colored and soft. Eye color still dark brown
	7	Eye color lightening from dark brown to gray. Contour feathers full grown, but blood quills still vascularized. Leg scales showing some black coloration.
	8	Body similar to adult size. Primary feathers about ¾ emerged and look worn with chick preening more. Chick conducting test flights/short hops. Legs at least 50% black and scales maturing and hardening.
3	9-10	Chick not yet capable of sustained flight, but conducting longer test flights and gliding close to the ground. Legs completely black and scales are matured. Eye color light gray or starting to appear yellow.
	11-13	Chick capable of sustained flight.
4	14+	Chick fully fledged. Crown typically feathered with short contour feathers, although red skin beginning to appear for some chicks.

Table 3.2. Summary of timing and average age (+SE) when Sandhill Crane chicks dissociated from their parents.

Age at dispersion	N (M:F:U)	Average±SE (range) age (days) when last dependent	Average±SE (range) age (days) when independent
Pre-fall migration	11 (6:5:0)	123±7 (73-176)	146±7 (116-191)
Over-winter (known)	8 (3:4:1)	169±9 (136-207)[a]	248±14 (198-295)
Over winter (likely)	68 (26:40:2)	163±3 (51-201)[a]	?
Post-spring migration	9 (4:5:0)	316±7 (301-365)	335±11 (304-385)

[a] Age (days) is when last observed with parents on breeding grounds before fall migration.

Table 3.3. Timing of chick dissociation from its parents and relation to first year dispersal pattern (philopatric or dispersive).

Dissociation		First Year Dispersal Pattern		
Timing	Sex ratio	Philopatric	Dispersive	Total
Fall	5 M: 3 F	4	4	8
Winter	24 M: 42 F: 3 U	35	34	69
Spring	4 M: 4 F	4	4	8

Table 3.4a. Results of mark-recapture analysis for radio-tagged chicks allowing sex and time to vary between models.

Model	AICc	ΔAICc	AICc weight	No. Parameters	Parameter	Estimate	SE
ϕ(constant) ρ(sex)	281.6052	0.00	0.36	3	ϕ	0.92	0.02
					ρ (Female)	0.80	0.04
					ρ (Male)	0.89	0.03
ϕ(constant) ρ(constant)	282.3405	0.74	0.25	2	ϕ	0.92	0.02
					ρ	0.84	0.03
ϕ(sex) ρ(sex)	282.6063	1.00	0.22	4	ϕ (Female)	0.90	0.03
					ϕ (Male)	0.94	0.02
					ρ (Female)	0.80	0.04
					ρ (Male)	0.89	0.03
ϕ(sex) ρ(constant)	282.9656	1.36	0.18	3	ϕ (Female)	0.89	0.03
					ϕ (Male)	0.94	0.02
					ρ	0.84	0.03
ϕ(constant) ρ(time)	300.5739	18.97	0.00	18			
ϕ(time) ρ(constant)	300.6581	19.05	0.00	18			
ϕ(time) ρ(sex)	300.9107	19.31	0.00	19			
ϕ(sex) ρ(time)	301.6796	20.07	0.00	19			
ϕ(time) ρ(time)	324.8045	43.20	0.00	33			
ϕ(constant) ρ(sex*time)	326.7602	45.16	0.00	35			
ϕ(sex) ρ(sex*time)	329.2667	47.66	0.00	36			
ϕ(sex*time) ρ(constant)	330.8056	49.20	0.00	35			
ϕ(sex*time) ρ(sex)	332.0452	50.44	0.00	36			
ϕ(time) ρ(sex*time)	362.6045	81.00	0.00	51			
ϕ(sex*time) ρ(time)	366.5929	84.99	0.00	51			
ϕ(sex*time) ρ(sex*time)	417.7682	136.16	0.00	67			

Table 3.4b. Results of mark-recapture analysis for non-radio-tagged chicks allowing sex and time to vary between models.

Model	AICc	ΔAICc	AICc weight	No. Parameters	Parameter	Estimate	SE
ϕ(constant) ρ(sex)	1494.30	0.00	0.44	3	ϕ	0.93	0.02
					ρ (Female)	0.53	0.02
					ρ (Male)	0.83	0.02
ϕ(time) ρ(sex)	1494.79	0.49	0.34	22	ϕ (1993)	1.00	0.00
					ϕ (1994)	1.00	0.00
					ϕ (1995)	1.00	0.00
					ϕ (1996)	0.96	0.04
					ϕ (1997)	1.00	0.00
					ϕ (1998)	0.93	0.05
					ϕ (1999)	0.97	0.03
					ϕ (2000)	1.00	0.00
					ϕ (2001)	0.92	0.04
					ϕ (2002)	0.89	0.05
					ϕ (2003)	0.92	0.05
					ϕ (2004)	1.00	0.00
					ϕ (2005)	0.92	0.05
					ϕ (2006)	0.89	0.06
					ϕ (2007)	0.88	0.06
					ϕ (2008)	0.98	0.04
					ϕ (2009)	0.89	0.06
					ϕ (2010)	0.72	0.07
					ϕ (2011)	1.00	0.00
					ϕ (2012)	1.00	0.00
					ρ (Female)	0.53	0.02
					ρ (Male)	0.83	0.02

Table 3.4b (cont.)

Model	AICc	ΔAICc	AICc weight	No. Parameters	Parameter	Estimate	SE
ϕ(sex) ρ(sex)	1495.66	1.36	0.22	4	ϕ (Female)	0.93	0.01
					ϕ (Male)	0.92	0.01
					ρ (Female)	0.52	0.02
					ρ (Male)	0.83	0.02
ϕ(constant) ρ(sex*time)	1507.79	13.49	0.00	41			
ϕ(sex) ρ(sex*time)	1508.18	13.88	0.00	42			
ϕ(time) ρ(sex*time)	1513.74	19.43	0.00	59			
ϕ(sex*time) ρ(sex)	1525.62	31.31	0.00	42			
ϕ(sex*time) ρ(sex*time)	1548.87	54.57	0.00	78			
ϕ(constant) ρ(time)	1565.78	71.48	0.00	21			
ϕ(time) ρ(time)	1566.32	72.02	0.00	39			
ϕ(sex) ρ(time)	1567.90	73.59	0.00	22			
ϕ(constant) ρ(constant)	1568.78	74.47	0.00	2			
ϕ(time) ρ(constant)	1569.66	75.36	0.00	21			
ϕ(sex) ρ(constant)	1570.77	76.46	0.00	3			
ϕ(sex*time) ρ(time)	1597.92	103.61	0.00	59			
ϕ(sex*time) ρ(constant)	1601.59	107.28	0.00	41			

Table 3.5a. Results of mark-recapture analysis for radio-tagged chicks allowing season of dissociation from parents and time to vary between models.

Model	AICc	ΔAICc	AICc weight	No. Parameters	Parameter	Estimate	SE
ϕ(constant) ρ(season)	314.06	0.00	0.62	4	ϕ	0.92	0.02
					ρ (Fall)	1.00	0.00
					ρ (Winter)	0.73	0.04
					ρ (Spring)	1.00	0.00
ϕ(season) ρ(season)	315.44	1.38	0.31	5	ϕ (Fall)	0.85	0.10
					ϕ (Winter)	0.92	0.02
					ϕ (Spring)	0.96	0.00
					ρ (Fall)	1.00	0.00
					ρ (Winter)	0.73	0.04
					ρ (Spring)	0.96	0.00
ϕ(constant) ρ(constant)	318.91	4.85	0.05	2			
ϕ(season) ρ(constant)	321.18	7.12	0.02	4			
ϕ(constant) ρ(time)	333.70	19.63	0.00	18			
ϕ(season) ρ(time)	336.87	22.81	0.00	20			
ϕ(time) ρ(season)	339.12	25.06	0.00	20			
ϕ(time) ρ(constant)	344.16	30.10	0.00	18			
ϕ(constant) ρ(season*time)	365.14	51.08	0.00	35			
ϕ(time) ρ(time)	365.63	51.57	0.00	33			
ϕ(season) ρ(season*time)	369.40	55.33	0.00	37			
ϕ(season*time) ρ(season)	371.99	57.93	0.00	36			
ϕ(season*time) ρ(constant)	377.76	63.69	0.00	34			
ϕ(time) ρ(season*time)	409.34	95.28	0.00	50			
ϕ(season*time) ρ(time)	413.55	99.48	0.00	50			
ϕ(season*time) ρ(season*time)	456.08	142.02	0.00	63			

Table 3.5b. Results of mark-recapture analysis for non-radio-tagged chicks allowing season of dissociation from parents and time to vary between models.

Model	AICc	ΔAICc	AICc weight	No. Parameters	Parameter	Estimate	SE
ϕ(constant) ρ(constant)	630.64	0.00	0.63	2	ϕ	0.92	0.01
					ρ	0.70	0.03
ϕ(constant) ρ(season)	633.02	2.38	0.19	4			
ϕ(season) ρ(constant)	633.68	3.04	0.14	4			
ϕ(season) ρ(season)	636.01	5.37	0.04	6			
ϕ(constant) ρ(time)	642.06	11.42	0.00	20			
ϕ(season) ρ(time)	645.25	14.61	0.00	22			
ϕ(time) ρ(constant)	652.87	22.23	0.00	20			
ϕ(time) ρ(season)	655.63	24.99	0.00	22			
ϕ(time) ρ(time)	670.40	39.76	0.00	37			
ϕ(constant) ρ(season*time)	696.53	65.89	0.00	55			
ϕ(season) ρ(season*time)	701.45	70.81	0.00	57			
ϕ(season*time) ρ(constant)	730.92	100.28	0.00	55			
ϕ(season*time) ρ(season)	735.60	104.96	0.00	57			
ϕ(time) ρ(season*time)	740.57	109.93	0.00	73			
ϕ(season*time) ρ(time)	762.41	131.77	0.00	73			
ϕ(season*time) ρ(season*time)	862.44	231.80	0.00	106			

Table 3.6a. Results of mark-recapture analysis for radio-tagged chicks allowing sex/season of dissociation from parents and time to vary between models.

Model	AICc	ΔAICc	AICc weight	No. Parameters	Parameter	Estimate	SE
ϕ(constant) ρ(constant)	216.13	0.00	0.75	2	ϕ	0.92	0.02
					ρ	0.84	0.03
ϕ(constant) ρ(sex/season)	218.61	2.48	0.22	6			
ϕ(sex/season) ρ(constant)	223.03	6.89	0.02	6			
ϕ(sex/season) ρ(sex/season)	224.01	7.88	0.01	9			
ϕ(constant) ρ(time)	238.35	22.22	0.00	18			
ϕ(time) ρ(constant)	239.35	23.21	0.00	18			
ϕ(time) ρ(sex/season)	243.89	27.76	0.00	22			
ϕ(sex/season) ρ(time)	247.08	30.94	0.00	22			
ϕ(time) ρ(time)	272.06	55.93	0.00	33			
ϕ(constant) ρ(sex/season*time)	337.67	121.53	0.00	53			
ϕ(sex/season*time) ρ(constant)	345.31	129.17	0.00	53			
ϕ(sex/season) ρ(sex/season*time)	355.65	139.51	0.00	57			
ϕ(sex/season*time) ρ(sex/season)	358.49	142.35	0.00	57			
ϕ(time) ρ(sex/season*time)	418.73	202.60	0.00	69			
ϕ(sex/season*time) ρ(time)	426.56	210.42	0.00	69			
ϕ(sex/season*time) ρ(sex/season*time)	797.08	580.95	0.00	102			

Table 3.6b. Results of mark-recapture analysis for non-radio-tagged chicks allowing sex/season of dissociation from parents and time to vary between models.

Model	AICc	ΔAICc	AICc weight	No. Parameters	Parameter	Estimate	SE
ϕ(constant) ρ(sex/season)	650.48	0.00	0.94	7	ϕ	0.92	0.01
					ρ (Female Fall)	0.47	0.10
					ρ (Female Winter)	0.61	0.04
					ρ (Female Spring)	0.52	0.09
					ρ (Male Fall)	0.79	0.08
					ρ (Male Winter)	0.84	0.04
					ρ (Male Spring)	1.00	0.00
ϕ(sex/season) ρ(sex/season)	656.06	5.59	0.06	12			
ϕ(time) ρ(sex/season)	669.21	18.74	0.00	25			
ϕ(constant) ρ(constant)	678.23	27.76	0.00	2			
ϕ(constant) ρ(time)	683.67	33.20	0.00	20			
ϕ(sex/season) ρ(constant)	683.77	33.29	0.00	7			
ϕ(sex/season) ρ(time)	690.13	39.65	0.00	25			
ϕ(time) ρ(constant)	695.86	45.39	0.00	20			
ϕ(time) ρ(time)	705.30	54.82	0.00	37			
ϕ(constant) ρ(sex/season*time)	803.83	153.36	0.00	95			
ϕ(sex/season) ρ(sex/season*time)	818.42	167.94	0.00	100			
ϕ(sex/season*time) ρ(sex/season)	859.17	208.70	0.00	97			
ϕ(time) ρ(sex/season*time)	861.54	211.07	0.00	112			
ϕ(sex/season*time) ρ(constant)	874.91	224.43	0.00	92			
ϕ(sex/season*time) ρ(time)	918.50	268.02	0.00	110			
ϕ(sex/season*time) ρ(sex/season*time)	1247.27	596.80	0.00	172			

Chapter 4

TRANSIENT NON-TERRITORIAL SANDHILL CRANES DISPERSE AND THEN RETURN NEAR THEIR NATAL AREA AS THEY APPROACH BREEDING AGE

ABSTRACT

Sandhill Cranes do not breed until at least three-years-old. I determined home range and linear distance from natal area for radio-tagged Sandhill Cranes that spanned the ages of one-year-old through three-years-old. Average total home range size decreased as birds aged from one-year-old (284 km^2) to two-years-old (86 km^2) and three-years-old (31 km^2). Similar results were observed with 95% home range size. All home range sizes were smaller than average 95% home range size for breeding adults (3 km^2). Overlap in home range used among years also decreased as birds aged (23% between one-year-old and two-year-old, 17% for two-year-old and three-year-old, 7% for one-year-old and three-year-old). These results suggest that older Sandhill Cranes travel less than younger Sandhill Cranes, but they are not focusing on a specific area to eventually breed. Average one-year-old females (22 km) and males (11 km) were located furthest from their natal area, then returned closer to their natal area as two-year-olds (females: 12 km, males: 4 km) and three-year-olds (females: 11 km, males: 3). These results suggest that older Sandhill Cranes may prospect for potential breeding areas as young birds, but as they age, prefer to use areas near their natal location and focus on these areas to set up a breeding territory. The average two-year-old Sandhill Crane (male and female) was observed paired, but these associations were short-term, lasting an average of only two and a half months. None of these associations persisted into adulthood. Nest mates were observed associating together as one-year-old and two-year-old birds, but these associations did not persist when they were three-years-old or older. Pairing by young birds allows them to practice behaviors that will be important as birds begin looking for a long-term mate.

INTRODUCTION

There are three main phases during the dispersal process: departure, transience, and settlement (Bowler and Benton 2005, Clobert et al. 2009); the departure and settlement phases are discussed in Chapters 3 and 5, respectively. During transience, individuals have become independent from their parents and departed from their natal site, but not yet settled on a breeding location and/or found a mate.

The length of time spent in transience is highly variable among avian species. While most passerine species attempt breeding during their first year of independence (e.g., Martin and Gavin 1995, Sheppard 1996, Summers-Smith 1988), Corvids, Piprids (i.e., Manakins) and many non-passerines do not attempt to breed until two-years-old or older, spending a minimum of one to three years as non-breeders (e.g., Cooke and Rockwell 1988, McCormack and Brown 2008, Poole 1989, Pyle 2001).

For those species that do not attempt reproduction for at least one breeding season, little is often known regarding behaviors exhibited by non-breeding individuals during transience. Different species of eagles (Falconiformes) do not reach sexual maturity until three to five-years-old (Gargett 1990, Gonzalez et al. 2006, McCollough 1989). Upon dispersing from their natal site, subadult Spanish Imperial Eagles (*Aquila adalberti*) and Golden Eagles (*Aquila chrysaetos*) travelled hundreds of km from their natal site as one-year-olds before returning near their natal area as they approached sexual maturity as three-year-olds (Gonzalez et al. 1989, Grant and McGrady 1999, Soutullo et al. 2006a, 2006b). Geese and swans (Anseriformes) do not start breeding until two-years-old or older (e.g., Conover et al. 2000, Forslund and Larsson 1992, Warren et al. 1992). Prior to breeding, geese and swan form large flocks, composed of sexually immature subadults, sexually mature but non-breeding adults, and failed breeding adults, in molting areas that are separated from main breeding areas (Sterling and Dzubin 1967, Bollinger and Derksen 1996, Nillson et al. 2001, Reed et al. 2003). Although the exact purpose of these large flocks is unclear, it has been suggested that they serve to provide a safe place to molt, to avoid food competition with breeding pairs and family groups, or to form initial pair bonds between non-breeding birds (Salomonsen 1968, Sterling and Dzubin 1967).

The Sandhill Crane (*Grus canadensis*) is a long-lived avian species that does not breed until at least two-years-old (Chapter 5, Radke and Radke 1986) with the average individual breeding at four-years-old or older (Chapter 5, Nesbitt 1992, Tacha et al. 1989). Movements of non-territorial birds following dissociation from their parents (between six-months-old and one-year-old; Chapter 3, Nesbitt et al. 2002) but before acquisition of a breeding territory have not been well documented. In non-migratory Sandhill Cranes in Florida and Georgia, home ranges of non-territorial birds that were one-year-old were significantly larger than home ranges of two-year-old and three-year-old non-territorial birds (Bennett 1989). Based on these results, I hypothesized that home range size would be largest when migratory, non-territorial birds were one-year-old and then shrink in size until the bird were three-years-old. Comparatively, home ranges of one-year-old, two-year-old, and three-years-old non-territorial birds were significantly larger than home ranges of breeding adults (Bennett 1989, Nesbitt and Williams 1990). Similarly, I hypothesized that non-territorial birds of any age would have a significantly larger home range than breeding adults in this migratory population as well.

Distances travelled between natal areas and locations used when birds were non-territorial is also unknown. Re-sightings of non-territorial Sandhill Cranes color-banded in

Alaska (Boise 1979) and Michigan (Hoffman 1985) suggest natal philopatry occurs for most birds, however, long-distance dispersal is possible as evidenced by one-year-old birds from each study being observed in Wisconsin. Male Sandhill Cranes obtained a breeding territory closer to their natal area than did females (Nesbitt et al. 2002, Chapter 5). Site fidelity to a breeding territory was high for migratory breeding male and female Sandhill Cranes as well. The furthest distance travelled among breeding territories by either sex was two km (Chapter 2). If natal philopatry allows males to benefit by gaining knowledge about local resources to acquire a territory and attract a female (Greenwood 1980, Nesbitt et al. 2002), I expected non-territorial male Sandhill Cranes to remain closer to their natal area until they obtained a breeding territory when compared to non-territorial females. For males to maximize their knowledge about local resource availability, I hypothesized males would not differ in the distance travelled from their natal area as they aged. For females to minimize the chance of inbreeding with a closely related male (Johnson and Gaines 1990), I hypothesized females would move an as yet undefined threshold distance away from their natal area as a one-year-old bird and remain this distance or further from their natal area as they aged.

Similar to moulting geese and swans, non-territorial Sandhill Cranes form flocks (Meine and Archibald 1996) composed of other sexually immature birds, sexually-mature non-territorial birds that may or may not be paired, and former territory holders that lost breeding status (Hayes and Barzen 2006). While these flocks likely serve multiple purposes, associations among non-territorial birds are often established in these flocks (Nesbitt and Wenner 1987). While Nesbitt and Wenner (1987) found that non-territorial Sandhill Cranes in Florida averaged 1.2 associations per year, the length of time that an association persisted among non-territorial birds and whether those associations transformed into long-term pair bonds were not reported. Perhaps as important, non-territorial birds may well form associations with territorial birds, allowing non-territorial birds to quickly fill vacancies on breeding territories when they occur (Chapter 2).

I investigated the transience phase of non-territorial Sandhill Cranes in south-central Wisconsin. Specifically, I wanted to measure the distances that non-territorial Sandhill Cranes dispersed from natal locations during their years in transience. I also wanted to quantify home ranges covered by non-territorial cranes of different ages and whether there was overlap in an individual's annual home ranges among years. If cranes were focusing on an area to later set up a breeding territory, I expected older, non-territorial cranes to have smaller home ranges than younger, non-territorial cranes. Finally, I wanted to determine the age at which associations occurred among non-territorial cranes, the length of time these associations persisted, and whether any of these associations transitioned into long-term pair bonds. Collectively, these data are useful in understanding flock dynamics in populations as they expand their range, as is currently being experienced in the Eastern Population of Sandhill Cranes (Ad Hoc Eastern Population Sandhill Crane Committee 2010, Chapter 6).

METHODS

Study Area

Sandhill Crane were color-banded near Briggsville, Wisconsin (N Lat. 43^{o} 36', W Long. 89^{o} 36'). This has been the site of a long-term study on Sandhill Crane breeding ecology and habitat selection by the International Crane Foundation since 1991. This area is primarily an agriculture-dominated landscape (primarily small family farms) intermixed with small woodlots or forest patches, grasslands, flow-through wetlands, and dispersed human residences (see Su 2003). During the summer, this area has a high density of territorial pairs (Su et al. 2004) and flocks of non-territorial birds.

Capture, Banding, and Radio Deployment

Sandhill Cranes were captured annually during two different seasons. In the summer, flightless chicks (age 35 to 70 days) were pursued by chasing them on foot until they hid (Hoffman 1985). In late summer and fall, after chick fledging, territorial adults with any fledged hatch-year chicks (older than 70 days) were captured using toe snares (Hereford et al. 2001) or alpha-chloralose (Bishop 1991), an oral tranquilizer (Fisher Scientific Company, Fairlawn, New Jersey, USA and Biosynth Ag, Switzerland) using a process described in Hayes et al. (2003).

Once captured, each crane received a unique combination of colored plastic leg bands to allow identification using binoculars and spotting scope. First, a 7.5 cm (3-inch) tall plastic band engraved with a unique three-digit number was placed above the joint between the tibiotarsus and tarsometatarsus of one leg. Additionally, either two or three 2.5 cm (1-inch) tall colored plastic leg bands, in a unique color combination for each bird, were added above the same joint on the opposite leg. U. S. Geological Survey aluminum bands (with an engraved unique nine-digit number) were either placed above the toes of either leg or within the combination of one-inch colored bands. For more detail on Sandhill Crane banding schemes, visit www.bandedcranes.org. Colored plastic leg bands had high retention which allowed long-term identification of individuals throughout the study period (Dickerson and Hayes 2014).

Age (adult or hatch-year chick) was determined through presence/absence of red skin on the crane’s head (Lewis 1979). Blood samples were collected from most birds captured between 1996 and 2012. Sex of birds with blood samples collected was determined through genetic analysis (Griffiths et al. 1998, Duan and Fuerst 2001). Birds without blood samples collected were sexed by behavior (posture during unison call; Archibald 1976) or relative size (males are typically larger than females [Nesbitt et al. 1992] especially within a breeding pair [ICF unpublished data]).

Two different mounting styles of radio transmitters were deployed on hatch-year chicks from targeted territories within the study area. From 1996-2001, 40-gram leg-band mounted transmitters (Advanced Telemetry Systems, Isanti, MN, USA; hereafter leg-band) were constructed so that the back of the radio was concave to fit the rounded edge of the one-inch colored leg bands (Melvin et al. 1983, Dickerson and Hayes 2014). The back of the radio was swabbed with PVC primer and glue and attached to two of the one-inch colored leg bands, then wrapped with stretch gauze until the glue dried, after which the gauze was removed before the crane was released. Based on manufacturer specifications, leg-band radios were expected to be active for a minimum of 270 days from initiation of signal transmission. While limited in battery life, these radios were versatile and deployable on chicks of age five weeks to volant adults because the transmitter weighed less than 2% of the total body weight (Table 4.1) as recommended for birds (Kenward et al. 2001, Bird Banding Lab 2012, but see Irvine et al. 2007).

From 2006-2008, 80-gram backpack transmitters (Communications Specialists, Orange, CA, USA; hereafter backpack) were deployed on fledged chicks. A Teflon ribbon figure-eight harness was wound through holes in the backpack and the straps were crossed near the furcula region of the bird’s thoracic cage to reduce slippage of the transmitter over the bird’s wings and body (Nagendran et al. 1994). The ends of the harness were sutured together with dental floss near the bird's shoulder. A short sleeve of Teflon ribbon was then slid over the suture point and the sleeve was sutured in place using dental floss. Before suturing with dental floss, we checked the fit of the harness by inserting two or three fingers (3-5 cm) between the backbone of the crane and the transmitter (Nagendran et al. 1994). This distance allowed fat deposition prior to fall migration and room for continued growth as the chick matured into adulthood with reduced concern about the harness being so loose that the bird could not fly (Burke et al. 1999). Based on manufacturer specifications, these radios were expected to be active for a minimum of 1100 days from the initiation of signal transmission. While the increased weight allowed longer battery life, this transmitter type could only be deployed on fledged hatch year chicks due to weight recommendations and body development restrictions (i.e., crane chicks do not attain near adult size until after fledging; Ricklefs et al. 1986, ICF unpublished data).

Each radio (leg-band and backpack) was tested for functionality with a radio frequency receiver prior to deployment. Following release from capture, radio-tagged birds were monitored daily until the bird was re-sighted through binoculars or spotting scope to ensure that it was behaving normally and neither the transmitter nor colored leg bands was causing morbidity. Following the first post-capture re-sighting, birds were monitored intermittently until fall migration and annually across subsequent years.

Radio Telemetry Protocol and Subsequent Re-sightings

Sandhill Cranes were monitored via radio telemetry from April through October annually. Triangulation (Mech 1983) was utilized to determine a bird's location when it was not in view, although every attempt was made to re-sight bands on focal birds. Azimuths and bird locations were collected via hand-held or truck-mounted antenna and portable receiver and then plotted on 1:24,000 U.S. Geological Survey topographical maps. Locations were collected in either Wisconsin Transverse Mercator (WTM 83/91; Wisconsin DNR) or Latitude/Longitude; the latter were converted to WTM 83/91 for home range construction and distance calculations (see below). To attain as accurate a location as possible, circles with an internal diameter $\leq$ 1 cm within the triangulated location (providing an estimated error of $\leq$ 240 m) were accepted. When a focal bird was in view, behavior information, flock size, presence of other banded cranes, and habitats used were recorded.

Locations were collected on focal birds every 1-2 hours on each sampling day starting before sunrise (AM roost) to after sunset (PM roost). Sampling days were randomly assigned to a full day of tracking once per one-week (leg-band) or two-week (backpack) intervals. Sampling intervals were designed to reduce possible autocorrelation among samples (Swihart and Slade 1985). When the signal from an individual's frequency was not located either on the target day of tracking or through scanning different frequencies while monitoring another target individual, telemetry via fixed-wing aircraft was conducted with the volunteer assistance of the Windway Capital Corporation (Sheboygan, WI). Efforts were made to maintain consistency in locating cranes prior to the day of assigned tracking. Once any transmitter was known to be non-functional (through visual observation of a focal bird without receiving a signal from the transmitter), birds were continually monitored through visual observation of colored leg bands. Additionally, attempts were made to regularly observe all color-banded Sandhill Cranes from March to November annually.

Behavioral Observations

Regular observations of Sandhill Crane flocks occurred from March through November each year while birds were on the breeding grounds (Su 2003). Two non-territorial Sandhill Cranes (at least one of which was color-banded) were considered paired when they were observed mutually associating, dancing, or unison calling (Archibald 1976) together. These behaviors were used to define the length of time that two banded, non-territorial cranes were observed pair-bonded. Mutual association was also used to define the length of time that nest mates were observed together in the same flock.

Statistical Analyses

I tested all data sets for normality using a Shapiro-Wilk test prior to statistical analysis (Shapiro and Wilk 1965). Significance was set at $p<0.05$. A deviation from normality was verified for all data using a Q-Q plot in R. Non-parametric tests were used to compare all data sets that were not normally distributed.

I used triangulation and re-sightings of radio-tagged cranes (while transmitters were still active) to investigate changes in and repeated use of individual home range through time. All radio telemetry points were visually scrutinized before analysis to verify correct identification of the bird and transcription of information into the database. Any points missing identification or location information were not used in analyses. Home ranges for each bird were constructed in ArcMap 10.1 (ESRI, Redlands, CA) using Minimum Convex Polygons (MCP; Jennrich and Turner 1969) encompassing all points in a specific year (e.g. one-year-old, etc.). I chose MCP because they use all points recorded for an individual bird and this is the definition of a home range (Burt 1943). Because MCP is susceptible to changes in area based on sample size (Burgman and Fox 2003), a 95% MCP was also created for each bird by finding the mean center location for one individual bird's cloud of points in a given year and measuring the distance (m) from each collected point for that bird to that mean center location. The mean (AVG) and standard deviation (SD) from all distances for each bird were calculated and any points outside the range of AVG±2*SD were removed. I then re-constructed 95% MCP using the remaining points for each individual.

Area (km^2) was calculated for each individual's home range at the 100% and 95% levels in ArcMap. Additionally, the portion of the home range that overlapped among years was calculated using the Intersection tool in ArcMap. A Kruskal-Wallis test was used to determine if home range size varied significantly with age or sex of the bird or the type of radio deployed and significant differences among group means were tested using a Mann-Whitney U test with Bonferonni correction. Inter-annual changes in home range size were assessed using a Wilcoxon Sign Rank test (Sokal and Rohlf 2001).

I measured the linear distance between a bird's natal territory and all telemetry and re-sighting locations for radio-tagged, non-breeding birds. A Kruskal-Wallis test (Sokal and Rohlf 2001) was used to determine if average annual dispersal distance was affected by the sex or age of the bird and the month and year the bird was tracked. *A posteriori* difference in means was calculated using a Mann-Whitney U test (Sokal and Rohlff 2001) with Bonferroni correction to test for significant differences among groups.

RESULTS

Radio transmitters were deployed on 41 hatch year Sandhill Cranes captured 1996-2008 (Appendix A). Of those 41 chicks, 33 (80.5%) were actively tracked beyond their hatch year. Of those eight not tracked, one radio fell off and was not recovered, two radios died prematurely before the bird initiated its first fall migration, three birds died between their hatch year and first year, and two birds remained unknown. Both unknown fated chicks (one male, one female) were observed alive through their first fall migration, but they were not seen nor their radio frequencies heard during the following spring. This led to an unknown error rate of 4.9% (n = 41 radios) where a lack of relocation could be due to either bird death, premature radio death, or dispersal beyond the range of detection.

Of 17 birds with leg-band transmitters, 15 (88%) were tracked and re-sighted as one-year-old birds and two (12%) as two-year-olds. For birds with backpacks, 17 (74%) of 23 birds were tracked as one-year-olds, 14 (61%) as two-year-olds, and nine (39%) as three-year-olds. Leg band transmitters were tracked for an average of 499±35 days while backpack transmitters were tracked for an average of 840±63 days. Eighteen radios (five leg-band and 13 backpacks) failed, but had an unknown end date because transmitters were active in the fall of one year before migration but not active the following spring. All 18 color-banded birds were re-sighted alive confirming radio failure. For radio transmitters with a known failure date, leg-bands (n = 9) were active for an average of 490±38 days (range = 308-655 days) while backpacks (n = 7) were active for an average of 939±64 days (range = 641-1198 days). Monitoring intervals differed among radio types. Cranes with leg-band transmitters were monitored an average of once every 14±1.1 days (range 1-116 days) while cranes with backpack mounted transmitters were monitored an average of once every 29±1.7 days (range = 2-175 days).

Changes in home range size and use over time

There was no difference (Mann-Whitney U = 120, p = 0.76) between average home ranges of one-year-old Sandhill Cranes with leg-band transmitters (331.4±175.4 km^2) and those with backpack transmitters (243.3±60.1 km^2). Similar results were observed with 95% home ranges (leg-band: 258.1±177.4 km^2, backpack: 144.1±48.7 km^2; Mann-Whitney U = 104, p-value = 0.76). Analyses could not be conducted for two and three-year-old birds as there were only two leg-band transmitters that were tracked for more than one year. Radio types were combined for further home range analyses.

When I tested the effect of sex, age, and sex*age on total home range, the only factor significantly contributing to home range size was age (Kruskal-Wallis = 5.4, df = 3, 48, $p = 0.003$; age slope = -0.57, $p < 0.001$). Average one-year-old birds (284.4 km^2) had significantly larger home ranges than average two-year-old birds (86.3 km^2) and home range of both age groups were significantly larger than average three-year-old birds (31.3 km^2; Figure 4.1). Similar results were found with 95% home ranges and age (Kruskal-Wallis = 3.5, df = 3, 48, $p = 0.02$; age slope = -0.49, $p = 0.004$) with trends similar to total home range (197.3 vs. 54.0 vs. 28.3; Figure 4.1). All non-territorial age groups had larger total home ranges (one-year-old: Mann-Whitney U = 360, $p < 0.001$; two-year-old: Mann-Whitney U = 180, $p < 0.001$; three-year-old: Mann-Whitney U = 82, $p < 0.001$) and 95% home ranges (one-year-old: Mann-Whitney U = 359, $p < 0.001$; two-year-old: Mann-Whitney U = 177, $p < 0.001$; three-year-old: Mann-Whitney U = 76, $p = 0.002$) than the average 95% home range of 2.85±0.6 km^2 (range = 0.25 – 7.94 km^2) of breeding adult Sandhill Cranes reported by Miller (2003; Figure 4.1).

Between year change in total home range was greatest for one-year-olds compared to other age groups (Figure 4.2; One-year-olds vs. Two-year-olds Mann-Whitney U = 315, $p = 0.03$, Two-year-olds vs. Three-year-olds Mann-Whitney U = 81, $p = 0.05$, One-year-olds vs. Three-year-olds Mann-Whitney U = 187, $p < 0.001$). This effect was more subtle for comparisons of

95% home range sizes (Figure 4.3; One-year-olds vs. Two-year-olds Mann-Whitney $U = 304$, $p = 0.06$, Two-year-olds vs. Three-year-olds Mann-Whitney $U = 71$, $p = 0.21$, One-year-olds vs. Three-year-olds Mann-Whitney $U = 175$, $p = 0.005$).

Individual cranes home range areas overlapped among consecutive years. All birds averaged higher overlap in total home range use between years one and two compared to years two and three or years one and three (Figure 4.4). Males and females did not differ in total home range use among any year comparison (Years one and two: Mann-Whitney $U = 30$, $p = 0.78$; years two and three: Mann-Whitney $U = 7$, $p = 0.57$; years one and three: Mann-Whitney $U = 4$, $p = 0.86$). Trends observed in 95% home range overlap between years were similar to total home range use (Figure 4.5). Also similar to total home range use, there was no difference between males and females in 95% home range overlap (years one and two: Mann-Whitney $U = 22$, $p = 0.61$; years two and three: Mann-Whitney $U = 8$, $p = 0.38$; years one and three: Mann-Whitney $U = 6$, $p = 0.86$).

Linear distance from natal area

Linear distance from natal area was significantly affected by sex, radio type, age, and sex*age (Kruskal-Wallis = 354.3, df = 4, 4978, $p < 0.001$). The slopes of all variables were highly significant (sex: -603.4, $p < 0.001$, radio: -358.0, $p < 0.001$, age: -0.13, $p < 0.001$, sex*age: -0.26, $p < 0.001$). One-year-old females (both radio types) were found the furthest distance from their natal area while three-year-old males with backpacks were found the closest (Figure 4.6). Most post-hoc Mann-Whitney U tests against all pairwise comparisons were significant after Bonferroni correction (Table 4.2). Radio type was a significant variable in the model as one-year-old males with backpacks were found nearly twice the distance from their natal area as one-year-old males with leg-band radios. However, I suspected that the significance of radio type was influenced by the lack of two-year-olds with leg-band radios. When I removed radio type as a variable and re-ran the model, I still found significant differences among all sex and age groups (Kruskal-Wallis = 334.6, df = 4, 4978, $p < 0.001$). Males were found closer to home than females and older birds (both males and females) moved closer to home as they aged (Figure 4.6). Again, post-hoc comparisons were significant after Bonferroni correction (Table 4.3).

Radio-tagged three-year-old male Sandhill Cranes were located an average linear distance of 2.5±0.3 km from their natal area. There was a statistical trend that the average linear distance for three-year-old males was longer than the average linear distance of 2.3±0.4 km between natal territory and breeding territory for males (Mann-Whitney U = 1662, $p = 0.07$; Figure 4.6). On average, males acquired a territory when 4.9 years (range 2-10 years; Chapter 5). So, by three-years-old, average males were located as close to their probable future breeding territories as they would get without obtaining a breeding territory. Radio-tagged three-year-old female Sandhill Cranes were located an average distance of 11.4±0.5 km from their natal area. This average distance for three-year-old females was significantly longer than the average distance of 10.7±4.0 km between natal territory and breeding territory for females (Mann-Whitney U = 3428, $p = 0.02$; Figure 4.6) that acquired a breeding territory at an average of 4.3 years (range 3-9 years; Chapter 5).

Associations among non-territorial Sandhill Cranes

The average age when non-territorial Sandhill Cranes were first observed pairing behavior was 24.5±1.5 months (range = 11 – 48 months). Females (average = 24.2±2.6 months, range = 11 - 48 months, n = 23) and males (24.6±1.3 months, range = 11 - 48 months, n = 33) were observed showing pairing behaviors at similar ages (Mann-Whitney U = 355.5, p = 0.69). Approximately 75% of both males and females showed pairing behavior as one-year-olds or two-year-olds (Figure 4.7). Eight birds (four males and four females) were not observed paired before they were observed defending a breeding territory at the ages of two to four-years-old. When pair bonds formed among two banded birds (n = 6 pairs), these bonds were ephemeral and lasted an average of 2.3±0.7 months (range = 1 - 5 months). None of these ephemeral bonds persisted to breeding status.

Prolonged post-independence associations among Sandhill Crane nest mates occurred as one-year-old and two-year-old birds, but associations in flock were more sporadic at older ages. Of 16 broods where two females fledged, only two (12.5%) were observed together in the same flock as independent birds. One pair of female nest mates was observed in the same flock on one day while the other pair were observed together as one-year-olds and two-year-olds on the wintering grounds. The length of time this pair of nest mates associated on wintering areas was unknown.

Of 23 broods where one male and one female fledged, nine broods (39%) were observed together as one-year-olds and five broods were observed together as two-year-olds. As one-year-olds, these male-female nest mates were observed an average of 5.2±1.8 times (range = 5-17 times) over an average span of 45.3±10.4 days (range = 17-66 days). As two-year-olds, only one brood of male-female nest mates was observed together on more than one day. These nest mates were observed 27 times over a span of 67 days and were observed unison-calling and defending a feeding territory together during this time. These nest mates separated at the end of their second year and the female was observed on a breeding territory as a three-year-old while the male dispersed from the study area and was not re-sighted until he was ten-years-old.

Of five broods containing two males, three (60%) were observed together both as one-year-olds and two-year-olds. Two of the one-year-old nest mates were each observed three times over an average consecutive span of 55±22 days. As two-year-old birds, however, these two sets of male brood mates were only observed in the same flock on one day. The third male-male brood mates were observed five times as one-year-old birds, but on sporadic days from March through November. As two-year-old birds, however, this third set of brood mates was observed 15 times over a consecutive period of 86 days.

DISCUSSION

Home range size of one-year-old birds were larger than those of two and three-year-old birds and all non-territorial birds had larger home ranges than breeding adults. These results supported my first two hypotheses. While home ranges of non-territorial Sandhill Cranes recorded in this study were larger than those reported for other populations (Bennett 1989, Nesbitt and Williams 1990), the trends were similar to those reported by Bennett (1989) and Nesbitt and Williams (1990). Total home range shrinkage across years was greater for males than it was for females while 95% home range shrinkage across years was greater for females than it was for males. Narrowing of a bird's home range (regardless of sex) over time could suggest that birds are gradually selecting the area where they plan to defend a breeding territory. Of interest, once birds reached three-years-old, they were located close to eventual breeding locations, even though they did not obtain a breeding territory, on average, for almost two additional years. From our understanding of mate switches (Chapter 2), this delay may be due to the limited availability of breeding territories in our dense breeding population and the fact that most birds gained access to a territory as an individual, not as a pair.

Sandhill Cranes used similar parts of their home range across multiple years. Average percent home range area shared was highest when birds were one-year-old and two-years-old for both total and 95% home ranges and then shared use was reduced between two-year-olds and three-year-olds. All age groups averaged less than 25% shared use among years. So, even though a bird's home range reduced as the bird aged, use of overlapping home range area among years reduced over time as well. Home range reduction, therefore, does not necessarily suggest a gradual selection of a preferred area (e.g., concentric rings on a target). Rather, these results suggest that most three-year-old birds are still searching for a preferred area to attempt breeding, but likely using resources from familiar areas used in past years (e.g., interlinking rings). These results are supported by the fact that of 40 birds that obtained breeding territories, only one male (2.5%) obtained a breeding territory at age two while nine birds (22.5%; four females and five males) obtained a breeding territory at age three (Chapter 5). Thus, 75% of the population obtained breeding territories after three-years-old. This is surprising given that, on average, birds began showing pairing behavior at two-years-old. Pairing by younger birds may be important for learning behaviors that will allow them to evaluate a prospective mate once they reach sexual maturity.

Similar to Spanish Imperial Eagles and Golden Eagles (Gonzalez et al. 1989, Grant and McGrady 1999, Soutullo et al. 2006a, 2006b), non-territorial Sandhill Cranes dispersed furthest from their natal area as one-year-old birds and then returned near their natal area as two and three-year-olds. While female Sandhill Cranes dispersed further distances from their natal area than males (for all age groups), both sexes returned to areas near their natal area as they aged. Neither sex, however, had moved as close to their natal area as the average breeding male or female. Distances moved by males did not support my hypothesis that non-territorial males of any age would maintain a set distance from their natal area to maximize knowledge about local resource availability. Similarly, females moved the furthest distance from their natal area as one-year-olds and returned closer to their natal area as two-year-olds and three-year-olds. This return near their natal area could possibly increase interactions among nest mates and/or full siblings from different years which would increase the chance of inbreeding. These results do not support my hypothesis that females would move a set distance away from their natal area to reduce the probability of inbreeding with a relative (Chapter 5). On average, however, both males and females remained very close (<11 km) to their natal range.

The results of the analyses of home range and linear distance from natal area suggest that non-territorial Sandhill Cranes of either sex would prefer to settle near their natal area when possible. While some birds (banded and radio-tagged) were observed long distances (>50 km) from their natal area, the average radio-tagged bird was re-located less than 25 km from their natal area and this distance shrank as the bird aged. Long-distance movements by one-year-old birds and then a return near the natal area by three-year-old individuals suggest that non-territorial birds may be evaluating different areas to determine their suitability as a breeding location but use their natal area as an alternative if they do not find better opportunities elsewhere.

Evaluation of a breeding site is also known as prospecting behavior, or informed dispersal, when an individual gathers information about a potential breeding site prior to occupying that site (Boulinier and Danchin 1997, Doligez et al. 2004, Valone and Templeton 2002). Boulinier and Danchin (1997) applied costs and benefits of prospecting and developed a threshold model that predicted when to expect prospecting behavior. This model incorporated habitat patch quality (e.g., proportion of “good” patches, stability of patch quality over time) as well as public information (e.g., reproductive success and survival rate of individuals currently breeding at the site) to predict a prospector’s lifetime reproductive success should they settle in an area. Boulinier and Danchin (1997) concluded that benefits of prospecting before first attempted breeding would outweigh costs of possible missed breeding opportunities while searching in species that are: (1) long-lived, (2) inhabit areas where there are few “good” patches, but (3) the quality of these patches is predictable among years. These criteria make sense because adults of long-lived species typically show high inter-annual site fidelity. Evaluating multiple sites to choose an area where you will potentially spend the remainder of your life should be beneficial. Having few patches of good quality would make those patches defensible and high predictability of patch quality would allow an individual to expect those resources to be available across years.

Sandhill Cranes are long-lived (20-30 years in the wild; Walkinshaw 1973). Sandhill Cranes nest in wetland patches surrounded by uplands (e.g., grasslands, agricultural fields) where they lead offspring to forage shortly after hatching (Baker et al. 1995, Lacy and Liying 2008). While Sandhill Cranes inhabiting agricultural areas face annual rotation of crop types, food availability in a territory is typically stable among years (Su 2003). Finally, Sandhill Cranes are highly territorial with high inter-annual site fidelity and form long-term pair bonds (Chapter 2). All of these characteristics suggest that prospecting should occur before a Sandhill Crane chooses a territory. Additionally, because of delayed sexual maturity, Sandhill Cranes have time to sample possible breeding areas and investigate the potential for successful reproduction in those areas to make an informed decision about choosing the best available location. An individual needs to balance the cost of investigating areas for too long, especially after reaching sexual maturity, because an individual risks experiencing mortality before it obtains the opportunity to breed.

In Sandhill Cranes, territory availability depends on the density and survival of breeding adults (Chapter 2). Breeding adult density in our study area is high (Chapter 2) and this high density reduces the probability that a non-territorial bird or pair can establish a breeding territory. When all available space is occupied by breeding birds, a non-territorial bird will need to either wait for an opening (through breeding adult death or breeding pair divorce) to occur or to force their way into an established breeding pair to gain access to a breeding territory. In our study area, experienced breeding birds were preferred as new mates compared to non-territorial birds (Chapter 2). Breeding birds from territories adjacent to a territory with an opening typically filled the gap (Chapter 2). These results suggest that prospecting occurs in non-territorial birds prior to territory acquisition and in breeding adults while on territory by observing their neighbors and evaluating whether to move or remain on their current territory when an opening occurs.

I was unable to accurately evaluate prospecting behavior in this population of Sandhill Cranes because radio transmitters lasted a maximum of three years. Although the highest proportion of non-territorial male and female Sandhill Cranes began showing pairing behaviors at two-years-old, the average age when a male or female obtained a breeding territory was 4.8 years (Chapter 5). These initial pairings were short-lived as the average pair bond among two banded, non-territorial cranes lasted two and a half months and the longest duration was five months. More information about movements made by non-territorial four-year-old and five-year-old Sandhill Cranes would fill in gaps to better evaluate territory site selection. To effectively evaluate prospecting behavior by non-territorial Sandhill Cranes, a study would need to determine steps taken by non-territorial cranes to achieve territorial status. This would include conducting more intense radio telemetry and observation of non-territorial birds that are four to six-years-old. Preferentially, these birds would also have been tracked between the ages of one and three. Being able to monitor these birds at a regular interval would allow comparisons and changes in home range area and linear distance from natal area as the birds aged. An intense observation interval would also allow scrutiny of associations that occurred among non-territorial cranes and the length of time that associations occurred among birds of different ages. By intensely observing these birds during this time frame, a better understanding of the transition from non-territorial to territorial crane could develop.

Secondly, recording habitat types used during transience could be important because young individuals may be evaluating an area’s potential as a breeding location (Doligez et al. 2004, Valone and Templeton 2002). Habitat quality can be imprinted at a young age (Davis and Stamps 2004, Glück 1984, Wecker 1963). While one-year-old Sandhill Cranes chose the same proportion of habitat types as they were exposed to as hatch year chicks (ICF unpublished data), more information is needed regarding how habitat selection by non-territorial birds changes as they age and begin searching for a territory. Incorporating breeding adult density into a habitat selection model would allow us to not only understand how their habitat needs change as they age, but also determine the probability that a non-territorial bird could actually settle in a preferred location.

Prolonged associations among nest mates occurred into the first and second year of independence when at least one male was part of the clutch. Why this behavior occurs in Sandhill Cranes is unknown but may be related to the high degree of natal philopatry observed in both males and females. Proportionally, the highest amount of association occurred when the brood mates were both males. However, nearly 40% of male-female broods were associated beyond their hatch year. This behavior could potentially increase inbreeding as evidenced between one set of male-female nest mates showed pairing behavior when they were two-years-old. For clutches that contain two males, it is possible remaining together could give them a feeding advantage in flock by working together to defend a resource, but more observation of nest mates in flock is needed to support or refute this hypothesis.

It is important to research the transience phase of a focal species because it can affect appropriate modelling of population growth over time. For example, recruitment of juveniles into breeding populations is often measured by counting the number of offspring (retained juvenal plumage) fledged per number of adults (definitive alternate or basic plumage) counted in the same flock (Cowardin and Blohm 1992, Drewein et al. 1995). One assumption of this methodology is that all definitive-plumaged adults were capable of breeding. Birds that are in definitive plumage, yet sexually immature or non-territorial, would suggest recruitment estimates were lower than the accurate value. By estimating the number of breeding adults relative to the number of birds in definitive plumage, yet non-breeding, would more accurately estimate recruitment rates.

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Table 4.1. Average (+SE) weights (g) of Sandhill Crane chicks of varying ages (weeks) banded near Briggsville, WI.

			Weight (g)	
Age (weeks)	n	Sex	Avg.	SE
5	13	Female	2251	35
	7	Male	2329	127
6	25	Female	2366	62
	26	Male	2437	78
7	27	Female	2547	56
	22	Male	2856	89
8	12	Female	2554	125
	8	Male	2848	141
9-10	9	Female	2664	76
	9	Male	2947	98
Post-fledge	46	Female	4126	54
	32	Male	4620	89

Table 4.2. P-values of group by group Mann-Whitney U tests determining effect of age, sex, and radio types on linear distance from natal area.

	OYO[a] F Back	OYO F Leg	OYO M Back	OYO M Leg	TwYO[a] F Back	TwYO F Leg	TwYO M Back	TwYO M Leg	ThYO[a] F Back	ThYO M Back
OYO F Back	-									
OYO F Leg	0.99	-								
OYO M Back	**<0.001**	**<0.001**	-							
OYO M Leg	**<0.001**	**<0.001**	**<0.001**	-						
TwYO F Back	0.02	0.09	**<0.001**	**<0.001**	-					
TwYO F Leg	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	-				
TwYO M Back	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.04	-			
TwYO M Leg	**<0.001**	**<0.001**	**<0.001**	0.11	**<0.001**	0.09	**<0.001**	-		
ThYO F Back	0.23	**0.005**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.34	**<0.001**	-	
ThYO M Back	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	-

Bold values = significant comparisons after Bonferroni correction.

[a] OYO = one-year old, TwYO = two-years old, ThYO = three-years old

Table 4.3. P-values of group by group Mann-Whitney U tests determining effect of age and sex on linear distance from natal area.

	OYO[a] Female	OYO Male	TwYO[a] Female	TwYO Male	ThYO[a] F Back	ThYO M Back
OYO Female	-					
OYO Male	**<0.001**	-				
TwYO Female	**<0.001**	**<0.001**	-			
TwYO Male	**<0.001**	**<0.001**	**<0.001**	-		
ThYO Female	**<0.001**	**<0.001**	**<0.001**	**<0.001**	-	
ThYO Male	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	-

Bold values = significant comparisons after Bonferroni correction.

[a] OYO = one-year old, TwYO = two-years old, ThYO = three-years old

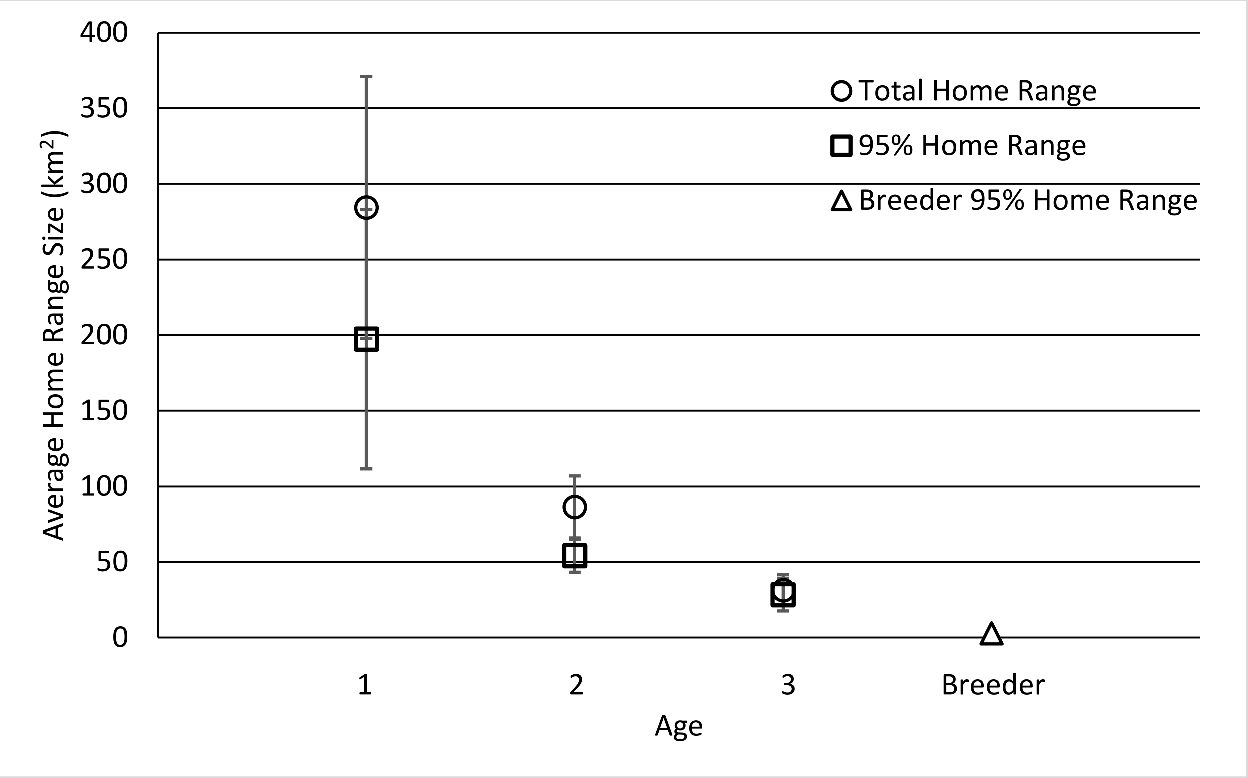

Figure 4.1. Average home range size (total MCP and 95% MCP in km2) of one-year-old, two-year-old, and three-year-old radio-tagged Sandhill Cranes. Average 95% kernel density estimate home range size of radio-tagged breeding adult Sandhill Cranes from Miller (2003).

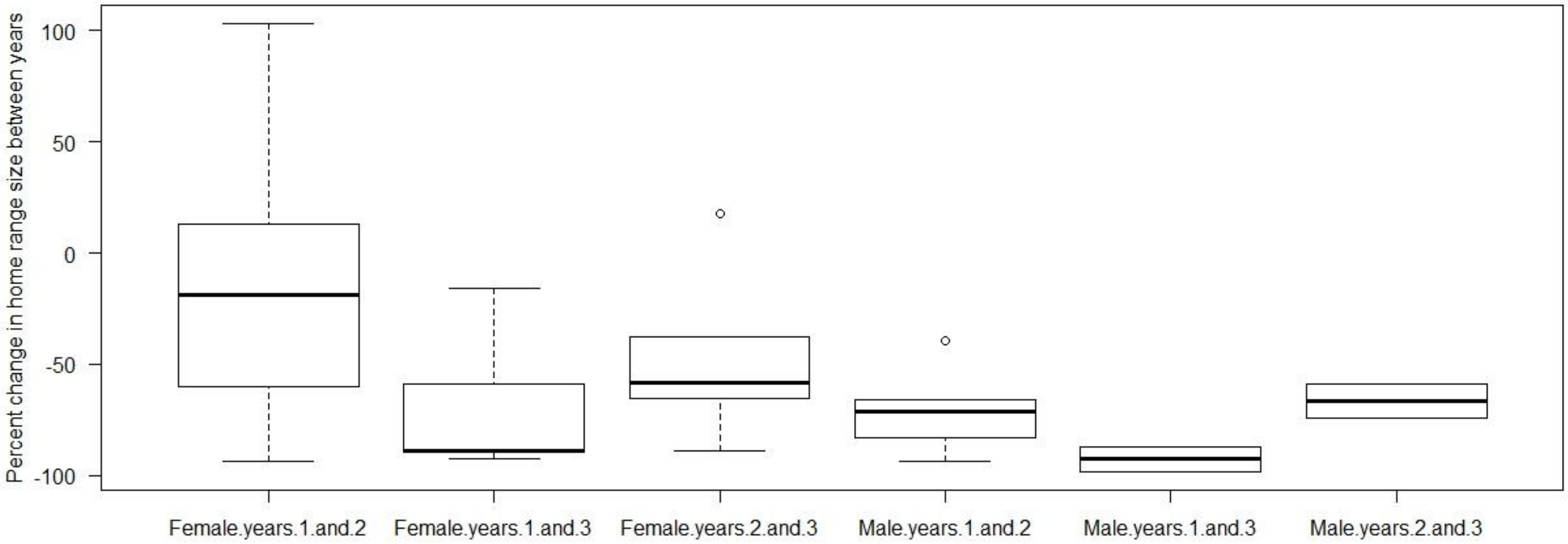

Figure 4.2. Average % change in total home range size (±SE) among age groups of non-territorial Sandhill Crane females, males, and males and females combined.

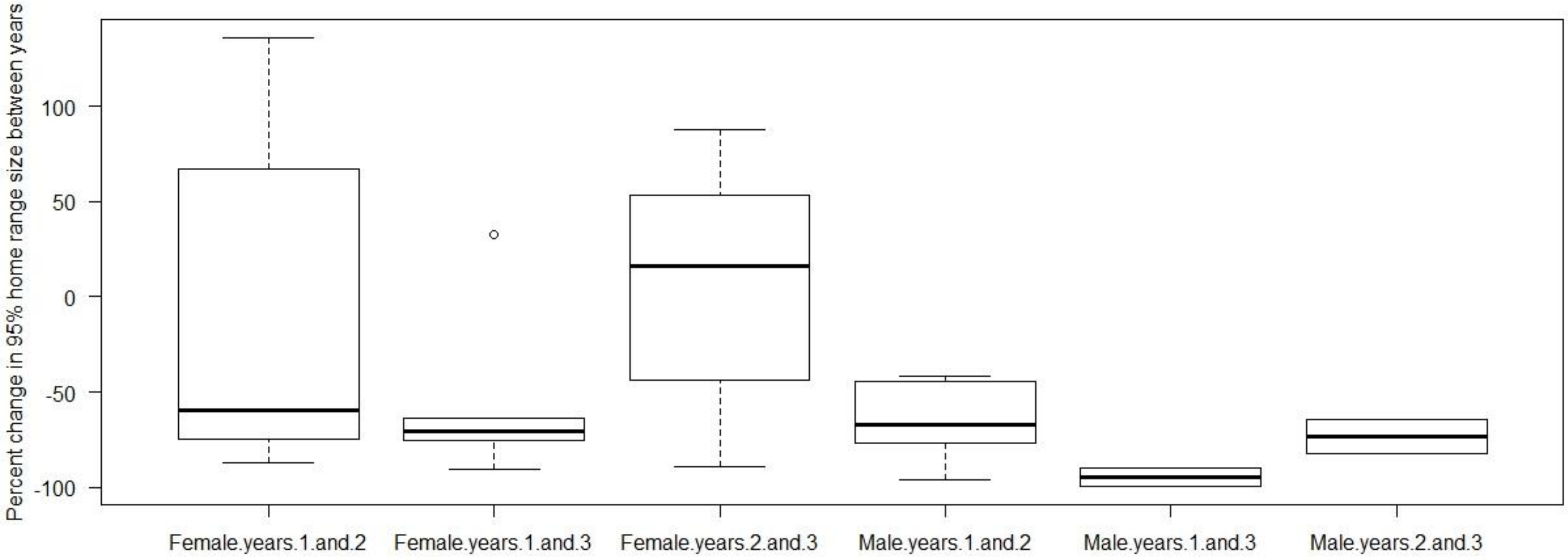

Figure 4.3. Average % change in 95% home range size (±SE) among age groups of non-territorial Sandhill Crane females, males, and males and females combined.

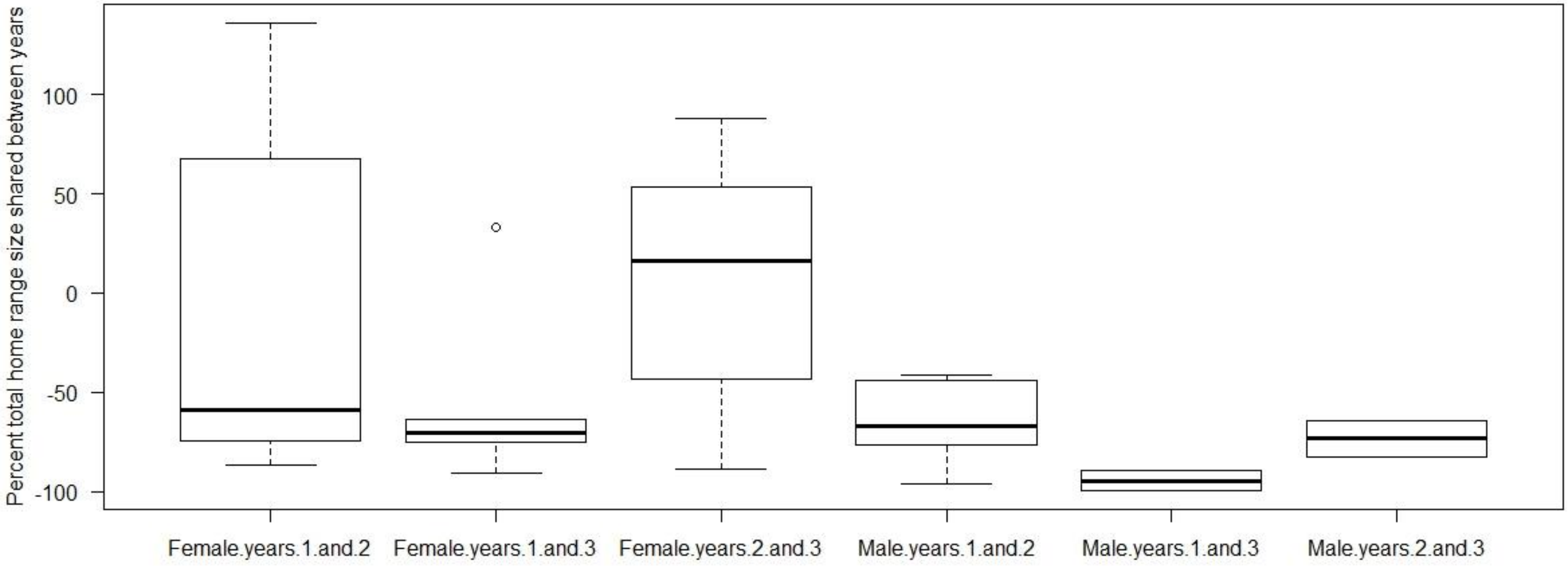

Figure 4.4. Average % total home range area (±SE) that was used among years for radio-tagged Sandhill Crane males, females, and combined males and females.

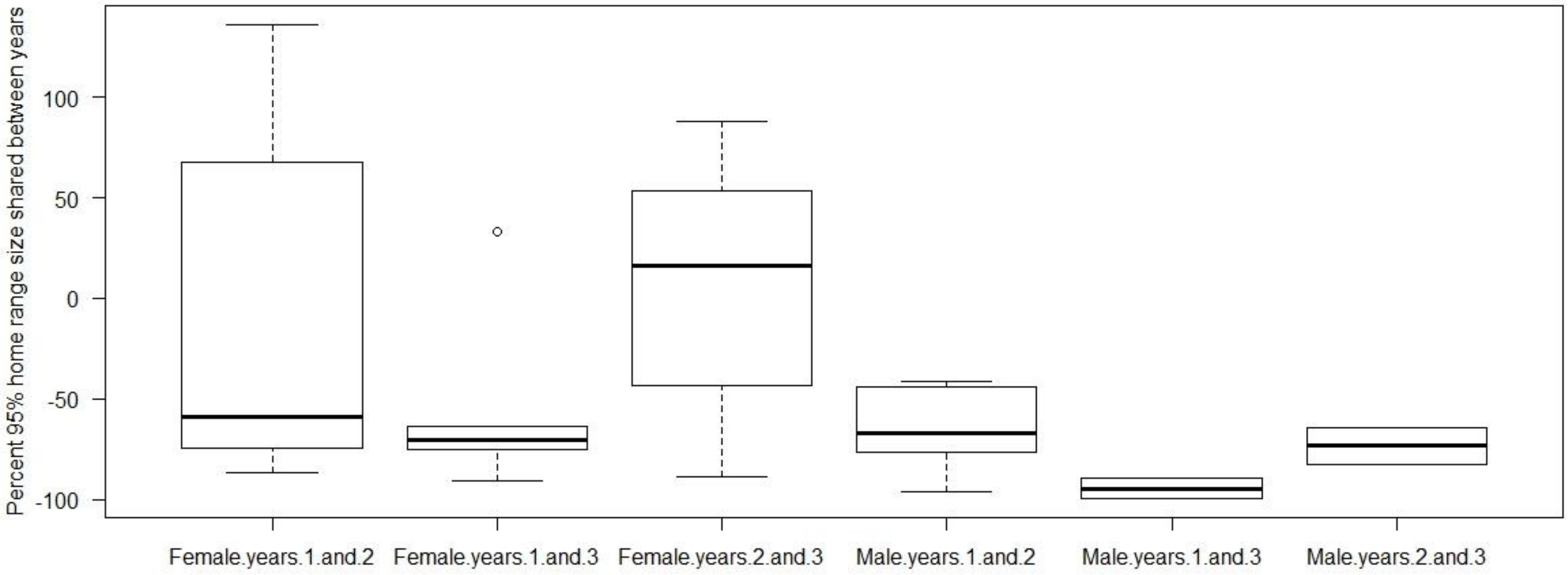

Figure 4.5. Average % 95% home range area (±SE) that was used among years for radio-tagged Sandhill Crane males, females, and combined males and females.

Figure 4.6. Average linear distance (+SE) from natal territory to locations recorded for one-year-old, two-year-old, and three-year-old radio-tagged Sandhill Cranes. Average effective natal dispersal distance between natal territory and breeding territory from Chapter 4.

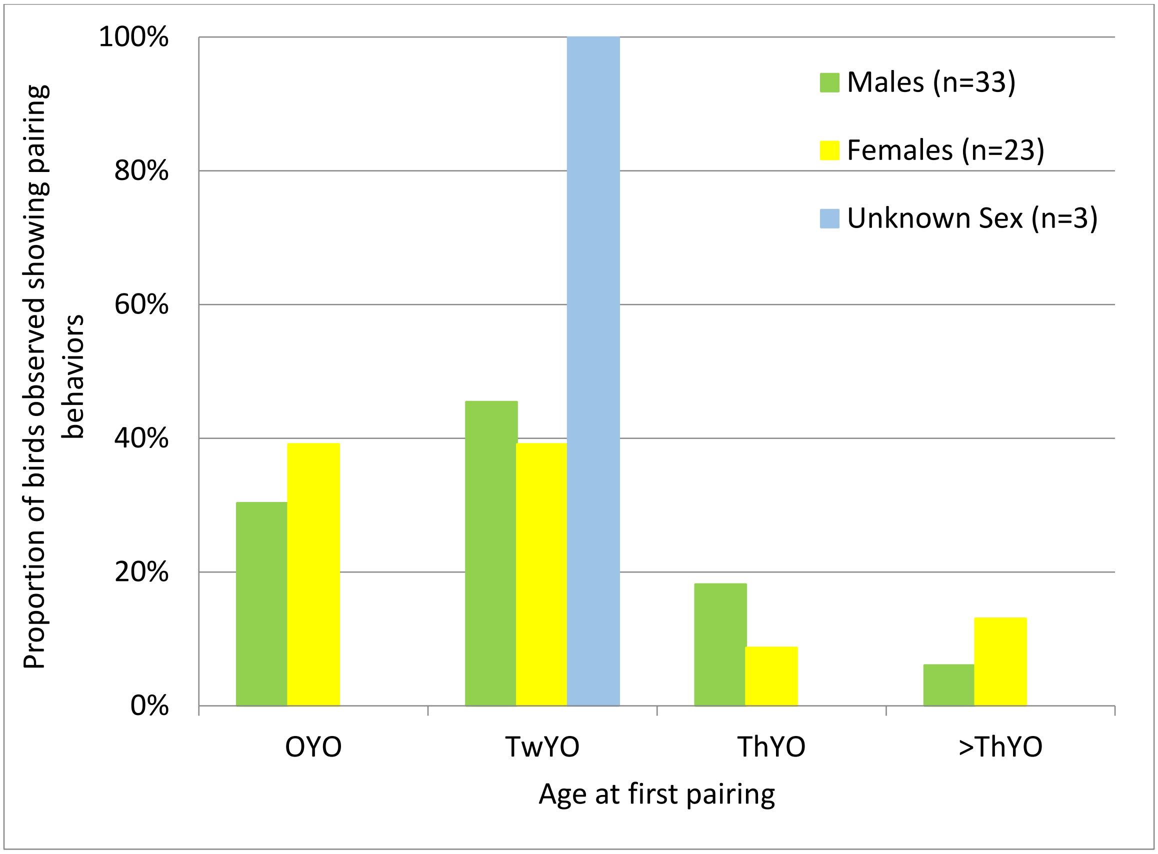

Figure 4.7. Proportions of non-territorial Sandhill Cranes that were observed showing pairing behaviors at one-year-old (OYO), two-years-old (TwYO), three-years-old (ThYO), and older than three-years-old.

Appendix A. Total home range sizes of Sandhill Cranes radio-tagged near Briggsville, WI.

					Home Range (km^2)					
USGS ID	Sex	Year Deployed	Year(s) Tracked	Radio	Year 1	No obs.	Year 2	No obs.	Year 3	No obs.
62945234	F	2006	2007-09	Backpack	104.547	72	101.19	73	11.38	36
62945233	F	2006	2007-09	Backpack	122.52	75	37.67	60	13.05	37
62947277	F	2008	2009-10	Backpack	61.89	21	112.66	67	-	-
62945244	F	2007	2008-10	Backpack	67.16	82	136.53	73	56.67	62
62945243	F	2007	2008-10	Backpack	171.48	58	113.60	56	70.71	81
62945240	F	2006	2007-09	Backpack	418.58	56	338.84	84	**0.83**	**15**
62947279	F	2008	2009	Backpack	241.08	37	-	-	-	-
62945246	F	2007	2008-10	Backpack	686.45	59	43.20	50	50.84	98
62947296	F	2008	2009-10	Backpack	25.31	65	28.67	90	-	-
62922164	F	1997	1998-99	Leg	108.27	295	43.13	153	-	-
62922151	F	1997	1998	Leg	183.54	75	-	-	-	-
62922117	F	1996	1997	Leg	40.90	150	-	-	-	-
62922122	F	1996	1997	Leg	41.71	85	-	-	-	-

Appendix A (cont.)

		Year	Year(s)		Home Range (km^2)					
USGS ID	Sex	Deployed	Tracked	Radio	Year 1	No obs.	Year 2	No obs.	Year 3	No obs.
62923449	F	2000	2001	Leg	317.54	204	-	-	-	-
62922143	F	1997	1998	Leg	37.27	48	-	-	-	-
62923418	F	1999	2000	Leg	2555.16	308	-	-	-	-
62947291	M	2008	2009-10	Backpack	85.97	39	29.40	81	-	-
62947286	M	2008	2009	Backpack	45.11	60	-	-	-	-
62947259	M	2007	2008-10	Backpack	33.96	77	10.70	72	4.39	41
62947290	M	2008	2009	Backpack	406.63	48	-	-	-	-
62945247	M	2007	2008-10	Backpack	772.68	66	48.01	68	12.33	73
62945222	M	2006	2007-08	Backpack	500.46	61	85.90	88	-	-
62945223	M	2006	2007-08	Backpack	150.46	90	90.59	85	-	-
62922173	M	1998	1999	Leg	19.70	48	-	-	-	-
62922155	M	1997	1998	Leg	167.72	204	-	-	-	-
62922121	M	1996	1997	Leg	108.37	196	-	-	-	-
62922175	M	1998	1999	Leg	99.93	142	-	-	-	-

Appendix A (cont.)

					Home Range (km^2)					
USGS ID	Sex	Year Deployed	Year(s) Tracked	Radio	Year 1	No obs.	Year 2	No obs.	Year 3	No obs.
62923444	M	2000	2001	Leg	558.80	70	-	-	-	-
62922153	M	1997	1998-99	Leg	291.49	199	75.03	132	-	-
62922125	M	1996	1997	Leg	108.46	171	-	-	-	-
		Total		Average	284.43		86.34		31.34	
				SE	86.62		20.46		10.23	
		Females		Average	323.96	Mann-Whitney U (W)	106.17	Mann-Whitney U (W)	40.53	
				SE	155.05	105	32.03	37	12.01	
		Males		Average	239.24	p-value	56.61	p-value	8.36	
				SE	62.19	0.79	13.26	0.27	3.97	

USGS band in **bold** was not included in the analysis for three-year old birds due to small number of observations collected for that year.

Appendix B. 95% home ranges of Sandhill Cranes radio-tagged near Briggsville, WI.

		Year	Years		Home Range (km^2)					
USGS ID	Sex	Deployed	Tracked	Radio	Year 1	No obs.	Year 2	No obs.	Year 3	No obs.
62945234	F	2006	2007-09	Backpack	94.91	68	78.87	69	8.81	32
62945233	F	2006	2007-09	Backpack	30.52	73	4.01	53	7.53	33
62947277	F	2008	2009-10	Backpack	61.89	21	103.85	66	-	-
62945244	F	2007	2008-10	Backpack	46.31	77	109.26	70	61.57	63
62945243	F	2007	2008-10	Backpack	171.48	54	40.63	51	136.31	74
62945240	F	2006	2007-09	Backpack	418.58	55	153.76	79	**0.83**	**15**
62947279	F	2008	2009	Backpack	23.54	37	-	-	-	-
62945246	F	2007	2008-10	Backpack	170.49	51	52.60	49	50.84	91
62947296	F	2008	2009-10	Backpack	13.01	63	28.67	85	-	-
62922164	F	1997	1998-99	Leg	72.13	264	29.40	147	-	-
62922151	F	1997	1998	Leg	19.11	73	-	-	-	-
62922117	F	1996	1997	Leg	19.11	141	-	-	-	-
62922122	F	1996	1997	Leg	41.71	85	-	-	-	-
62923449	F	2000	2001	Leg	196.95	196	-	-	-	-

Appendix B (cont.)

					Home Range (km^2)					
USGS ID	Sex	Year Deployed	Years Tracked	Radio	Year 1	No obs.	Year 2	No obs.	Year 3	No obs.
62922143	F	1997	1998	Leg	5.19	41	-	-	-	-
62923418	F	1999	2000	Leg	2555.16	283	-	-	-	-
62947291	M	2008	2009-10	Backpack	85.97	39	31.31	73	-	-
62947286	M	2008	2009	Backpack	32.84	57	-	-	-	-
62947259	M	2007	2008-10	Backpack	23.86	73	6.87	70	2.46	41
62947290	M	2008	2009	Backpack	253.84	42	-	-	-	-
62945247	M	2007	2008-10	Backpack	772.68	66	28.43	66	4.96	69
62945222	M	2006	2007-08	Backpack	135.78	54	50.24	84	-	-
62945223	M	2006	2007-08	Backpack	95.73	85	56.11	81	-	-
62922173	M	1998	1999	Leg	10.92	46	-	-	-	-
62922155	M	1997	1998	Leg	64.08	187	-	-	-	-
62922121	M	1996	1997	Leg	60.95	183	-	-	-	-
62922175	M	1998	1999	Leg	84.83	126	-	-	-	-
62923444	M	2000	2001	Leg	149.19	59	-	-	-	-

Appendix B (cont.)

		Year	Years				Home Range (km^2)			
USGS ID	Sex	Deployed	Tracked	Radio	Year 1	No obs.	Year 2	No obs.	Year 3	No obs.
62922153	M	1997	1998-99	Leg	112.78	188	62.74	127	-	-
62922125	M	1996	1997	Leg	75.87	164	-	-	-	-
		Total		Average	197.30		54.03		28.26	
				SE	85.71		10.81		10.65	
		Females		Average	255.37	Mann-Whitney U	62.12	Mann-Whitney U	38.08	
				SE	155.58	107	16.37	35	12.39	
		Males		Average	130.94	p-value	37.40	p-value	3.71	
				SE	50.59	0.85	9.08	0.39	1.25	

USGS band in **bold** was not included in the analysis for three-year old birds due to small number of observations collected for that year.

Appendix C. Percent area shared among Sandhill Cranes total home ranges in different years.

USGS ID.	Sex	Radio Type	Area (km^2) Year t	Area (km^2) Year t+1	Shared Area (km^2)	Total Area (km^2)	% shared	Interactions
62922164	F	Leg	108.27	43.13	32.80	118.61	27.65%	Years 1 and 2
62945233	F	Backpack	122.52	37.67	0.00	160.19	0.00%	Years 1 and 2
62945234	F	Backpack	104.55	101.19	22.60	183.14	12.34%	Years 1 and 2
62945240	F	Backpack	418.58	338.83	209.59	547.82	38.26%	Years 1 and 2
62945243	F	Backpack	171.48	113.60	43.74	241.33	18.13%	Years 1 and 2
62945244	F	Backpack	67.16	136.53	49.20	154.48	31.85%	Years 1 and 2
62945246	F	Backpack	686.45	43.20	6.38	723.27	0.88%	Years 1 and 2
62947277	F	Backpack	61.89	112.66	53.93	120.63	44.71%	Years 1 and 2
62947296	F	Backpack	25.31	28.67	17.70	36.28	48.79%	Years 1 and 2
62922153	M	Leg	291.49	75.03	51.86	314.66	16.48%	Years 1 and 2
62945222	M	Backpack	500.46	85.90	75.58	510.78	14.80%	Years 1 and 2
62945223	M	Backpack	150.12	90.59	65.83	174.88	37.64%	Years 1 and 2
62945247	M	Backpack	772.68	48.01	28.44	792.25	3.59%	Years 1 and 2
62947259	M	Backpack	33.96	10.70	10.70	33.96	31.49%	Years 1 and 2
62947291	M	Backpack	85.97	29.40	25.91	89.46	28.96%	Years 1 and 2
62945233	F	Backpack	37.67	13.05	6.34	44.38	14.28%	Years 2 and 3
62945234	F	Backpack	101.19	11.38	3.68	108.88	3.38%	Years 2 and 3
62945243	F	Backpack	113.60	154.87	11.79	256.68	4.59%	Years 2 and 3

Appendix C (cont.)

USFWS	Sex	Radio Type	Area (km^2) Year t	Area (km^2) Year t+1	Shared Area (km^2)	Total Area (km^2)	% shared	Interactions
62945244	F	Backpack	136.53	69.88	23.53	182.88	12.87%	Years 2 and 3
62945246	F	Backpack	43.20	65.98	31.31	77.87	40.21%	Years 2 and 3
62945247	M	Backpack	48.01	129.74	11.64	166.12	7.01%	Years 2 and 3
62947259	M	Backpack	10.70	4.40	3.77	11.32	33.29%	Years 2 and 3
62945233	F	Backpack	122.52	13.05	0.00	135.57	0.00%	Years 1 and 3
62945234	F	Backpack	104.55	11.38	11.38	104.55	10.88%	Years 1 and 3
62945243	F	Backpack	171.48	154.87	47.84	278.51	17.18%	Years 1 and 3
62945244	F	Backpack	67.16	69.88	9.60	127.43	7.54%	Years 1 and 3
62945246	F	Backpack	686.45	65.98	1.51	750.92	0.20%	Years 1 and 3
62945247	M	Backpack	772.68	129.74	11.91	890.51	1.34%	Years 1 and 3
62947259	M	Backpack	33.96	4.40	4.40	33.96	12.94%	Years 1 and 3

Appendix D. Percent area shared among Sandhill Cranes 95% home ranges in different years.

USGS ID	Sex	Radio Type	Area (km^2) Year t	Area (km^2) Year t+1	Shared Area (km^2)	Total Area (km^2)	% shared	Interactions
62922164	F	Leg	72.13	29.40	26.67	74.86	35.63%	Years 1 and 2
62945233	F	Backpack	30.52	4.01	0.00	34.54	0.00%	Years 1 and 2
62945234	F	Backpack	94.91	78.87	22.53	151.24	14.90%	Years 1 and 2
62945240	F	Backpack	418.58	153.76	47.84	524.49	9.12%	Years 1 and 2
62945243	F	Backpack	171.48	40.63	2.81	209.29	1.34%	Years 1 and 2
62945244	F	Backpack	46.31	109.26	38.73	116.84	33.15%	Years 1 and 2
62945246	F	Backpack	170.49	43.20	3.84	209.86	1.83%	Years 1 and 2
62947277	F	Backpack	61.89	103.55	46.66	118.77	39.29%	Years 1 and 2
62947296	F	Backpack	13.01	23.38	8.09	28.30	28.60%	Years 1 and 2
62922153	M	Leg	112.78	62.74	51.04	124.48	41.01%	Years 1 and 2
62945222	M	Backpack	135.78	50.24	39.31	146.71	26.79%	Years 1 and 2
62945223	M	Backpack	95.73	56.11	30.83	121.01	25.48%	Years 1 and 2
62945247	M	Backpack	772.68	28.43	25.48	775.62	3.29%	Years 1 and 2
62947259	M	Backpack	23.85	6.87	6.54	24.18	27.05%	Years 1 and 2
62947291	M	Backpack	85.97	20.00	19.99	85.98	23.24%	Years 1 and 2
62945233	F	Backpack	30.52	7.53	3.33	34.72	9.60%	Years 2 and 3
62945234	F	Backpack	94.91	8.81	3.60	100.12	3.60%	Years 2 and 3
62945243	F	Backpack	171.48	62.19	8.48	225.18	3.76%	Years 2 and 3

Appendix D (cont.)

USFWS	Sex	Radio Type	Area (km^2) Year t	Area (km^2) Year t+1	Shared Area (km^2)	Total Area (km^2)	% shared	Interactions
62945244	F	Backpack	46.31	61.57	23.29	84.59	27.54%	Years 2 and 3
62945246	F	Backpack	170.49	50.30	30.80	189.99	16.21%	Years 2 and 3
62945247	M	Backpack	772.68	4.96	4.32	773.32	0.56%	Years 2 and 3
62947259	M	Backpack	23.85	2.46	1.96	24.36	8.03%	Years 2 and 3
62945233	F	Backpack	30.52	7.53	0.00	38.06	0.00%	Years 1 and 3
62945234	F	Backpack	94.91	8.81	8.81	94.91	9.29%	Years 1 and 3
62945243	F	Backpack	171.48	62.19	45.80	187.86	24.38%	Years 1 and 3
62945244	F	Backpack	46.31	61.57	9.52	98.37	9.68%	Years 1 and 3
62945246	F	Backpack	170.49	50.30	0.33	220.46	0.15%	Years 1 and 3
62945247	M	Backpack	772.68	4.96	4.96	772.68	0.64%	Years 1 and 3
62947259	M	Backpack	23.85	2.46	2.06	24.25	8.51%	Years 1 and 3

Appendix E. Effect of age, sex, and radio type on linear distance among a Sandhill Crane's natal area and locations observed during radio telemetry.

			Distance (km)			
Age	Sex	Radio Type	Average	SE	Minimum	Maximum
One-year-old	Female	Backpack	22.85	1.30	0.17	137.37
		Leg-band	22.23	0.67	0.11	79.62
		Average	22.44	0.62		
	Male	Backpack	10.55	0.73	0.31	73.00
		Leg-band	5.84	0.23	0.25	67.75
		Average	7.26	0.28		
Two-year-old	Female	Backpack	14.93	0.62	0.32	82.57
		Leg-band	2.96	0.11	0.05	8.27
		Average	12.44	0.52		
	Male	Backpack	3.04	0.13	0.19	10.24
		Leg-band	5.64	0.37	0.23	18.1
		Average	3.90	0.16		
Three-year-old	Female	Backpack	11.40	0.52	1.77	81.96
	Male	Backpack	2.53	0.26	0.07	31.08

Chapter 5

SHORTER EFFECTIVE NATAL DISPERSAL DISTANCE DOES NOT LEAD TO YOUNGER AGE AT FIRST TERRITORY ACQUISITION IN SANDHILL CRANES

ABSTRACT

I investigated the effective natal dispersal distance (ENDD) travelled between a Sandhill Crane's natal area and breeding territory and whether this distance affected the age at which it obtained a breeding territory. Sandhill Crane chicks were color-banded on their natal territory and I was able to re-locate 35 chicks (21 male and 14 female) on a breeding territory. Average male ENDD (2.3 km) was significantly shorter than average female ENDD (10.7 km). When two long-distance dispersive females (>25 km) were removed, male ENDD was still significantly shorter than the adjusted female ENDD (5.3 km). There was no observable direction pattern detected for males or females. Average males (4.9 years old) and average females (4.3 years old) obtained breeding territories at similar ages. There was no relationship between ENDD and age at territory acquisition. There was also no relationship between when a bird first showed pairing behavior (average = 24.5 months) an age at first territory acquisition. While males remained closer to their natal territory to breed than females, both sexes were generally philopatric. Higher detectability of dispersive birds (> 25 km) could change this trend. For philopatric birds, ENDD may be driven by territory availability. In our study area, territory availability is low due to 1) high breeding adult survival, 2) few mate changes per year, and further restricted by 3) preference for experienced birds after a mate switch. These results suggest non-territorial birds balance potential costs of dispersing (e.g., possibly lowered survival) against costs of being philopatric (e.g., obtaining a breeding territory after reaching sexual maturity).

INTRODUCTION

Individuals undergo three phases while dispersing: departure, transience, and settlement (Bowler and Benton 2005, Clobert et al. 2008); the departure and transience phases were discussed in Chapters 3 and 4 respectively. For this study, the settlement phase occurs as a result of effective dispersal (Greenwood 1980) when an individual has moved from its natal area and attempted reproduction at its new location. Alternatively, gross dispersal (Greenwood 1980) does not require reproduction after departure from a natal area.

The settlement phase is important because this drives population genetic structure and gene flow among populations. Typically, once an adult animal acquires a breeding location, they remain on or near that territory for the remainder of their life (Greenwood 1980, Greenwood and Harvey 1982) and this has been observed in Sandhill Cranes (Chapter 2). Breeding adults of some species exhibit breeding dispersal or long-distance movement among successive breeding attempts (Haas 1998, Pärt and Gustaffson 1989, Serrano et al. 2001), but this phenomenon is rare. For most species, any gene flow that occurs among populations is the result of long-distance movement by juvenile and non-territorial individuals (Greenwood and Harvey 1982). Therefore, quantifying the effective natal dispersal distance (ENDD) travelled between natal and breeding location is a key factor in understanding population dynamics and population genetic structure.

Theoretical economic costs and benefits for dispersive versus philopatric individuals have been well developed. Compared to dispersing individuals, a philopatric individual is expected to have increased survival and reproductive success because it is already familiar with its natal area (Greenwood 1980). For species with high breeding adult site fidelity, however, philopatric individuals can experience high cost because they may compete with other philopatric relatives for limited resources (West et al. 2001). In dense breeding populations, where breeding locations are limited, philopatric individuals may delay breeding opportunities, even if sexually mature, because they are unable to obtain a breeding location (Zack and Stutchbury 1992, Russell and Rowley 1993, Negro et al. 1997). This is particularly true for long-lived species in which adults use the same breeding location across multiple years and have few mate changes over their lifetime (see Kimball et al. 2003), such as Sandhill Cranes (Chapter 2, Nesbitt and Tacha 1997). Each missed breeding opportunity can be detrimental for an individual's reproductive fitness because they risk mortality without first reproducing. Alternatively, dispersing individuals risk high cost through reduced survival in new areas compared to philopatric individuals (Belichon et al. 1996, Byrom and Krebs 1999, Ferreras et al. 2004, but see Townsend et al. 2003). Dispersing can be beneficial, however, because successful dispersers can have higher reproductive success (Nilsson 1989) or reproduce at a younger age (Steiner and Gaston 2005) which can lead to high lifetime reproductive success (Brommer et al. 1998, Krüger 2005, Oli et al. 2002) compared to philopatric individuals.

The sex of the individual is an important driver of ENDD in birds, as females usually disperse further from their natal area than do males (Greenwood 1980, Greenwood and Harvey 1982). Proximate explanations for male-biased philopatry include: experience with nesting location availability which could lead to faster acquisition of a mate (Pärt 1994), increased knowledge about local resources and habitat quality (Becker et al. 2008), and information regarding number and density of intraspecific competitors also vying for open breeding locations (Doligez et al. 2004). One main exception to male-biased philopatry in birds occurs in waterfowl, where philopatry is female-biased (Anderson et al. 1992). Mate choice in waterfowl occurs on wintering areas or spring migratory stopover locations, which forces a paired male to follow his female mate back to her natal area (Rohwer and Anderson 1988). Similar to philopatric males of other avian species, female ducks, geese, and swans are expected to show 1) increased feeding ability and survival of offspring due to local knowledge of nesting habitat and 2) increased probability of positive kin selection with closely-related females breeding nearby (Anderson et al. 1992). This second point may explain the willingness of females of many waterfowl species to adopt unrelated chicks (Eadie et al. 1988, Kalmbach 2006, Kraaijeveld 2005).

Not all avian species show a sex-bias in male or female philopatry. In monogamous species with equal parental care and no sexual dimorphism between males and females, neither sexual selection nor dominance should cause sex-biased ENDD to evolve (Gauthreaux 1978, Greenwood 1980). For example, a lack of sex-bias in ENDD was found in several species of Charadriiformes (Black-necked Stilt [*Himantopus mexicanus*], James 1995; Dunlin [*Calidris alpina*], Soikkeli 1970; Semipalmated Sandpipers [*C. pusilla*], Gratto 1988; and Western Sandpiper [*C. mauri*], R. T. Holmes in Oring and Lank 1982). The lack of sex-biased ENDD in these species is confounding in the context of kin competition and inbreeding potential. However, if male offspring disperse in one direction and female offspring disperse in a different direction, the likelihood of encountering a relative, especially a brood mate, is decreased. For example, male and female Ortolan Bunting (*Emberiza hortulana*) siblings showed similar ENDD, but dispersed from natal areas in different cardinal directions (Dale 2010).

Cranes (Gruidae) are long-lived and highly territorial (Walkinshaw 1973). Pair bonds are monogamous and long-term with males and females sharing parental duties (Walkinshaw 1965, Layne 1982). Males and females are sexually monomorphic in plumage, however males are typically larger than females (Nesbitt et al. 1992) as well as have a deeper pitch to their voice and display different postures during an antiphonal breeding duet (unison call; Archibald 1976). All of these characteristics suggest that there should be no observed sex-bias in ENDD in Gruidae.

Surprisingly, patterns of ENDD in crane populations that have been studied are similar to other avian species with females dispersing farther from natal areas than males. Female ENDD was three times longer than male ENDD in non-migratory Sandhill Cranes in Florida (*Grus canadensis*; Nesbitt et al. 2002) and to five times longer in non-migratory Red-crowned Cranes (*Grus japonensis*; Masatomi 2003). Alternatively, there was no difference between male and female natal distances in both a wild population (Johns et al. 2005) and re-introduced population (WCEP, unpublished data) of migratory Whooping Cranes (*Grus americana*). So, migratory behavior might alter ENDD in male and female cranes.

While Sandhill Cranes are capable of producing viable eggs and sperm at two-years-old (Mirande et al. 1996, Radke and Radke 1986), age at first breeding does not typically occur until four or five-years-old or older (Nesbitt 1992, Tacha et al. 1989). Low mate and breeding site availability constrains when non-territorial birds obtain their first territory. Within a territory, nearly 80% of breeding pair bonds were maintained among years (Chapter 2). When a mate and/or territory becomes available through death or divorce, experienced birds from nearby territories were typically chosen as new mates (Chapter 2). Once a breeding territory was acquired, a bird bred on or within a two km diameter of that territory for the remainder of its life (Chapter 2). All of these characteristics could constrain age at first breeding by non-territorial cranes because this presents limited openings for territory acquisition.

I investigated ENDD in a migratory population of color-banded Sandhill Cranes that has been studied for over 20 years (Hayes et al. 2003). I did not expect male and female Sandhill Cranes in this population to differ in ENDD. If ENDD did not differ, then I hypothesized that males and females would disperse in different directions from their natal area. If ENDD did differ, then I hypothesized that males would be closer to their natal area than females, as observed in Florida Sandhill Cranes. If males were more philopatric, then I hypothesized that males would breed later than females (due to high density) and have lower lifetime reproductive success.

METHODS

Capture and Banding

During this study, two different methods were used to capture Sandhill Cranes near Briggsville, Wisconsin, site of a long-term research project on Sandhill Crane ecology and behavior. Flightless chicks (age 35 to 70 days) were pursued by chasing them on foot until they hid (Hoffman 1985). Territorial adults with any fledged hatch-year chicks (older than 70 days) were captured using alpha-chloralose, an oral tranquilizer (Fisher Scientific Company, Fairlawn, New Jersey, USA and Biosynth Ag, Switzerland) using a process described in Hayes et al. (2003). Once captured, each crane received a three-inch plastic band engraved with a unique three-digit number that was placed above the tarsal-metatarsal joint of one leg. Either two or three one-inch colored plastic leg bands, in a unique color combination for each bird, were added on the opposite leg above the same joint. U. S. Geological Survey aluminum bands (with an engraved unique nine-digit number) were either placed above the toes of either leg or within the combination of one-inch colored bands. Overall, the three unique ways of identifying banded birds persisted across multiple years (Dickerson and Hayes 2014) and were ideal for receiving observations from audiences that ranged from novice to professional (see www.bandedcranes.org) to monitor long-term movements made by dispersing chicks.

Blood samples were collected from most birds captured between 1996 and 2012. Sex of birds with blood samples collected was determined through genetic analysis (Griffiths et al. 1998, Duan and Fuerst 2001). All other birds were sexed by behavior, specifically posture during a unison call (an antiphonal duet between paired birds; Archibald 1976). Age (adult or hatch-year chick) was determined by differences in plumage and presence or absence of red skin on the bird’s head (Lewis 1979, Nesbitt and Schwikert 2005).

Behavioral observations

Sandhill Cranes were classified as “paired, but non-territorial” when they separated themselves from a larger flock (any grouping of cranes that numbered greater than two), showed synchronized maintenance behaviors (e.g., preening), or were observed unison-calling together but not defending a territory. Paired Sandhill Cranes were re-classified as “breeding” when they actively defended a breeding territory from conspecifics, nested, and/or raised offspring with a mate in an established pair bond. A nesting event was suspected through observation of a lone bird that was known to be paired in an area that had been defended by that pair and was subsequently verified by observing the pair re-united together later in the same breeding season either with or without chicks. From 2001-2003, nesting was verified for many individuals through observation of color-banded birds during nest surveys via helicopter (Lacy and Su 2008). For most pairs, I had continued observations over multiple years to increase my confidence that a pair defended a breeding territory.

Statistical Analyses

Because I typically recorded a small number of samples, I wanted to all data sets with a Shapiro-Wilk test (Shapiro and Wilk 1965) and set significance at $p<0.05$. A deviation from normality was verified for all data using a Q-Q plot in R. A non-parametric test was used when the results of the Shapiro-Wilk test were significant (i.e., if the resulting p-value was less than 0.05, then the data were not normally-distributed). Significance for all statistical tests was set at $p \leq 0.05$.

In ArcMap 10.1 (ESRI, Redlands, CA), ENDD was quantified by measuring the distance between the center of a bird's natal location and center of its breeding territory location. Following Shields (1982), cranes were classified as philopatric when their ENDD was less than 10 times the diameter of an average territory and dispersive when their ENDD exceeded this distance. Average territory diameter used was 1.2 km and calculated by assuming each territory was a circle with area πr^2. For territory size, I used the 95% fixed kernel home range sizes (converted to km^2) of 12 breeding adult Sandhill Cranes during incubation and while their chicks were flightless reported by Miller (2003). I used the home range sizes collected during the incubation and flightless chick stage because this is when adult mobility is most restricted due to chick mobility and represented a pair's breeding territory.

I used a Kruskal-Wallis test (Sokal and Rohlff 2001) to evaluate if the sex of the bird or the age when that bird acquired a breeding territory affected natal dispersal distance. I also used a Kruskal-Wallis test to determine the relationship between the age when a bird first started showing pairing behavior and the age when it acquired its first breeding territory. Finally, I used a Kruskal-Wallis test to determine if there was any effect of natal dispersal distance, sex, age at first observed pairing behavior, age at first territory acquisition, and length of time on a breeding territory on reproductive success. Following all Kruskal-Wallis tests, any variables that were significant were further evaluated using a Mann-Whitney U test (Sokal and Rohlff 2001).

In addition to ENDD, angle of movement between a crane's natal and breeding territory was also measured to determine if there were overall differences between males and females. To compare males and females, I categorized each bird's angle of movement between natal and breeding area into either two (North, South), four (North, East, South, West), or eight (North, Northeast, East, Southeast, South, Southwest, West, Northwest) cardinal directions. Directions were categorized using this methodology instead of considering measurements as continuous data because of the nature of a 360° circle. While 0° and 359° would both point directionally North, the average of these two data points would be 180°, or due south. Cutoff points for two direction categories (North or South) were placed at 90° and 270° (Direction 2; Figure 5.1). Cutoff points for four direction categories (North, East, South, or West) were placed at the four main cardinal directions, so the line between West and North was at 0°, North and East at 90°, East and South at 180°, and South and West at 270° (Direction 4a; Figure 5.1). I then rotated these categories counterclockwise by 45° and re-categorized each bird's angle of dispersal (Direction 4b; Figure 5.1). This was done to account for the artificial lines separating these four directions. I then divided the 360° circle into eight groups where each direction spanned 45°

(Direction 8a; Figure 5.1) and re-categorized the angle of dispersal. These eight groups were then rotated by 22.5^o (Direction 8b; Figure 5.1), and re-categorized a fourth time. Differences between sexes, distance a bird dispersed between natal and breeding location (categorized as 0-3 km, 3.1-6 km, 6.1-9 km, 9.1-12 km, and >12 km blocks), and the age that a bird acquired its first breeding territory (categorized as 2-3 years, 4-5 years, and >5 years) were examined with a χ^2 test (Sokal and Rohlff 2001). Average values reported in the RESULTS are $\underline{+}$ SE.

RESULTS

We banded 234 hatch-year chicks (95 M: 123 F: 16 U) on 71 territories 1991-2012. Of these 234 chicks, 44 (19%) died or disappeared during their hatch year, 16 (7%) were not observed after their hatch year, and four (2%) died as one-year-old or two-year-old birds. Of the remaining 170 chicks, 40 (23%, 22 M: 18 F) were confirmed defending a breeding territory and/or hatching a chick. I was able to locate the breeding territory for 35 of these chicks (21 M: 14 F; Table 5.1). Five cranes banded as chicks (four males, one female) joined a banded breeding bird on their territory (Chapter 2). Prior to obtaining their breeding territories, each of these five non-territorial cranes was paired with an unbanded mate. Only one non-territorial pair (a banded nine-year-old and an unbanded female) was observed entering the breeding population together. This pair was regularly observed on the fringe of an established territory during the breeding season prior to acquiring that territory. I could not determine if the remaining 30 chicks joined unbanded birds on previously unknown territories or paired with a bird and then established a new territory.

Effective natal dispersal distance was affected (Kruskal-Wallis = 10.7, df = 2, 31, $p < 0.001$) by the sex of the bird (slope p-value < 0.001, $R^2 = 0.40$). Average female ENDD ($10.7\underline{+}4.0$

km) was longer than average male ENDD (2.3±0.4 km; Mann-Whitney U = 238, $p < 0.001$). Two females were considered dispersive because their ENDD exceeded 12.1 km (Table 5.1, Figure 5.2); the remaining 33 birds were considered philopatric to their natal area. The removal of these dispersive females cut the average female ENDD in half (5.3±0.8 km; Figure 5.3), but this distance was still significantly longer than average male ENDD (Mann-Whitney U = 198, p = 0.002). Proportionally, greater than 75% of males were found breeding less than three km from their natal area where as less than 10% of females nested this same distance away (Figure 5.4).

Average age that male (4.9±0.4 years old, range = 2 - 10 years) and female Sandhill Cranes (4.3±0.4 years old, range = 3 - 9 years) obtained a breeding territory were similar (Mann-Whitney U = 15.5, p = 0.29). Effective natal dispersal distance was not affected by age at first territory acquisition (Kruskall-Wallis = 1.6, df = 1, 32, p = 0.22). For males and females, there was no relationship between the age at territory acquisition and ENDD (males: slope = -0.35, p = 0.14, Figures 4.2, 4.3; females: slope = 0.033, p = 0.91, Figure 5.2). When the two dispersive females were removed, the relationship did not change (slope = -0.43, p = 0.18; Figure 5.3).

Males and females did not disperse from their natal area in any observed directional pattern (Figure 5.5). There was no significant relationship between the angle that a bird travelled from its natal territory to its first breeding territory and: 1) the sex of the bird (Table 5.2), 2) distance travelled between natal and breeding territory (Table 5.3), or 3) age when a bird gained its first territory (Table 5.4).

With males and females combined, there was no relationship between age at first pairing behavior (average = 24.5±1.5, range = 11-48 months; Chapter 4) and age at first territory acquisition (Kruskal-Wallis = 0.11, df = 1, 26, p = 0.75). Separately, neither males (Kruskal-Wallis

= 0.4, df = 1, 15, slope = -0.16, p = 0.55) nor females (Kruskal-Wallis = 2.1, df = 1, 9, slope = 0.43, p = 0.18) showed a relationship between age at first pairing behavior and age at first territory acquisition (Figure 5.6).

An individual crane's reproductive success was significantly affected (Kruskall-Wallis = 2.6, df = 5, 22, p = 0.06) by sex (slope = -7.5, p = 0.004) and length of time that a Sandhill Crane chick spent as a breeding bird (slope = -0.4, p = 0.03), but the variation explained by this model was low (R^2 = 0.23). Females (0.38±0.12 chicks/territory/year, range = 0.00 – 1.25) had a higher average reproductive success than males (0.13±0.07 chicks/territory/year, range = 0.00 – 1.00; Mann-Whitney U = 137.5, p = 0.03). There was also a trend that females from known natal areas (5.5±1.1 years) defended a territory longer than males (4.3±0.6 years; Mann-Whitney U = 129.5, p = 0.09). There was no effect of age at first territory acquisition on average annual reproductive success or total number of chicks fledged over the lifetime of a bird from a known natal area (Figure 5.7).

DISCUSSION

While effective natal dispersal distance was significantly longer for female Sandhill Cranes than it was for males, natal philopatry was strong for both sexes. A majority (71%) of banded Sandhill Cranes nested less than six km from their natal area and the farthest ENDD was 57 km. These distances are minimal given the flight capabilities of Sandhill Cranes. Caution needs taken with these data as them are reflective of measurable ENDD which could be short-distance dispersal biased. Five birds (one male and four females) successfully fledged chicks at a known age, but their territory location was unknown, suggesting they were nesting outside the study area and greater than 15 km from their natal area. Additionally, 130 birds banded as chicks were observed alive, and even paired, yet I could not determine if they had obtained a breeding territory or attempted reproduction because they were not regularly observed in the study area during spring or fall migration.

Natal philopatry was also observed in non-migratory Sandhill Cranes in Florida (Nesbitt et al. 2002). While natal philopatry seems the general rule with Sandhill Cranes, important exceptions have occurred. For example, a one-year-old non-territorial banded male was found dead 200 km north of his natal area, while a twenty-year-old banded female died 150 km north of her natal area. While ICF has never received a report of one of its banded Sandhill Cranes being observed outside of Wisconsin except on migratory stopover or wintering areas (Chapter 6), long-distance dispersal by juvenile Sandhill Cranes has been recorded. One flightless juveniles banded in the lower peninsula of Michigan (Hoffman 1985) and another banded in southeastern Alaska (Boise 1979) were each re-sighted as one-year-old birds in central Wisconsin. Whether these birds returned to these new summering areas to breed is unknown.

Why would males nest closer to their natal area and females further from their natal area? Higher male philopatry could suggest that males have higher investment in the breeding territory than females (Greenwood 1980). Greenwood (1980) hypothesized that males that stay closer to their natal area gain more knowledge about available resources, establish and defend a territory, and then females then choose a mate based on that territory. Male territory establishment and female choice based on that territory has been documented in serially monogamous bird species (e.g., Sedge Warbler *Acrocephalus schoenobaenus*, Buchanan and Catchpole 1997; House Wren *Troglodytes aedon*, Eckerle and Thompson 2006) and polygynous species (Red-winged Blackbirds (*Agelaius phoeniceus*; Yusakawa 1981, Searcy et al. 1995), which typically re-pair following one or a few breeding attempts. Nesbitt et al. (2002) also found longer ENDD for female Florida Sandhill Cranes than males and concluded that this supported Greenwood's (1980) hypothesis.

The conclusion of male territory establishment and female choice based on that territory is surprising given the monogamous mating system utilized by cranes. First, male and female Sandhill Cranes share in territory defense and chick provisioning (Walkinshaw 1965, Layne 1982) suggesting equal investment in the territory and resource allocation. If males had higher investment in the territory than females, I would expect more females than males would leave their territory following mate death or divorce to obtain a new mate and territory. While this was observed in Florida Sandhill Cranes (Nesbitt and Wenner 1987, Nesbitt and Tacha 1997), there was no difference in territory retention for males and females following a mate switch in Sandhill Cranes in Wisconsin (Chapter 2). Widowed or abandoned females were not only able to retain their territory, but attract a male (non-territorial or neighboring territory holder) to pair with her (Chapter 2). Second, Sandhill Cranes form long-term pair bonds (Nesbitt and Tacha 1997, Chapter2). How could you evaluate a long-term mate based only on territory quality which may vary annually? Typically, long-term pair bonds are established through ritualized display and behavior evaluation and reinforced through specific behaviors (e.g., Barnacle Geese *Branta leucopsis*; Black et al. 1996). Additionally, Greenwood (1980) suggested that territory allocation would need to occur prior to mate choice. With cranes, however, sexually immature, subadult cranes often form pair bonds prior to obtaining a territory (Bishop and Blankinship 1982, Chapter 4). While these pair bonds rarely result in an established breeding pair, why would a female pair with a male if her mate choice occurs after a male has established a territory?

It is possible that female Sandhill Cranes are attempting to avoid inbreeding, but the distances travelled between natal and breeding area in our study are not sufficient to avoid interaction with a nest mate (Chapter 4). Additionally, there was no directionality of dispersal from a natal territory for either males or females and this was also observed by Nesbitt et al. (2002). Genetic estimates of inbreeding, using Amplified Fragment Length Polymorphisms (Chapter 6), are minimal for this study area and other sites in the Eastern Population of Sandhill Cranes. Shields (1982) argued that moderate inbreeding can be beneficial as it allows individuals to adapt to local environments while mitigating negative effects from outbreeding with migrants. While the life history characteristics of Sandhill Cranes (e.g., long-lived, small clutch size, high natal philopatry) imply that Sandhill Cranes should be susceptible to inbreeding depression, the results of both ENDD and genetic analysis suggest that currently, these risks are not negatively affecting this population.

Why female Sandhill Cranes move farther than males is unknown. While ENDD was significantly longer for females than it was for males, this may be an artifact of territory availability. Our study area is extremely dense with territorial and non-territorial birds (Su 2003). Birds typically acquire breeding territories by pairing with widowed or divorced birds (Chapter 2) and rarely as an established pair. Additionally, experienced breeding birds are typically chosen as new mates rather than inexperienced, non-territorial birds (Chapter 2). As non-territorial females also moved farther from their natal area than males (Chapter 4), longer ENDD for females observed in this study may be a result of encountering a territory opening and their ability of a nearby non-territorial bird to capitalize on that opening. More intense behavioral observations are needed to test this hypothesis.

While females moved farther from their natal area than males, they were not penalized by starting to breed later than males. My study area has a high density of breeding birds (Su et al. 2004) which could explain why there was no difference in age at first territory acquisition for males or females. Males that remain in a dense breeding area may need to wait for a territory opening compared to females that disperse to less dense areas and can acquire a breeding territory at an earlier age. This could also explain why some non-territorial birds adopted the strategy of remaining philopatric for the first one or two years after reaching independence and then dispersing away outside of the study area (Chapter 4). Each year they are sexually mature, but not breeding, they risk experiencing mortality before successfully reproducing. However, birds that are unable to acquire a territory until well after sexual maturity were not negatively affected in terms of reproductive success. This is contrary to Northern Goshawks (*Accipiter gentilis*) which had lower reproductive success if they began breeding earlier than the mean for the population (Kruger 2005).

How do these results help explain the current range expansion in the Eastern Population of Sandhill Cranes? Estimates of ENDD are short and could explain the slow growth of the EP (Su et al. 2004) from the demographic bottleneck in the early 1900's (Henika 1936, Walkinshaw 1949). If males and females are, on average, only dispersing 5.5 km from their natal area to breed, then diffusion of birds to new areas would be relatively slow, especially given the low reproductive potential of fledging one or two chicks per year and average age of first breeding at nearly five-years-old. This would explain the slow, diffusive growth that has occurred in the

Midwest throughout the 1900’s (Chapter 6). However, long-distance movements by a few individuals would further explain the rapid re-colonization in the northeastern U.S. and Canada that has recently occurred (Melvin 2002, 2008). For example, Sandhill Cranes were found breeding in Ohio (1988) and northwestern Pennsylvania (1994; Meine and Archibald 1996) then spread to Maine (2000), New York (2003), and into New England (Melvin 2002, 2010). Anecdotal observations showed Sandhill Cranes arriving as singles (sex unknown) or as pairs in new areas one to two years before chicks were observed (ebird 2011). While these settlers are likely long-distance dispersers, whether they represent differences in personality and dispersal ability as observed in Great Tits (*Parus major*; Dingemanse et al. 2003) is unknown. It is also possible that flocks of subadult cranes could “disperse” together or get pushed off course during migration to colonize previously unoccupied areas as hypothesized to explain colonization and rapid speciation in Hawaiian Honeycreepers (Fringillidae; Lerner et al. 2011) and Darwin’s finches on the Galapagos (Fringillidae, Grant and Grant 1979).

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Table 5.1. Natal dispersal distance, natal dispersal angle, and age when displaying reproductive behaviors for Sandhill Cranes.

USGS ID	Hatch territory	Hatch Year	Sex	Natal Dispersal Distance (km)	Natal Dispersal Angle (°)	Age when gained first territory[1]	Age when first hatched a chick[1]	Age when first fledged a chick[1]
62922105	Bonnie Oaks	1995	F	28.72	3.5	8	UNK	UNK
62922116	Wianecki	1996	M	2.40	351.1	5	UNK	NA
62922117	Earl Brancel	1996	F	1.73	97.7	4	7	7
62922118	Earl Brancel	1996	M	0.55	70.9	8	9	9
62922121	Gromme	1996	M	2.34	48.3	7	10	NA
62922138	Joyce	1996	F	7.79	351.6	3	3	3
62922139	New Foote	1997	M	0.72	0.6	10	10	NA
62922140	New Foote	1997	F	7.66	22.2	3	3	NA
62922151	Davison	1997	F	5.92	305.3	5	7	8
62922153	Summer	1997	M	2.01	249.7	4	NA	NA
62922155	Gray East	1997	M	6.18	116.4	4	6	6
62922157	Wade	1997	M	4.93	111.3	6	6	6
62922165	Burns II	1997	M	0.72	161.8	5	5	5

Table 5.1 (cont.)

USGS No.	Hatch territory	Hatch Year	Sex	Natal Dispersal Distance (km)	Natal Dispersal Angle (^{o})	Age when gained first territory[1]	Age when first hatched a chick[1]	Age when first fledged a chick[1]
62922173	Davison	1998	M	2.11	200.6	6	6	6
62922175	Johnston	1998	M	1.18	328.2	4	NA	NA
62922188	New Foote	1999	F	4.76	264.8	9	9	11
62922192	Reichhoff	1999	M	4.01	261.3	6	6	6
62922199	Luger	1999	M	1.60	37.5	4	NA	NA
62923402	Gromme	2001	F	3.37	190.6	4	5	5
62923435	Considine North	2000	F	6.07	27.7	4	4	NA
62923452	Lindner	2001	F	3.64	26.4	5	NA	NA
62923487	New Foote	2003	M	0.093	110.8	7	7	NA
62938703	Foote	1993	F	11.65	11.1	3	3	3
62938722	Earl Brancel	1993	F	4.68	331.5	3	3	6
62938743	Burns	1994	M	6.30	188.8	2	3	NA
62938750	Summer X	1995	F	3.00	48.6	4	5	5

Table 5.1 (cont.)

USGS No.	Hatch territory	Hatch Year	Sex	Natal Dispersal Distance (km)	Natal Dispersal Angle (^{o})	Age when gained first territory[1]	Age when first hatched a chick[1]	Age when first fledged a chick[1]
62945206	Anacker II	2004	M	2.15	239.1	4	4	4
62945211	Earl Brancel	2004	M	2.56	179.3	3	3	6
62945222	New Foote	2006	M	0.45	177.1	5	5	NA
62945234	Betty Brancel	2006	F	3.29	141.8	4	4	4
62947251	Davison	2007	F	57.45	243.8	5	5	NA
62947259	Gerbitz East	2007	M	1.87	212.4	3	3	3
62947271	Anacker II	2008	M	2.25	233.9	3	NA	NA
62947286	Burgess West	2008	M	1.41	272.2	3	NA	NA
62947328	Abbott	2009	M	1.51	156.2	3	3	NA

[1] NA = not applicable (i.e. never observed at this stage)

asdffdTable 5.2. Azimuths between natal and breeding location for Sandhill Cranes categorized by sex.

Direction 4a		M	F
	N	4	6
	E	6	2
	S	8	2
	W	3	4

χ^2 = 4.9, df = 3, p = 0.18

Direction 4b		M	F
	N	4	7
	E	5	2
	S	6	2
	W	6	3

χ^2 = 3.9, df = 3, p = 0.27

Direction 8a		M	F
	N	2	5
	NE	2	1
	E	3	1
	SE	5	1
	S	3	1
	SW	4	2
	W	1	1
	NW	1	2

χ^2 = 6.1, df = 7, p = 0.52

Direction 8b		M	F
	N	2	4
	NE	2	3
	E	3	1
	SE	2	1
	S	5	1
	SW	3	1
	W	3	1
	NW	1	2

χ^2 = 6.0, df = 7, p = 0.54

Table 5.3. Azimuths between natal and breeding territory for Sandhill Cranes based on distance from natal to breeding territory.

		0-3 km	3-6 km	6-12 km	>12 km
Direction 4a	N	4	2	3	2
	E	5	2	1	0
	S	6	3	1	0
	W	2	3	1	1

$\chi^2 = 6.7$, df = 9, p = 0.67

		0-3 km	3-6 km	6-12 km	>12 km
Direction 4b	N	4	2	4	2
	E	4	2	1	0
	S	5	2	1	0
	W	4	4	0	1

$\chi^2 = 8.4$, df = 9, p = 0.49

		0-3 km	3-6 km	6-12 km	>12 km
Direction 8a	N	2	1	3	1
	NE	2	1	0	0
	E	2	1	1	0
	SE	5	1	0	0
	S	2	1	1	0
	SW	3	2	0	1
	W	0	2	0	0
	NW	1	1	1	0

$\chi^2 = 17.7$, df = 21, p = 0.67

		0-3 km	3-6 km	6-12 km	>12 km
Direction 8b	N	2	0	3	1
	NE	2	2	1	0
	E	3	1	0	0
	SE	1	1	1	0
	S	4	1	1	0
	SW	3	0	0	1
	W	1	3	0	0
	NW	1	2	0	0

$\chi^2 = 22.8$, df = 21, p = 0.36

Table 5.4. Azimuths between natal and breeding location for Sandhill Cranes categorized by age at first territory acquisition.

		2-3 yrs	4-5 yrs	>5 yrs
Direction 4a	N	2	4	4
	E	2	4	2
	S	3	4	3
	W	3	4	0

$\chi^2 = 3.8$, df = 6, p = 0.70

		2-3 yrs	4-5 yrs	>5 yrs
Direction 4b	N	4	5	4
	E	0	3	2
	S	4	3	3
	W	2	5	0

$\chi^2 = 6.2$, df = 6, p = 0.40

		2-3 yrs	4-5 yrs	>5 yrs
Direction 8a	N	2	3	2
	NE	0	1	2
	E	0	2	2
	SE	2	4	0
	S	2	1	1
	SW	1	3	2
	W	1	1	0
	NW	2	1	0

$\chi^2 = 11.9$, df = 14, p = 0.61

		2-3 yrs	4-5 yrs	>5 yrs
Direction 8b	N	3	1	2
	NE	0	4	1
	E	0	1	3
	SE	1	2	0
	S	2	3	1
	SW	2	2	0
	W	1	1	2
	NW	1	2	0

$\chi^2 = 15.7$, df = 14, p = 0.33

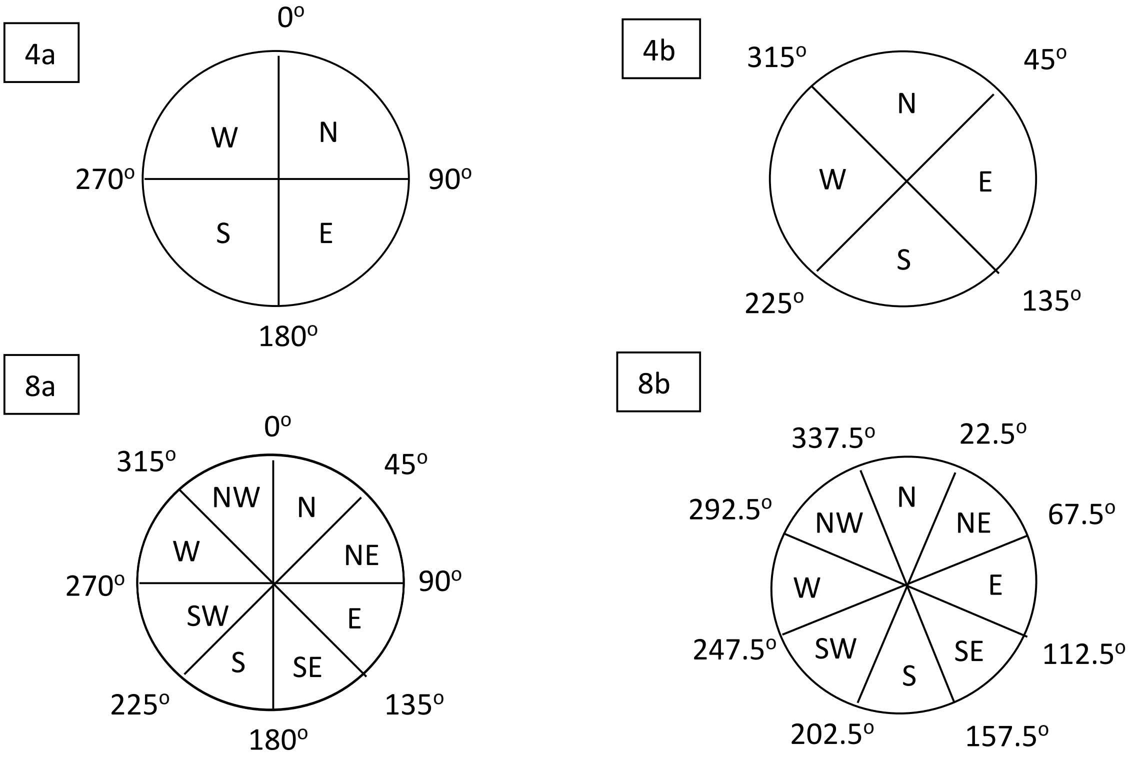

Figure 5.1. Four methods used to categorize the angle of dispersal (North, Northeast, East, Southeast, South, Southwest, West, and Northwest) from natal area to first breeding area.

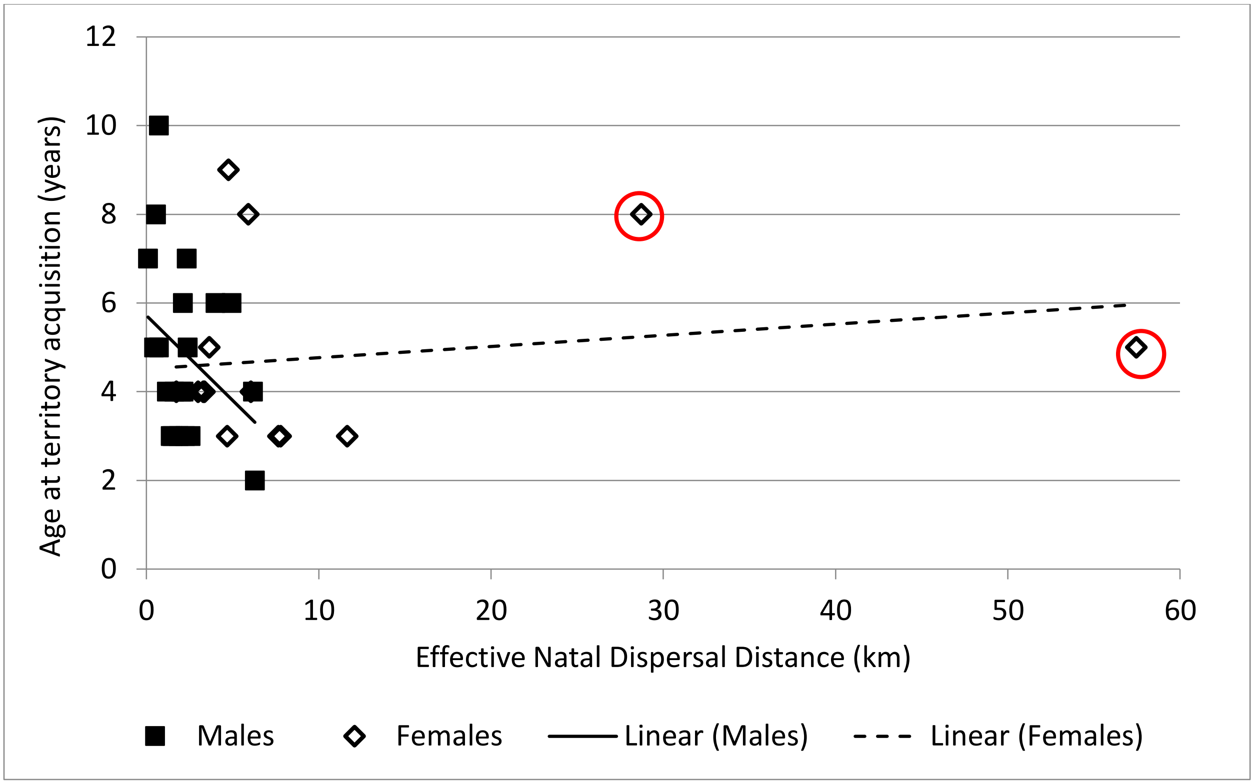

Figure 5.2. Effect of sex and effective natal dispersal distance on age when a Sandhill Crane first acquired a breeding territory. Dispersive females are circled in red.

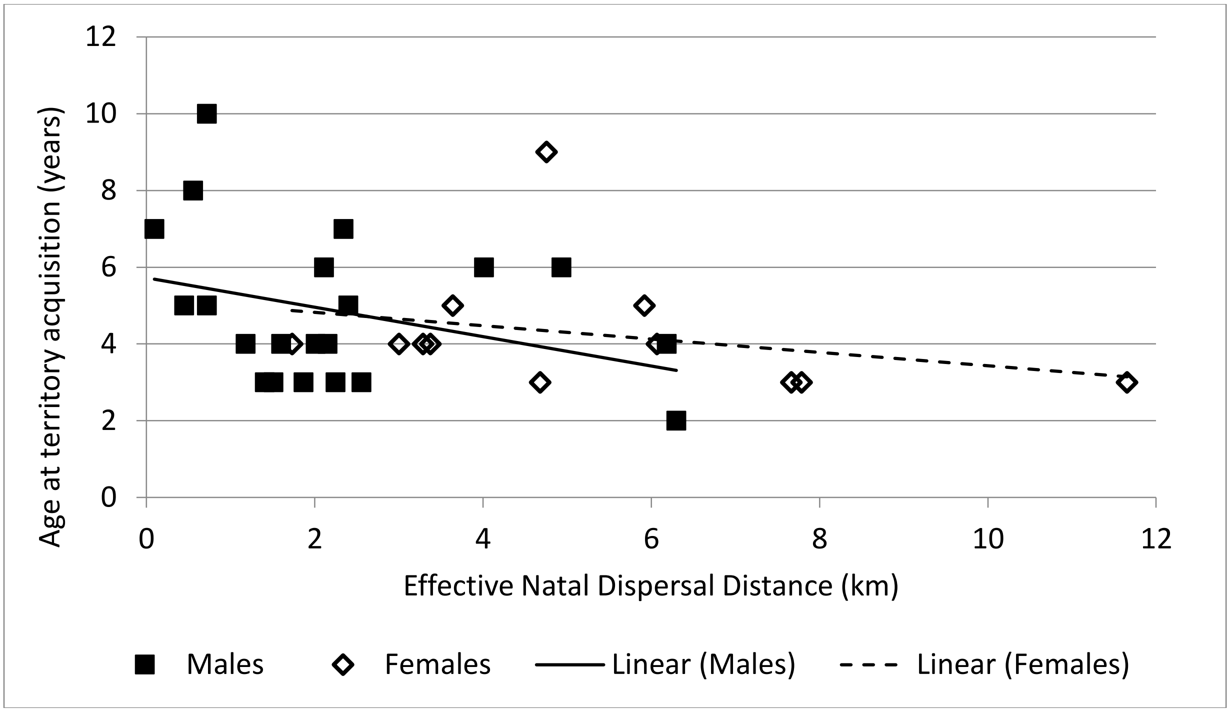

Figure 5.3. Effect of sex and effective natal dispersal distance on age when a Sandhill Crane first acquired a breeding territory after influential females were removed.

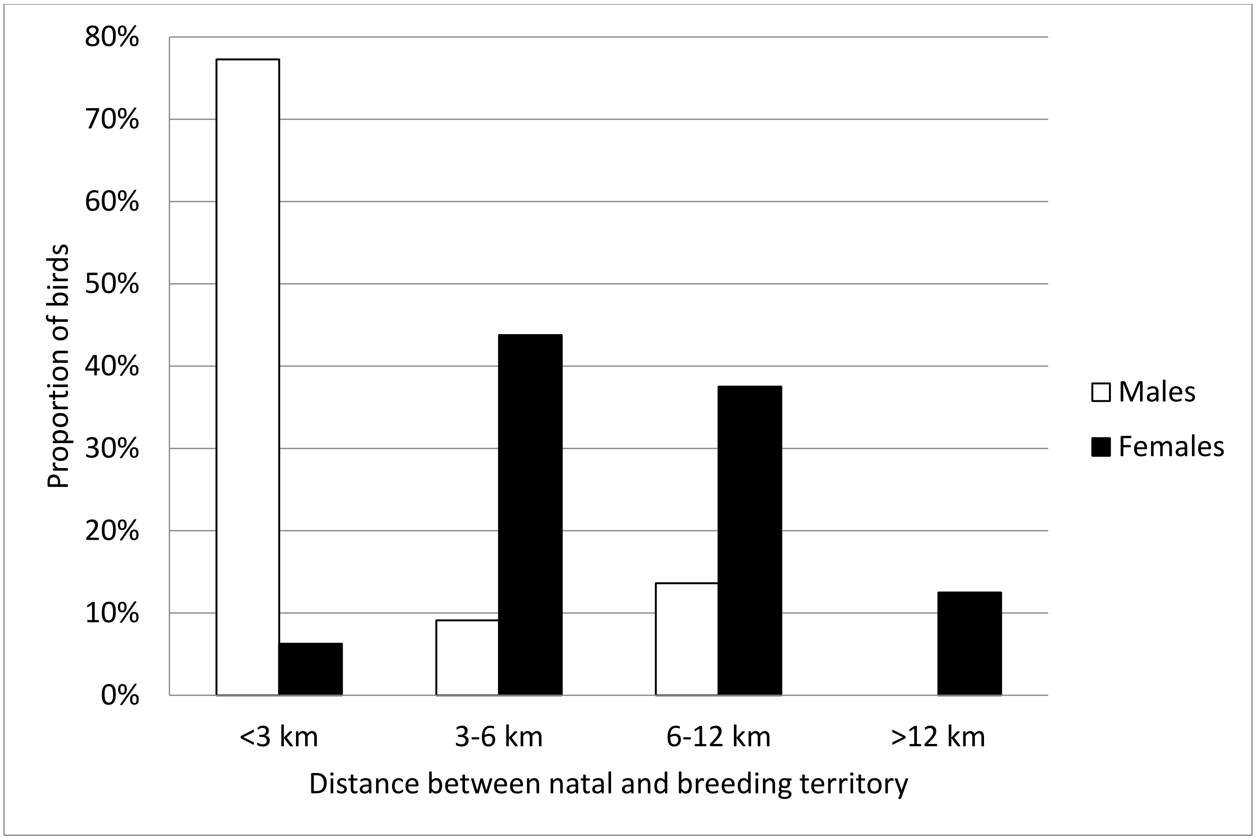

Figure 5.4. Proportions of male and female Sandhill Cranes observed on breeding territories at varying distances from their natal area.

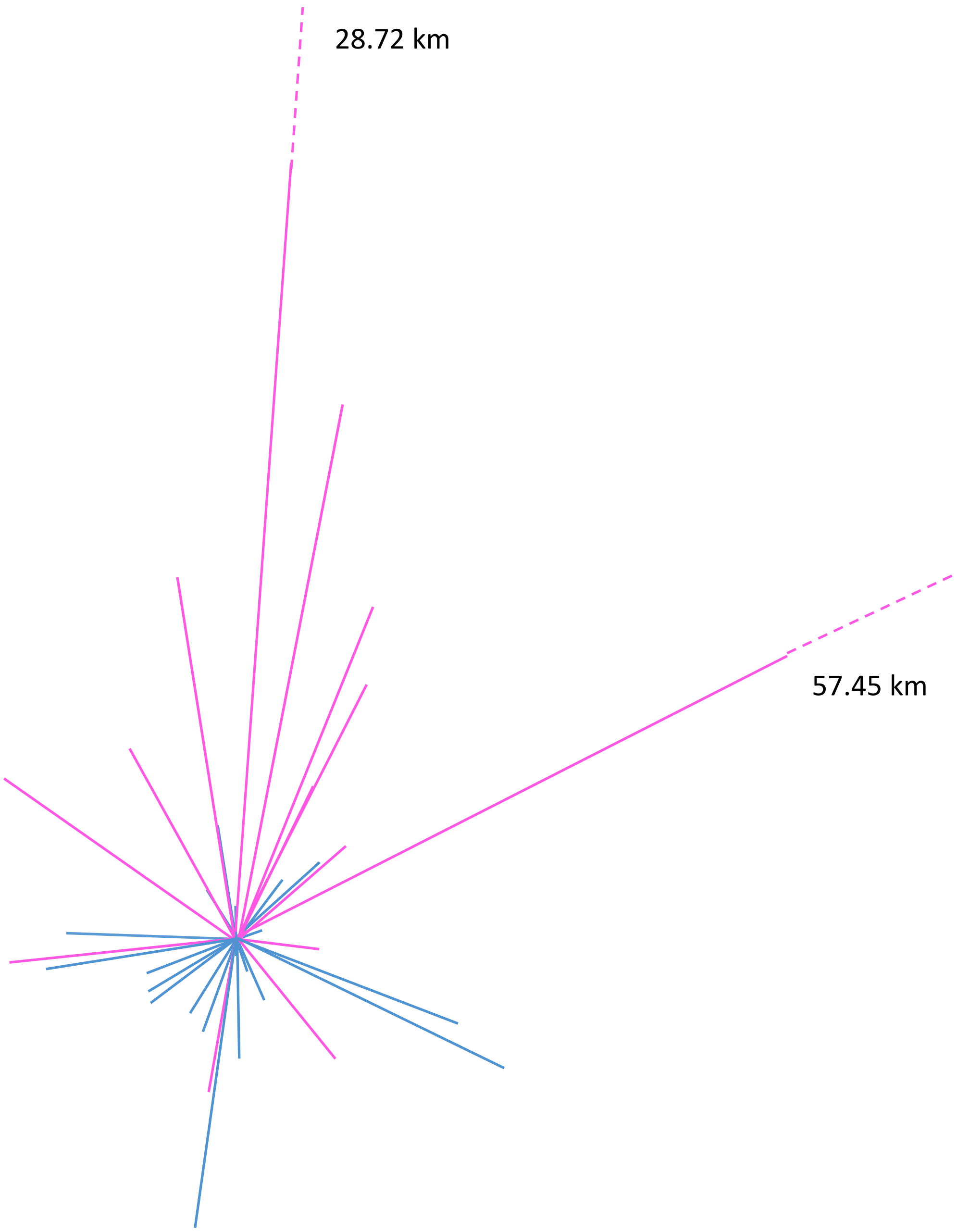

Figure 5.5. Natal dispersal distance and angle of dispersion from natal territory (centered) for birds listed in Table 5.1. Blue lines represent males and pink lines represent females.

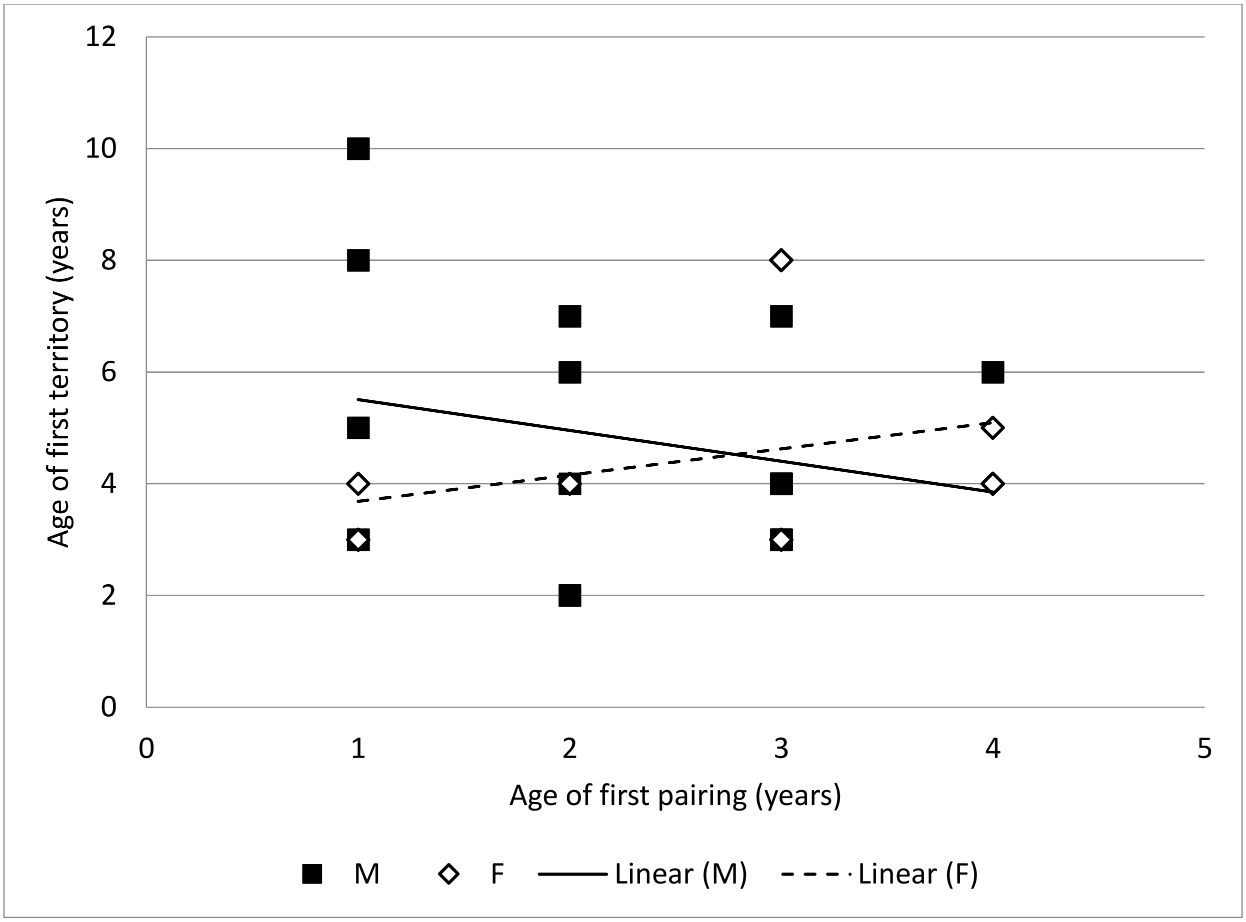

Figure 5.6. Effect of sex and age of first pairing on age of first territory acquisition by Sandhill Cranes.

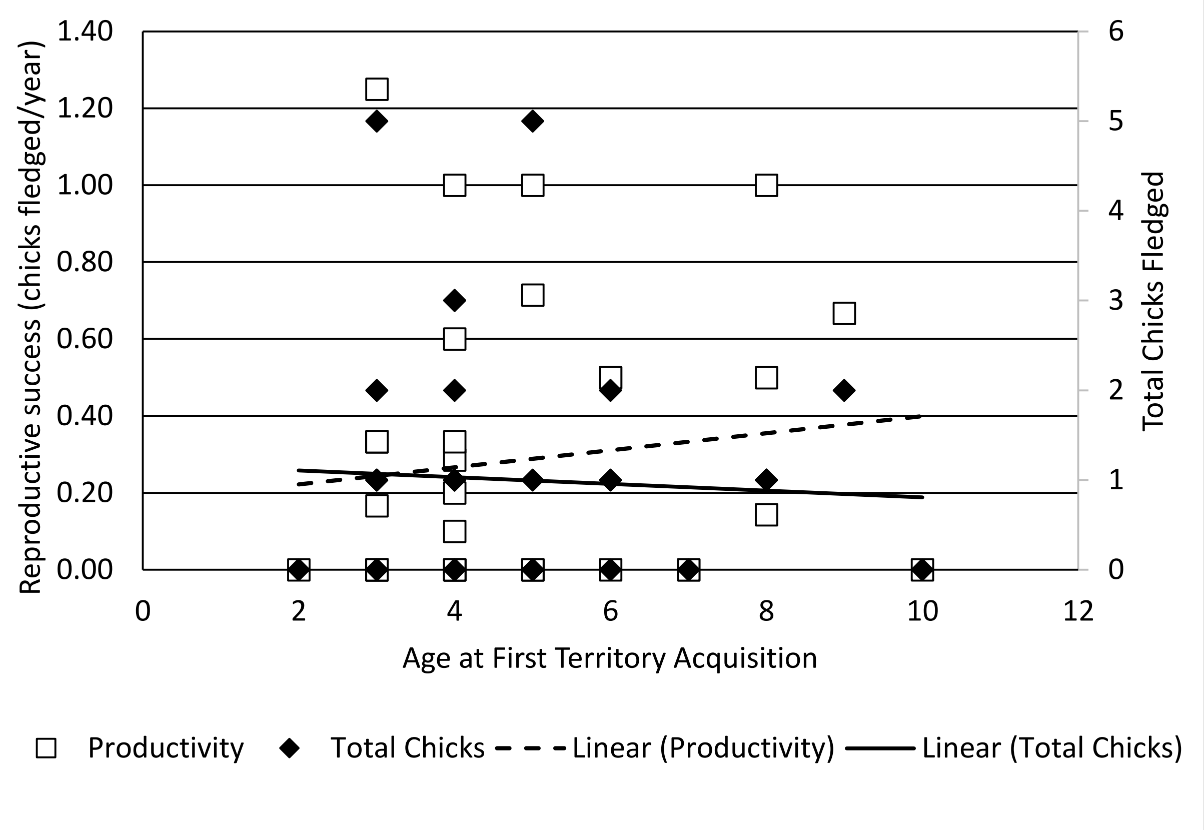

Figure 5.7. Effect of age at first territory acquisition on average annual reproductive success and total number chicks fledged for Sandhill Cranes.

Chapter 6

POPULATION GENETIC STRUCTURE IN THE EASTERN POPULATION OF SANDHILL CRANES

ABSTRACT

The Eastern Population (EP) of Sandhill Cranes (*Grus canadensis*) suffered a population bottleneck in the early 1900's and was reduced to fewer than 50 breeding pairs in Wisconsin, Michigan, and Minnesota. This population has recovered and is now estimated at >60,000 birds and has re-colonized other states in the Midwest (Illinois, Iowa, Indiana, Ohio, Ontario) and northeast (Pennsylvania, New York, Maine, Massachusetts, Vermont). I used Amplified Fragment Length Polymorphisms to test 251 Sandhill Cranes from 14 samples sites (six remnant and eight re-colonized) in the EP for population genetic structure. Significant overall Fst and pairwise Fst among all sample sites suggest there is population genetic structure within the EP. There was significant isolation-by-distance (matrix correlation = 0.48, p = 0.007) among sample sites, however, genetic and geographic distance did not correlate for all sites. There was no difference in estimated heterozygosity or private alleles per number of samples between re-colonized and remnant sites. Using 1,000 replicate runs, GENELAND found 11 genetic clusters among 14 sites. Nine clusters were composed of individuals from re-colonized sites and the closest remnant area. Two clusters contained only re-colonized sites. Sherburne in central Minnesota was likely re-colonized by an unsampled remnant area further north. Samples from the northeastern U.S. formed their own cluster and were likely re-colonized from EP birds dispersing east as well as birds from Hudson's Bay dispersing south. Results of these analyses suggest that potential harvest should be minimized on breeding areas to reduce loss of private alleles and risk of another population bottleneck.

INTRODUCTION

When a population suffers a bottleneck through reduction in population size, it can lead to a genetic bottleneck which reduces heterozygosity and allelic richness compared to non-bottlenecked populations (e.g., Bouzat et al. 1998, Nyström, et al. 2006, Whitehouse and Harley 2001). The effects of a genetic bottleneck on population genetic structure are less understood, however, an increase in population differentiation should occur. As population size is reduced and continuous range is fractured, breeding sites become more isolated thereby limiting exchange of individuals (e.g., Segelbacher et al. 2003). Without exchange of individuals, populations are more susceptible to random allele fixation through genetic drift which can increase genetic differentiation among populations over time. For example, samples from Golden-cheeked Warblers (*Setophaga chrysoparia*) collected throughout the continuous range 1890-1915 showed no significant population genetic structure (Athrey et al. 2011). Samples collected in 2005 throughout the fractured extant range showed significant differentiation among sample sites (Lindsay et al. 2008, Athrey et al. 2011). This change in population genetic structure was likely caused by a demographic bottleneck resulting in reduced population size, range, and connectivity among breeding sites due to low habitat availability (Lindsay et al. 2008).

Populations that were once continuous but become heavily fragmented can avoid (Busch et al. 2007) or quickly recover from a bottleneck (Keller et al. 2002) through exchange of individuals among breeding sites (i.e., the “rescue effect”; Brown and Kodric-Brown 1977, Ingvarsson 2001). While the rescue effect is dependent on vagility and philopatry of the species involved, this exchange of individuals would reduce the detection of population genetic structure because increased exchange with other sites should balance allele frequencies and distribute any pre-bottleneck private alleles. For example, populations of Cerulean Warblers (*Setophaga cerulea*, Veit et al. 2005, Deane et al. 2013) and White-backed Woodpeckers (*Dendrocopos leucotos*, Ellegren et al. 1999) did not show significant population genetic structure despite increased fragmentation of their range due to long-term habitat destruction. In these species, lack of population genetic structure development was likely driven by natal dispersal of juveniles among patches (Virkkala et al. 1993, Girvan et al. 2007). Similarly, Brown et al. (2013) found that fires caused major disturbances leading to multiple serial bottlenecks and heavy fragmentation of the range of Mallee Emu-wrens (*Stipiturus mallee*). These serial bottlenecks reduced overall genetic diversity, but also forced individuals to constantly move to re-locate suitable habitat, thereby reducing genetic differentiation among breeding sites (Brown et al. 2013).

For populations that successfully recover from a bottleneck, the presence or absence of population genetic structure following the bottleneck can depend on a species' life history characteristics, length of time the bottleneck persisted, as well as interaction among breeding sites. For example, Hailer et al. (2006) found significant population genetic structure and retained heterozygosity in White-tailed Eagles (*Haliaeetus albicilla*) 25 years post-bottleneck and hypothesized that this resilience of genetic diversity resided in individuals that survived the bottleneck and reproduced during recovery. Significant population genetic structure was also found in a recovered population of Black-capped Vireos (*Vireo atricapilla*) and Barr et al. (2008) suggested that genetic differentiation among sites was a result of strong natal philopatry of both males and females in conjunction with preference for early successional habitat.

As populations recover and grow, they can potentially re-colonize areas with appropriate habitat requirements. After re-colonized populations become established, they can show genetic differentiation and reduced heterozygosity and allelic diversity from source populations because they are often colonized by few individuals from a similar breeding site (i.e., the "founder effect"; see Mayr 1954, Hedrick and Kalinowski 2000). For example, an introduced island population of Desert Bighorn Sheep (*Ovis canadensis mexicana*) showed reduced heterozygosity and strong population genetic differentiation from the mainland source after 25 years of separation (Hedrick et al. 2001).

The Eastern Population (EP) of Sandhill Cranes (*Grus canadensis*) has a well described demographic history in the last century. While pre-1900 population size remains unknown, observations of nests and family groups along with flocks and harvested birds suggested a widely-distributed range across the Midwest U.S. (Figure 6.1); historic population distribution across southern Canada was not well documented. Due to unregulated hunting and wetland conversion for agriculture, the EP went through a population bottleneck in the early 1900's (Walkinshaw 1949). By the 1930's, the breeding population was estimated at approximately 50 breeding pairs in small, isolated populations in Michigan, Minnesota, and Wisconsin (Figure 6.2; Henika 1936, Walkinshaw 1949).

Following the population bottleneck, recovery of the EP was not well documented, however Sandhill Cranes adapted their foraging behaviors to utilize agricultural food sources adjacent to remnant wetlands. Su et al. (2004) showed that range expansion in Wisconsin 1982-2003 was a result of birds diffusing outward from refugia that survived the bottleneck. While growth and recovery in Michigan and Minnesota was not well documented, it can be assumed that range expansion diffused from refugia in a similar manner. Although Sandhill Cranes are capable of flying hundreds of km per day during migration (Melvin and Temple 1982), natal philopatry and site fidelity are strong in this species and can explain the slow spread of the EP. On average, most male and female Sandhill Cranes nested within 10 km of their natal area (Nesbitt et al. 2002, Chapter 5). Some individuals, however, moved up to 50 km from their natal area to nest (Chapter 5). When a bird obtained a breeding territory, it typically remained on or within two km of that breeding territory for the remainder of its life (Chapter 2).

When the U.S. Fish and Wildlife Service began counting EP Sandhill Cranes in fall 1979, there were nearly 15,000 birds. Currently, there are an estimated 40,000-70,000 birds in the EP (Kruse et al. 2012) and the population is still growing. Not only have Sandhill Cranes recovered and spread throughout much of central/southeastern Minnesota, Wisconsin, and Michigan, but birds have re-colonized previously occupied states and are now breeding in Ontario (since the early 1970's), Illinois (since 1979), Indiana (since 1982), Ohio (since 1988), and Iowa (since 1992; Tebbel and Ankney 1982, Mumford and Keller 1984, Meine and Archibald 1996). The population has also spread to the northeast U.S. and New England, now breeding in Pennsylvania (since 1992), Maine (since 2000), New York (since 2003), and Massachusetts and Vermont (since 2007 and 2008; Melvin 2002, 2008). This spread into New England is particularly encouraging as Sandhill Cranes re-colonized a historic portion of their geographic range where they have been absent since the 1700's (Melvin 2002).

The goal of this chapter was to determine if there is currently population genetic structure present in the EP. While previous genetic analyses showed that the EP exhibited low levels of gene flow with the Mid-Continent Population, Rocky Mountain Population (using microsatellite markers; Jones et al. 2005), and Central Valley Population (using amplified fragment length polymorphisms; Chapter 7), there was significant differentiation between the EP and all other tested populations. The EP samples used in the above analyses, however, were adults nesting near Briggsville, Wisconsin. Population genetic structure and genetic differentiation among different breeding locales within the EP itself have never been investigated.

Because of strong natal philopatry exhibited by Sandhill Cranes, I hypothesized genetic differentiation would occur among sampled breeding areas in the EP. Specifically, I hypothesized that gene flow would follow the “isolation-by-distance” or “stepping-stone model” (Wright 1943, Kimura and Weiss 1964) based on diffusive growth and slow geographic spread of Sandhill Cranes as they expanded in Wisconsin (Su et al. 2004) and throughout the rest of the range (Meine and Archibald 1996). If isolation-by-distance was detected, then I expected birds sampled from a single breeding area would be assigned to a single genetic cluster. I also hypothesized that birds from re-colonized breeding areas would be placed in the same genetic cluster as birds from the nearest remnant breeding area.

METHODS

Study sites, capture and banding

I sampled (with assistance from ICF staff and UW undergraduates) flightless Sandhill Crane chicks at multiple locations throughout the EP (sites 1, 2, 3, 5, 6, 8, 9, 11, 12; Figure 6.3, Table 6.1). Flightless chicks were targeted because they were known to have hatched locally and not immigrated from other populations. The status (immigrant or local) of most parents, however, was unknown. Additional samples from flightless chicks (sites 4, 7, 13, 14) and adults (site 10) were collected through collaborative effort with researchers from other institutions (Table 6.1). Sample areas were categorized as either remnant [Sandhill Cranes persisted in the area during the population nadir in the 1930's], or recolonized [Sandhill Cranes were extirpated from the area but then re-established by immigration of birds from remnant areas].

Flightless Sandhill Crane chicks were chased on foot until they hid and could be handled (Hoffman 1985). Once in hand, each chick was processed (including collection of morphological measurements [anterior and posterior nare culmen (mm), diagonal and total tarsus (mm), and weight (g)], banding, and blood drawing) and released back to its parents within 30 minutes of capture. Every attempt was made to release each chick in the vicinity of its parents and the confirmed reunion rate of family groups following capture of flightless chicks banded near Briggsville, Wisconsin (site 3) was 90% (n=176 chicks 1995-2013). This estimate is likely conservative as some territories are not easily observable due to vegetation or topography and some family groups become increasingly reclusive following capture. Therefore, it is possible that a reunion occurred between a chick and its parents, but mortality occurred before the family unit was re-sighted. Capture protocols were conducted under the auspices of the Institutional Animal Care and Use Committee at the International Crane Foundation.

Once in hand, each chick received unique combinations of bands for long-term identification (Dickerson and Hayes 2014). Each chick received one to three short (1-inch, 2.5 cm) colored plastic bands in a unique combination above the tarsal-metatarsal joint of one leg. A tall (3-inch, 7.5 cm) band engraved with a unique three-digit number was placed above the same joint on the opposite leg. The color of the tall band that each chick received was based on geographic sampling area. The color of the tall band overlapped among some sampling locations because there were limited available bright colors with highly contrasting cores for engraving to make observation of engraved numbers easily visible in the field. For example, chicks banded at Waterloo State Recreational Area in southeastern Michigan and Gun Lake Tribal Lands in southwestern Michigan both received white plastic tall bands engraved with black numbers. The tall bands for Waterloo were placed on the right leg and engraved with "0##" while those at Gun Lake were placed on the left leg and engraved with "1##". Additionally, each chick from Waterloo received a red short band as the top band of its three-short band color combination while each chick from Gun Lake received a white short band as the top band of its color combination. These differences in banding scheme increased the probability that the sampling location could be identified if a partial band combination was recorded. Finally, an aluminum U.S. Geological Survey (USGS) band (size 9 rivet) engraved with a unique nine-digit number was placed either on the toes of either leg or in the combination of short bands for permanent identification. See www.bandedcranes.org for a description of each color banding scheme used at each location.

Regular re-sightings of color-banded cranes only occurred near Briggsville, Wisconsin (site 3) because it is the site of a long-term research project on Sandhill Cranes by the International Crane Foundation (Hayes et al. 2003, Su 2003). Re-sightings on other breeding areas, migratory stopover areas, or wintering areas were sporadic and based on reports from the interested parties.

Genetic Analysis

A blood sample was collected from each bird and stored in a lysis buffer solution (Longmire et al. 1991) until DNA was extracted using the Promega Wizard DNA Isolation kit (Promega Corp., Madison, WI, USA). Purified, pelleted DNA was re-hydrated in 10 mM Tris pH 8.0 and heated at 65^{o}C for up to 48 hours to completely solubilize the DNA. Complete solubilization of DNA was verified by electrophoresis on a 1% agarose gel at 25-30 mAmps. I measured DNA concentration on a BioRad SmartSpec Plus spectrophotometer (BioRad Laboratories, Hercules, CA, USA). Each sample was diluted to 50 ng DNA/μl in 10 mM Tris pH 8.0 and diluted samples were electrophoresed to confirm uniformity of dilution. Sex of each bird was determined by results of PCR run on a 1% agarose gel (Duan and Fuerst 2001).

I used amplified fragment length polymorphism (AFLP; Vos et al. 1995) to determine the neutral genetic variation present in each individual and groups of individuals. Generation of AFLP fragments followed modified protocols described in Berres (2003). First, 200 ng of DNA was digested with 20 U *EcoRI* and 5 U *BfaI* at 37^{o}C overnight (minimum of 16 hours) to ensure complete digestion of the DNA, followed by a 20 minute deactivation at 65^{o}C. Eco/Bfa adaptors were then ligated to the digested DNA fragments with T4 DNA ligase at 16^{o}C overnight (minimum 16 hours). Ligated samples were then diluted with 160 μl 10 mM Tris pH 8.0. Ten μl of each diluted ligated sample were pre-selectively amplified in a 50 μl total reaction with primers *EcoRI*+G and *BfaI*+T. Ten μl of each pre-selective PCR product was electrophoresed on 1% agarose gel to determine complete digestion of DNA and sufficient amplification. The remaining 40 μl of each PCR product was diluted with 10 mM Tris pH 8.0 at 1:9 to 1:18 depending on amplification efficiency based on visual scrutiny of the gel. Selective amplification of fragments was performed with two primer combinations, *EcoRI*+GG/*BfaI*+TAT and *EcoRI*+GC/*BfaI*+TCT. PCR products were purified over columns of Sephadex G-75 (Sigma-Aldrich, St. Louis, MO, USA) to remove any salts and unincorporated primers. One μl of cleaned PCR product was mixed with 0.5 μl Geneflo 625 lane standard (CHIMERx, Molecular Biology Products, Milwaukee, WI) and diluted to a final volume of 15 μl with fresh, deionized formamide. Automated electrophoresis was performed on an Applied Biosystems, Inc. 3730 capillary sequencer. Fragments produced using these parameters were typically between 20,000 and 30,000 relative fluorescent intensity (RFI).

Fragments in AFLP fingerprints were visualized using DAx v. 9.0 (Van Mierlo Software Consultancy, The Netherlands). Loci with appropriate baseline resolution (Berres 2003) between 50 and 625 bp were used for analysis. Presence (1) or absence (0) of AFLP fragment traces were evaluated using peak height (based on RFI) and bins were constructed automatically using the DAx program. Bin tolerance in DAx was set at ±1.0 bp. Visual scrutiny of the fluorescent traces was performed to detect and correct trace alignment errors. AFLP loci generated by both data sets were combined for all analyses.

Statistical analyses

An average inbreeding coefficient (Fis; Wright 1951) was estimated for each sampling location in the EP using I4A (Inbreeding for AFLP; Chybicki et al. 2011). I used 10,000 rejection steps and 50,000 rejection steps for Fis calculations as reported by Chybicki et al. (2011). Increasing each of these steps to 100,000 did not change the output (unpublished data). The average Fis for the EP (calculated from the average Fis for each sampling location) was then incorporated into AFLP-SURV 1.0 (Vekemans 2002) to estimate genetic diversity and overall and pairwise Fst among geographic sampling areas (Wright 1951). To minimize bias due to the use of dominant markers, a Bayesian method with non-uniform prior distribution (Zhivotovsky 1999) was used in AFLP-SURV. Birds were grouped based on geographic sampling area. I used 10,000 permutations for Fst calculation and 10,000 bootstrap simulations for genetic distances. AFLP loci with private alleles for each geographic sampling area were determined in Genetic Data Analysis 1.1 (GDA; Lewis and Zaykin 2002). I compared expected heterozygosity and private allele frequency between remnant and recolonized populations using a Mann-Whitney U test (Sokal and Rohlff 2001).

I tested for isolation-by-distance among most sampling locations in the EP by plotting pairwise Fst/(1-pairwise Fst) against the natural log of pairwise linear distances (in km) between the mean center of each sampling location (calculated in ArcMap 10.1; ESRI, Redlands, CA). These adjusted parameters are more appropriate for a two-dimensional stepping stone dispersal model (Slatkin 1993) as expected for the EP of Sandhill Cranes. I conducted a Mantel test (Mantel 1967) using the ade4 package in R 3.0.2 (Dray and Dufour 2007). Significance of the correlation between matrices ($p \leq 0.05$) was evaluated using 10,000 randomizations. I excluded samples collected from eastern Wisconsin, Ohio, and northeastern U.S. from the test for isolation-by-distance because the sample sizes per location were small (Table 6.1) and the area of sampling was broad causing the variance of the average distance between the location of each sample and the mean center for all samples from that geographic location to be greater than other geographic sampling areas (Figure 6.4).

I performed a principal components analysis (PCA) using the adgenet package in R 3.0.2 (Jombart 2008). PCA offers a non-genetic model approach to group individuals based on shared AFLP loci. PCA does not assume Hardy-Weinberg Equilibrium or linkage equilibrium among loci

(Hannelius et al. 2008, Rutledge et al. 2010). Each ellipse represented 95% of the inertia (i.e., squared length of the vector) which in PCA represents the total variance attributed to each corresponding group.

As a comparative to the PCA analysis, a Bayesian clustering analysis, with allele autocorrelation, was performed in GENELAND (Guillot et al. 2005, Guillot and Santos 2010). I used 1,000,000 iterations of the algorithm with 1,000 random replicates with a variable K (1-20). When a spatial model was previously used in GENELAND, birds aligned well with geographic sampling area (Berres and Barzen 2013). I used a non-spatial model to determine if cluster membership was solely the result of analysis of the genetic data.

A bird was assigned to a genetic cluster when that cluster contained the highest probability of population assignment as estimated by an iterative MCMC calculation. While most studies using GENELAND choose the MCMC run with the highest likelihood, this does not include any variation of individual assignment in other replicate runs. To account for this variation, the pairwise cumulative proportion of same-cluster membership for individuals from 1,000 independent MCMC replicate runs was calculated. Relationships among individuals were then visualized by a topology created by applying an agglomerative hierarchical clustering procedure to estimate the unweighted average distance among individuals (UPGMA). These topologies do not depict phylogenetic relationships or population genetic structure, but overall relationships among individuals based on shared membership in a common cluster as determined by GENELAND. The mean posterior probability of cluster membership among individuals was visualized by a heat map. The scale for the map is 0 (always placed in the same cluster; colored red) to 1 (never placed in the same cluster; colored green). Pie charts showing the proportional distribution of each sampling area per cluster were constructed in Microsoft Excel.

RESULTS

A total of 251 birds (246 chicks from 157 family groups and five adults) were sampled from 14 different sample areas in the EP (Table 6.1, Figure 6.3). Proportionally, most of these chicks (48%) and family groups (34%) were sampled near Briggsville, Wisconsin, the site of a long-term research project by the International Crane Foundation. For Briggsville chicks, females dispersed five times longer than males based on linear distance between natal and breeding area (Chapter 5). Both sexes, however, remained philopatric to natal areas. Only two of 14 females (14%) dispersed longer than 20 km between natal and breeding area (Chapter 5). Greater than 75% of males bred within three km from their natal area while less than 10% of females bred within this same distance from their natal area (Chapter 5).

For chicks sampled from other areas in the EP, two females have been confirmed on breeding territories. One female Sandhill Crane banded 9 July 2007 on Sherburne National Wildlife Refuge, Minnesota was observed on 27 March 2012 breeding with an unmarked mate near Elk River, Minnesota, 14.7 km south of her natal territory. This pair fledged one chick in 2012 and two chicks in 2013. The other female banded 21 June 2008 near the Gun Lake Tribal Lands, Michigan was observed with an unmarked mate on 13 July 2013 near Freemont, MI, 102.9 km northwest of her natal territory. This pair fledged one chick in 2014.

Other EP chicks have also been re-sighted near their natal areas. For example, 104, a male banded in Crex Meadows, Wisconsin on 22 June 2007 was re-sighted alone on 22 June 2010 less than 5 km from his natal site. Another example is B2, a male banded near

Pymatuning Lake in northwestern Pennsylvania on 26 June 2011 was observed in April 2013 paired with an unmarked female 7.9 km southeast of his natal area near Erie National Wildlife Refuge, PA. Because these two birds were only three and two-years-old, respectively, it was unlikely they were breeding when re-sighted.

Re-sightings of color-banded Sandhill Cranes have also occurred at multiple migratory staging locations and wintering areas (n = 314; Figure 6.5). Most of these re-sightings (83%) were of birds banded near Briggsville, Wisconsin. Re-sighting locations were spread throughout southern U.S. states east of the Mississippi River with a majority clustered in Florida and Georgia (20%), Jasper-Pulaski State Wildlife Area in northwestern Indiana (28%), and Hiwasee Wildlife Refuge in southeastern Tennessee (39%). Cranes from different sampling locations mixed together at migratory staging locations and wintering areas (Figure 6.5). The most interesting re-sighting was of B2 who was observed in January 2014 in east-central Florida (Figure 6.5), a major wintering area for the rest of the EP. This is the first re-sighting of a banded bird from the northeastern U.S. on wintering grounds.

Population genetic structure in the Eastern Population

I generated 195 and 255 loci using primer pairs *EcoRI*+GG/*BfaI*+TAT and *EcoRI*+GC/*BfaI*+TCT, respectively. Of these, 144 (74%) and 206 (81%) met my scoring criteria and were combined for all further genetic analyses. Of these combined 350 loci, 141 (98%) and 197 (96%) were polymorphic, respectively.

Expected heterozygosity and percent polymorphic loci were highest in birds from eastern Wisconsin and lowest in birds from Ohio (Table 6.2). There was no difference in expected heterozygosity between remnant (0.143±0.010) and re-colonized locations

(0.136+0.010; Mann-Whitney U = 22, p = 0.57). Frequency of private alleles was highest in eastern Wisconsin and the northeastern U.S. and low (less than 0.5 private alleles/sample size) among most other locations (Table 6.2). Three sampling locations (Crex Meadows, Waterloo, and Ohio) held zero private alleles. Similar to heterozygosity, there was no difference in private allele frequency between remnant (0.27+0.18) and re-colonized locations (0.35+0.17; Mann-Whitney U = 13, p = 0.47).

Overall Fst and all pairwise Fst comparisons were significantly different from zero (Table 6.3). Of 36 pairwise Fst comparisons, 91.7% showed moderate or great genetic differentiation. The highest estimated gene flow was observed between Briggsville, Wisconsin and northeastern Illinois followed by Seney, Michigan and southeastern Ontario. The lowest estimated gene flow was between Necedah, Wisconsin and Gun Lake, Michigan. The results of the Mantel test showed significant isolation-by-distance (p = 0.007) with an observed correlation of 0.48 (Figure 6.6). Sampling locations with a longer geographic distance typically showed higher genetic distance compared to sampling locations with a shorter geographic distance. One exception was Necedah, Wisconsin because it showed large genetic distance (0.16) with Briggsville, Wisconsin (80 km away) but small genetic distance (0.05) with Crex Meadows, Wisconsin (247 km away). Each re-colonized area had the smallest genetic distance with its geographically closest remnant area (Table 6.3).

The results of the PCA with all 14 sampling locations showed one big cluster containing all locations (Figure 6.7). It was difficult to determine any fine scale structure that might be present among most sampling locations because the samples were highly clumped. So, I added the third principal component to plot a three-dimensional graph. Combined, the first three eigenvalues explain 58% of the variation observed in the AFLP data. When the samples were grouped based on sampling location, there was a lot of overlap among groups (Figure 6.8). There were observable patterns, however. For example, the birds sampled from Necedah formed a close group, as did the birds from Ohio, and the Northeastern U.S. There was, however, a lot of integration among sample groups.

When I ran a non-spatial model including all 251 birds in GENELAND, there was difficulty with completing the MCMC chain for many replicates because there were too many individuals included to allow the model to converge. With 116 chicks sampled from Briggsville, Wisconsin, I had the potential to reduce the number of samples from this site while still retaining the genetic information in GENELAND. So, I ran the 116 chicks from Briggsville in GENELAND to determine whether there was population genetic structure present at this site alone and if we could use representatives from clusters obtained to represent Briggsville in the run with the other EP chicks. When I ran a non-spatial model of 116 chicks in 52 family groups from Briggsville, Wisconsin, a modal K=10 clusters was estimated from 1,000 GENELAND MCMC replicates (Figure 6.9). A total of 25 representatives were chosen from these 10 clusters to represent Briggsville in the larger GENELAND model. I scaled the number of representatives that were randomly chosen from each cluster based on how many chicks total were present in the cluster and the overall stability of cluster membership among replicate runs, gauged by the size and amount of dark red represented in the heat map (Figure 6.9). For example, in Figure 6.9, the fifth cluster had 21 individuals present, but the cluster was stable among runs with few individuals switching to other clusters. So, only two individuals were randomly chosen from this cluster. The tenth and last cluster had 23 individuals present, but there were more individuals switching among different clusters during the replicate runs (Figure 6.9). So, a proportional amount of representative individuals (23/116 = 0.20*25 = 5 individuals) was randomly chosen from cluster 10. Once all 25 representatives from Briggsville were chosen, I included them with the remaining 135 individuals from the remaining EP sites.

I ran a non-spatial model of 160 individuals three times: once with 83 replicates, once with 197 replicates, and once with 1,000 replicates. During each time, a modal K=11 clusters was estimated. Two different clusters were split depending on which data set was analyzed. For example, cluster 2 remained intact during the runs of 83 and 999 replicates while the run with 197 replicates split cluster 2 into two clusters: one with three Briggsville birds and the bird from Maine while the other included six Briggsville birds, nine Illinois birds, one from Eastern Wisconsin, and one from Gun Lake. Secondly, cluster 8 remained intact during the runs 83 and 197 replicates while the run of 999 replicates split cluster 8 into two clusters: one with two Briggsville birds and eight Eastern Wisconsin birds and the other with four Briggsville birds, three Illinois birds and one Eastern Wisconsin bird.

The heat map in Figure 6.10 shows the variation in cluster membership of 1,000 replicate runs for 160 EP cranes. The heat maps summarizing cluster membership for 83 and 197 replicates are not shown because individual cluster assignment was similar. Overall, cluster membership was fairly stable with few individuals switching among clusters during different runs. The dendrogram shown in Figure 6.11 simplifies cluster membership based on 1,000 replicates. The breakdown for consistent membership (occurred in that cluster at least two out of three times GENELAND was run with 83, 197, or 1,000 replicates) in each cluster is shown in Figure 6.12. I color-coded the pie charts so sampling areas were designated as remnant (blue) or re-colonized (yellow; Figure 6.12). Cluster membership was consistent for 91.3% of all 160 birds across all three replicate groups. These clusters were supported by a three-dimensional PCA plot of the first three principal components with birds assigned to groups based on cluster membership in GENELAND (Figure 6.13).

Clusters formed containing primarily birds from Sherburne (cluster 4), Ontario (cluster 3), Necedah (cluster 7), and Pennsylvania/New York (cluster 10). Other geographic sampling areas (e.g., Briggsville, Illinois, eastern Wisconsin, Crex Meadows, Waterloo, and Gun Lake) were distributed among multiple clusters. Most clusters included a remnant and re-colonized portion and, typically, an area that was re-colonized was included in the same cluster as the nearest remnant area. Only two clusters do not have a remnant portion included: cluster 4 included 10 of 11 birds from Sherburne, Minnesota and cluster 10 included all seven birds from Pennsylvania/New York. The bird from Maine did not cluster with birds from Pennsylvania/ New York (cluster 10), but with birds from Briggsville, Illinois, and eastern Wisconsin (cluster 2).

Birds that shifted among clusters during different replicate runs were distributed among multiple sampling areas including: Waterloo (two birds between clusters 5 and 6), Gun Lake (one bird between clusters 2 and 6), Necedah (one bird between clusters 7 and 11), New York (two birds between clusters 8 and 10), Sherburne (two birds between clusters 4 and 5), Briggsville (three birds between clusters 8 and 11) and eastern Wisconsin (one bird between clusters 8, 9, and 11).

DISCUSSION

I found significant population genetic structure within the EP of Sandhill Cranes. Overall and pairwise Fst comparisons were significant. Although the EP was known to suffer a bottleneck, 11 genetic clusters were found, suggesting that some of the historic lineages persisted through the bottleneck. Typically, sample sites that were geographically near each other showed low genetic distance while geographically distant locations showed moderate to great genetic distance. There was significant correlation between genetic and geographic distances suggesting isolation-by-distance. Re-colonized areas had the smallest genetic distances with the geographically closest remnant area. Although birds from different breeding areas thoroughly mixed on migratory stopover and wintering areas, banded birds from multiple breeding areas showed strong natal philopatry and returned near their breeding area during summer and eventually to breed (Chapter 5). These results are supported by the diffusive growth pattern observed during population recovery in Wisconsin during the 1970's and 1980's (Su et al. 2004).

Relationships among breeding areas in the EP of Sandhill Cranes, however, are also dynamic and complex. Pairwise Fst results among remnant breeding areas did not follow a straightforward isolation-by-distance pattern, helping to explain the overall correlation of 48% between genetic and geographic distance matrices. For example, Necedah, Wisconsin showed higher estimated gene flow with Crex Meadows, Wisconsin (geographically distant) than with Briggsville, Wisconsin (geographically near, Table 6.1, Figure 6.3). Crex Meadows, Wisconsin showed higher estimated gene flow with Waterloo, Michigan (geographically far) than with Seney, Michigan (geographically near, Table 6.1, Figure 6.3). Mixing among geographically distant sampling areas was also supported PCA groups (based on sampling area) and assignment of individuals from 14 sample areas in the EP into 11 different genetic clusters by GENELAND.

What would cause these close genetic relationships among distant geographic areas in the EP? One hypothesis is that current gene flow exists among very distant breeding areas in the EP. There is some support for this hypothesis through examples of long distances movements made by banded cranes. A bird banded in southern Michigan as a flightless chick was observed in central Wisconsin the following year (R. Hoffman, pers. comm.). Similarly, a crane banded in southern Alaska as a flightless chick was observed in central Wisconsin as a one-year-old bird (Boise 1979). Lastly, a banded chick raised at Necedah was observed copulating with a bird at Crex Meadows as a three-year-old bird (D. Fronczak, U.S. Fish and Wildlife Service, pers. comm.). While these examples represent long distance dispersal within the EP as well as between the EP and other populations, these observations appear to be the exception rather than the rule. Sandhill Crane chicks show strong natal philopatry and typically disperse less than 20 km between natal and breeding areas (Nesbitt et al. 2002, Chapter 5).

Since the pre-bottleneck range of the EP was more continuous, another hypothesis could be that there was historically more exchange of individuals among geographically distant breeding sites. Similar to above, for this hypothesis to be supported, Sandhill Cranes in the EP would have regularly dispersed great distances among breeding sites prior to the bottleneck. A change in dispersal behavior could have been a result of the population bottleneck, where philopatric individuals would more readily locate a mate from birds concentrated in small, localized breeding sites. This would provide philopatric birds with increased reproductive fitness relative to dispersive birds and could explain a difference in natal dispersal behavior. Analyses of AFLP loci show more historic relationships among sites compared to faster mutating microsatellite loci (Alacs et al. 2011).

An alternative hypothesis is there was an alteration in mate choice behaviors during the population nadir in the early 1900's. During the population bottleneck, there was unquestionably a reduction in the number of available mates. Mate choice that occurred on migratory staging areas or wintering grounds could result in one bird following its new mate to their breeding area. Mate following is a common occurrence in waterfowl (Anseriformes), where males pair with females on migratory stopover sites and follow females back to her natal area to breed (Anderson et al. 1992). Mate following may also occur in Sandhill Cranes as evidenced by pair formation between different Sandhill Crane subspecies (Lesser [*G. c. canadensis*], Canadian [*G. c. rowani*], Greater [*G. c. tabida*]) during spring migration and on breeding areas (Tacha et al. 1985). Different subspecies are typically stratified based on latitude with Lessers breeding in the high arctic, Canadians in the subarctic, and Greaters in the temperate grasslands (Meine and Archibald 1996, Krapu et al. 2011). However, re-pairing between widowed or divorced breeding Greaters near Briggsville, WI occurred throughout the year, not just during spring migration (Chapter 2). Typically, the new mate was from an adjacent breeding territory or at least a resident in Briggsville (Chapter 2). This suggests that birds are more likely to choose a new mate from a local pool of available known neighbors rather than birds from unknown locations.

A refugee model described by Porter (1999) suggests a fourth hypothesis. When habitat is destroyed, not all individuals from the patch succumb to mortality, but can relocate to remaining habitat patches. The movement of refugees to remnant patches can have significant effects on population genetic structure (Porter 1999). This model may best explain the assignment of individuals to genetic clusters by GENELAND. Birds from all geographic locations, aside from Ohio, were assigned to more than one genetic cluster. This was surprising given strong natal philopatry found in Sandhill Cranes. The presence of multiple clusters found within each geographic location could support a refugee model. Because Sandhill Cranes are long-lived, with long generation times, allelic diversity can remain in surviving individuals, similar to White-tailed Eagles (Hailer et al. 2006). If refugees relocated to remnant areas during the bottleneck and then subsequently reproduced, their genes would survive in these remnant areas. This refugee model could also support the hypotheses above because surviving individuals from destroyed patches could be forced to move long distances to locate a suitable patch and then pair with individuals found within that patch or follow mates they acquired off breeding areas to their remnant patch. Similar movements were observed in Mallee Emu-wrens following fire regimes (Brown et al. 2013). Unfortunately, we cannot know whether dispersal behavior was altered or if social dynamics changed following the bottleneck.

Two clusters only included birds from re-colonized areas: Sherburne, Minnesota and New York and Pennsylvania birds from northeastern U.S. The placement of cranes sampled from Sherburne into its own genetic cluster is surprising given the small genetic distance with the closest geographic remnant area, Crex Meadows, Wisconsin. However, Sherburne is also geographically close to an unsampled remnant area at Crane Meadows NWR near Little Falls, Minnesota (J. Holler, U.S. Fish and Wildlife Service, personal communication; B. Lidell, Minnesota DNR, personal communication). If Crane Meadows served as the source for Sherburne colonizers, this could explain why most birds from Sherburne were assigned to their own cluster.

The reason for the placement of cranes sampled from Pennsylvania and New York into their own cluster is less clear. Sandhill Cranes were historically extirpated from these states (Melvin 2002, 2008) and surrounding states (Walkinshaw 1949, Meine and Archibald 1996) prior to recolonization. If the founders of this recently colonized population came from the EP, then these birds should have been assigned to one of the sampled sources. The birds from Pennsylvania and New York were not placed in the same cluster as the birds from Ohio. The birds sampled from Ohio were all adults, however, so it is possible these adults were migrants from another population. More samples from Ohio and Pennsylvania would help determine relationships between these two breeding sites.

The population in the northeast and New England is newly colonized. Population genetic structure can arise quickly in newly founded populations, but then may erode over time as contact is re-established with source populations (Short and Petren 2011). This has been termed "gene surfing" and occurs when rare alleles present in founders increase in frequency, possibly being fixed by genetic drift, in a newly established population leading to genetic differentiation from the initial source population (Klopfstein et al. 2006, Gracia et al. 2013). For example, in a reintroduced population of Asiatic Wild Ass (*Equus hemionus*), Gueta et al. (2014) found significant population genetic structure and differentiation compared to the source population after only four generations post-introduction.

With all of the above studies, founding events still led to reduced heterozygosity and allele richness compared to source populations (Short and Petren 2011, Gracia et al. 2013, Gueta et al. 2014). The individuals sampled from New York and Pennsylvania, however, were among the highest in expected heterozygosity and frequency of private alleles compared to other EP sample sites. These private alleles could only have originated from an unsampled source which may have originated from within the EP. However, an equally likely possibility exists that another population may have helped found this new population. While the EP was expanding and re-colonizing areas around the Great Lakes, cranes in the eastern portion of the Mid-continent population (MCP) were simultaneously expanding east around James Bay from Ontario into Quebec in the 1970's (Ouellet and Bourget 1975) and continued expansion south and east has occurred into southern Quebec, New Brunswick, and Newfoundland/ Labrador in the 2000's. Data from E-bird and sightings posted to the American Birding Association (Bannon et al. 2000, 2001, 2002, 2003, 2005; McTavish 1999, 2002, 2003, 2006, 2007, 2008; Dalzell 2009, 2010) show an increased frequency of flocks, pairs, and nests into eastern Canada (Figure 6.14) moving in a trajectory towards New England. These birds in the MCP morphologically measure as Canadian subspecies (*G. c. rowani*; Ouellet and Bourget 1975, Krapu et al. 2011) while those in the EP measure as Greater subspecies (*G. c. tabida*; Johnson et al. 2005). While no adult cranes have been morphologically measured, the possibility exists that both Canadian and Greater subspecies migrate through New York and Pennsylvania in the fall (Figure 6.15). These results suggest that possibly both the MCP and EP assisted in re-colonizing this fledgling population. Collection of more samples from throughout the northeastern U.S. and New England as well as Atlantic Provinces in Canada would help determine genetic relationships among these populations.

MANAGEMENT IMPLICATIONS

Understanding genetic relationships among breeding sites in the EP can be useful for management of Sandhill Cranes in the EP. A preliminary regulated harvest of EP Sandhill Cranes began in Kentucky in 2011 followed by Tennessee in 2013. This is the first harvest of Sandhill Cranes east of the Mississippi River following a moratorium on hunting following the signing of the Migratory Bird Treaty Act of 1918. There has also been discussion of opening hunting seasons in other states within the EP range. Before more states within the range of the EP initiate a harvest, a priority information need for the EP was to document the extent of breeding, migration, and wintering ranges of the EP through color-banding birds at multiple breeding sites throughout the population (Case and Sanders 2009, Ad Hoc Eastern Population Sandhill Crane Committee 2010). By uniquely color-banding birds at breeding sites within the EP, managers can re-sight color banded birds to determine movements made among breeding sites and the amount of mixing that occurs on migratory stopover locations and wintering grounds. This can allow managers to determine if certain migratory stopover or wintering sites are disproportionately used by birds from certain breeding areas. For example, Sauvie Island on the border between Washington and Oregon is a wintering location solely utilized by Canadian Sandhill Cranes from the coast of British Columbia (Ivey et al. 2005).

Two main management recommendations can emerge from the results of this study. First, if Sandhill Cranes in the EP are going to be harvested on breeding areas, caution should be undertaken to minimize effects of overharvest on breeding areas. The EP has already suffered a population bottleneck that has likely affected the genetic structure of this population. Because of low recruitment, high natal philopatry, and high site fidelity of breeding birds, the EP is susceptible to another bottleneck if not properly managed. Sandhill Cranes exhibit strong natal philopatry and with most chicks returning to natal areas to breed, overharvest at any breeding area could affect local population genetic structure. Hunting should be minimized or avoided near Sherburne Minnesota, Necedah Wisconsin, and southeastern Ontario. These populations have unique population genetic structure that may be lost if overharvest occurs in these areas. Caution should also be taken with populations in Eastern Wisconsin. This area has a high expected heterozygosity and number of private alleles which can be used a proxy for overall genetic diversity. Guidelines should be put in place to minimize loss of this unique genetic diversity.

Harvest should definitely be avoided in the Northeastern U.S. This is a small, but growing population, and there is so little information currently known about this population. What is the current number of breeding pairs? What is the fledgling rate? What is their migratory timing and route? Do birds in Pennsylvania and New York interact with populations in New England and how do these birds relate to wintering populations on the east coast? More information is needed throughout this area to fully understand the demography of this population and how harvest on wintering areas may impact its current and future growth and sustainability.

If hunting in the EP is going to increase, a second recommendation would be to focus harvest on migratory stopover and wintering areas. Based on re-sightings of color-banded cranes, a lot of mixing from different breeding sites occurs on migratory stopover areas and throughout the winter range. By focusing harvest on these congregation areas, there is reduced risk of overharvest from any one breeding site. Caution needs to be extended with this recommendation because a majority of re-sightings were from one breeding site near Briggsville, Wisconsin. At local sites with small overwintering populations, there may be an unequal distribution of birds from any one breeding areas. More observations and research needs to occur on migratory stopover and wintering sites to determine if there is an overabundance from any one breeding site utilizing any one wintering site. Finally, continued banding and monitoring needs to occur throughout the EP to determine natal dispersal and gene flow occurring among breeding sites.

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Table 6.1. Sample locations and numbers for the Eastern Population of Sandhill Cranes. Location number corresponds with the numbered location in Figure 6.3.

Location Number	Location Name	Sample Dates	No. chicks sampled	No. families sampled	Remnant or Re-colonized?	Source
1	Sherburne National Wildlife Refuge, central MN	7/9 - 7/12/2007	11	10	Re-colonized	This study
2	Crex Meadows, Fish Lake, Amsterdam Slough State Wildlife Areas, northwestern WI	7/13 - 7/16/2007	8	8	Remnant	This study
3	Briggsville, central WI	1996 – 2011[a]	116	54	Remnant	Hayes et al. 2003, This study
4	Necedah National Wildlife Refuge, central WI	2000	23	16	Remnant	Urbanek et al. 2005
5	Waterloo State Recreation Area, southeast MI	6/16 - 6/18/2008	14	10	Remnant	This study
6	Gun Lake Tribal Lands, southwest MI	6/20 - 6/23/2008	10	7	Re-colonized	This study
7	Northeastern IL	2009 – 2010	25	19	Re-colonized	Fox 2011
8	Seney National Wildlife Refuge, Upper Peninsula MI	7/5 – 7/8/2009, 7/12 – 7/15/2010	7	6	Remnant	This study

Table 6.1 (cont.)

Location Number	Location Name	Sample Dates	No. chicks sampled	No. families sampled	Remnant or Re-colonized?	Source
9	Thessalon and surrounding areas, southeastern ON	7/5 – 7/8/2009	13	10	Re-colonized	This study
10	North-central OH	7/14 – 8/10/2010	5 (adults)	UNK	Re-colonized	Sherman 2011
11	Central NY (Montezuma NWR and surrounding areas)	6/16 – 6/20/2011	2	2	Re-colonized	This study
12	Northern PA (Pymatuning Lake and Dushore)	6/21 – 6/27/2011	5	3	Re-colonized	This study
13	Central ME	July 2007	1	1	Re-colonized	L. Brennan, Brandywine Zoo, DE
14	Eastern WI	2010-2011	11	11	Remnant	P. Fisher, The Feather (rehabilitator)

[a] Samples from flightless chicks banded as part of a long-term research project on Sandhill Cranes by the International Crane Foundation.

[b] Samples from chicks hatched from eggs collected from Necedah NWR that were trained to follow ultralight aircraft or released with wild flocks of Sandhill Cranes.

Table 6.2. Genetic diversity estimates for Sandhill Cranes in the Eastern Population.

Sampling Location	Status	N[a]	n[b]	PL[c]	%PL	PA[d]	He[e]	S.E.	Avg. Fis (95% CI)	Avg. loci/ind[f]	PL/N	PA/N
Sherburne NWR, MN	Re-colonized	11	350	172	49.1	1	0.119	0.008	0.016 (0.0002, 0.080)	116±1.5	15.6	0.09
Crex Meadows SWA, WI	Remnant	8	350	176	50.3	0	0.139	0.009	0.021 (0.0002, 0.104)	120±2.0	22.0	0.00
Briggsville, WI	Remnant	116	350	152	43.4	21	0.140	0.008	0.210 (0.137, 0.292)	107±1.2	1.3	0.18
Necedah NWR, WI	Remnant	23	350	166	47.4	3	0.123	0.008	0.011 (0.0002, 0.54)	116±1.7	7.2	0.13
Waterloo SWA, MI	Remnant	14	350	170	48.6	0	0.140	0.009	0.097 (0.014, 0.260)	116±2.6	12.1	0.00
Gun Lake, MI	Re-colonized	10	350	167	47.7	2	0.128	0.008	0.019 (0.0002, 0.091)	107±2.3	16.7	0.20
Northeastern IL	Re-colonized	25	350	177	50.6	11	0.153	0.009	0.111 (0.026, 0.238)	107±2.5	7.1	0.44
Seney NWR, MI	Remnant	7	350	155	44.3	1	0.127	0.009	0.030 (0.0003, 0.152)	105±2.5	22.1	0.14
Southeastern ON	Re-colonized	13	350	152	43.4	3	0.128	0.008	0.022 (0.0003, 0.098)	107±2.4	11.7	0.23
Northern OH	Re-colonized	5	350	132	37.7	0	0.112	0.008	0.034 (0.0003, 0.152)	98±1.4	26.4	0.00
Eastern WI	Remnant	11	350	226	64.6	13	0.190	0.010	0.118 (0.019, 0.296)	125±3.5	20.5	1.18

Table 6.2 (cont.)

Northeast US	Re-colonized	8	350	199	56.9	9	0.174	0.009	0.106 (0.013, 0.300)	118±4.3	18.1	1.13

[a] number of individuals analyzed

[b] number of loci analyzed

[c] polymorphic loci

[d] private alleles (0 = absence of a fragment, 1 = presence of a fragment)

[e] Nei's gene diversity, or expected heterozygosity

[f] average number of loci (±SD) present in each individual

Table 6.3. Pairwise Fst[a] (± 95% CI) [above diagonal] and linear distance (km) among mean centers of sampling locations [below diagonal] in the Eastern Population of Sandhill Cranes. Location corresponds with the numbered location in Figure 6.3 and Table 6.1.

Location	1	2	3	4	5	6	7	8	9	Overall Fst: 0.104 (0.091, 0.107)
1	-	0.052* (0.017, 0.062)	0.151** (0.139, 0.166)	0.124* (0.100, 0.134)	0.091* (0.065, 0.115)	0.153** (0.120, 0.180)	0.127* (0.106, 0.158)	0.105* (0.070, 0.133)	0.138* (0.108, 0.158)	
2	87.73	-	0.116* (0.101, 0.136)	0.050* (0.022, 0.057)	0.062* (0.034, 0.096)	0.112* (0.075, 0.137)	0.111* (0.088, 0.148)	0.107* (0.066, 0.134)	0.112* (0.080, 0.138)	
3	372.36	330.09	-	0.111* (0.103, 0.119)	0.101* (0.091, 0.113)	0.099* (0.086, 0.114)	0.029 (0.022, 0.037)	0.109* (0.093, 0.132)	0.114* (0.103, 0.127)	
4	291.9	246.85	83.25	-	0.136* (0.117, 0.154)	0.182** (0.156, 0.207)	0.125* (0.110, 0.148)	0.112* (0.082, 0.132)	0.120* (0.097, 0.132)	
5	799.95	741.73	436.19	510.04	-	0.045 (0.019, 0.061)	0.070* (0.052, 0.095)	0.088* (0.059, 0.119)	0.096* (0.073, 0.116)	
6	690.39	635.2	323.93	399.3	112.89	-	0.079* (0.058, 0.107)	0.130* (0.089, 0.158)	0.122* (0.090, 0.142)	
7	543.26	506.51	176.99	260.01	308.6	200.96	-	0.089* (0.065, 0.129)	0.100* (0.081, 0.125)	
8	547.22	461.7	375.93	371.91	463.98	408.81	453.37	-	0.037 (0.001, 0.055)	
9	747.7	662.46	534.17	550.16	444.46	438.94	558.16	200.81	-	

Table 6.3 (cont.)

[a] 0 to 0.05 indicates little genetic differentiation, *0.05 to 0.15 indicates moderate genetic differentiation, **0.15 to 0.25 indicates great genetic differentiation, ***0.25 indicate very great genetic differentiation (Wright 1978).

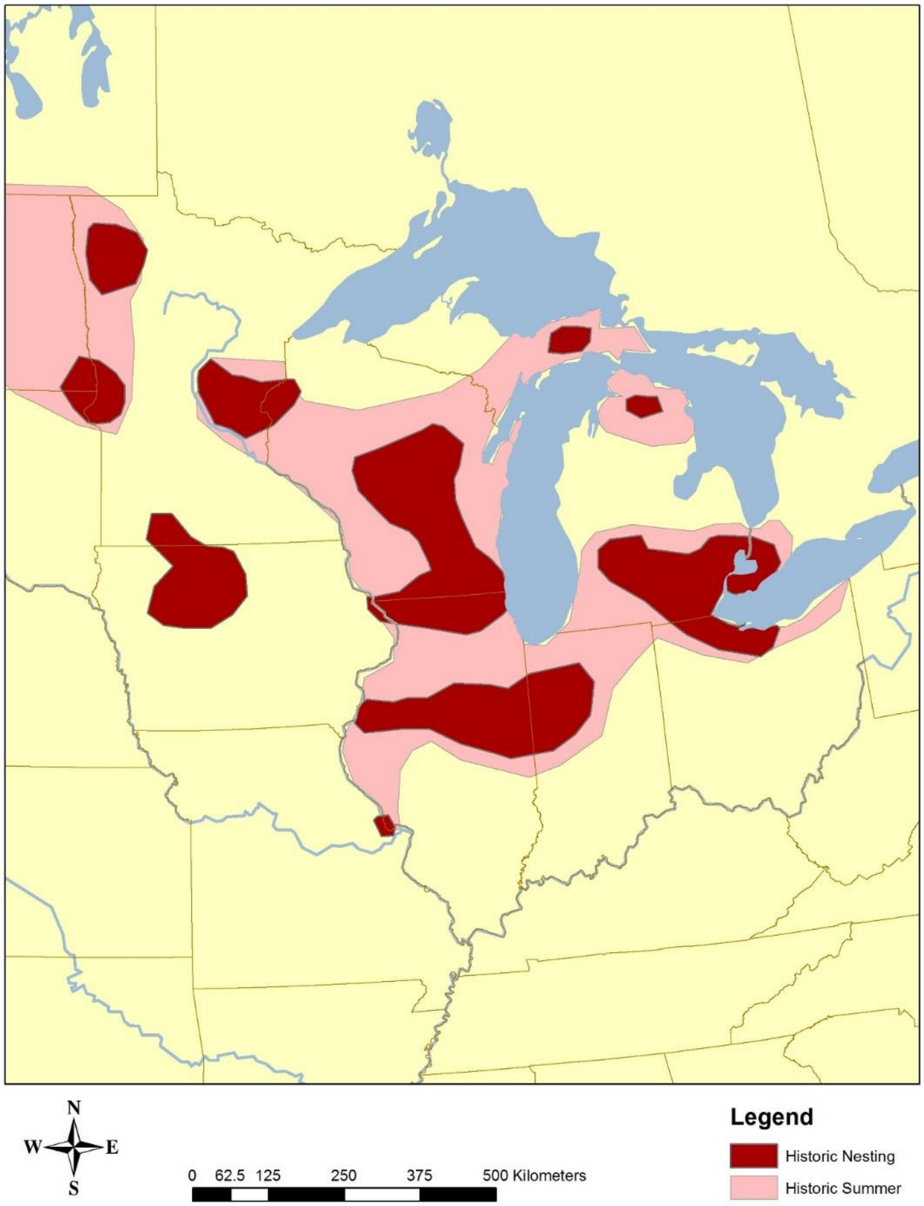


Figure 6.1. Pre-1930's estimated geographic breeding range of Sandhill Cranes in the Eastern Population. Nesting range drawn from sites of nests or families with chicks. Summer range drawn from birds observed in these areas during summer months, but nesting observations did not occur. Re-drawn from data published in Anderson 1907; Barrows 1912; Bent 1926; Bogardus 1878; Cory 1909; Ford 1956; Henika 1936; Kennicott 1854; Walkinshaw 1949, 1960; Widmann 1907.

Figure 6.2. Estimated geographic distribution of Sandhill Cranes in the Eastern Population during the population nadir in the 1930's. Redrawn from data published in Henika (1936) and Walkinshaw (1949).

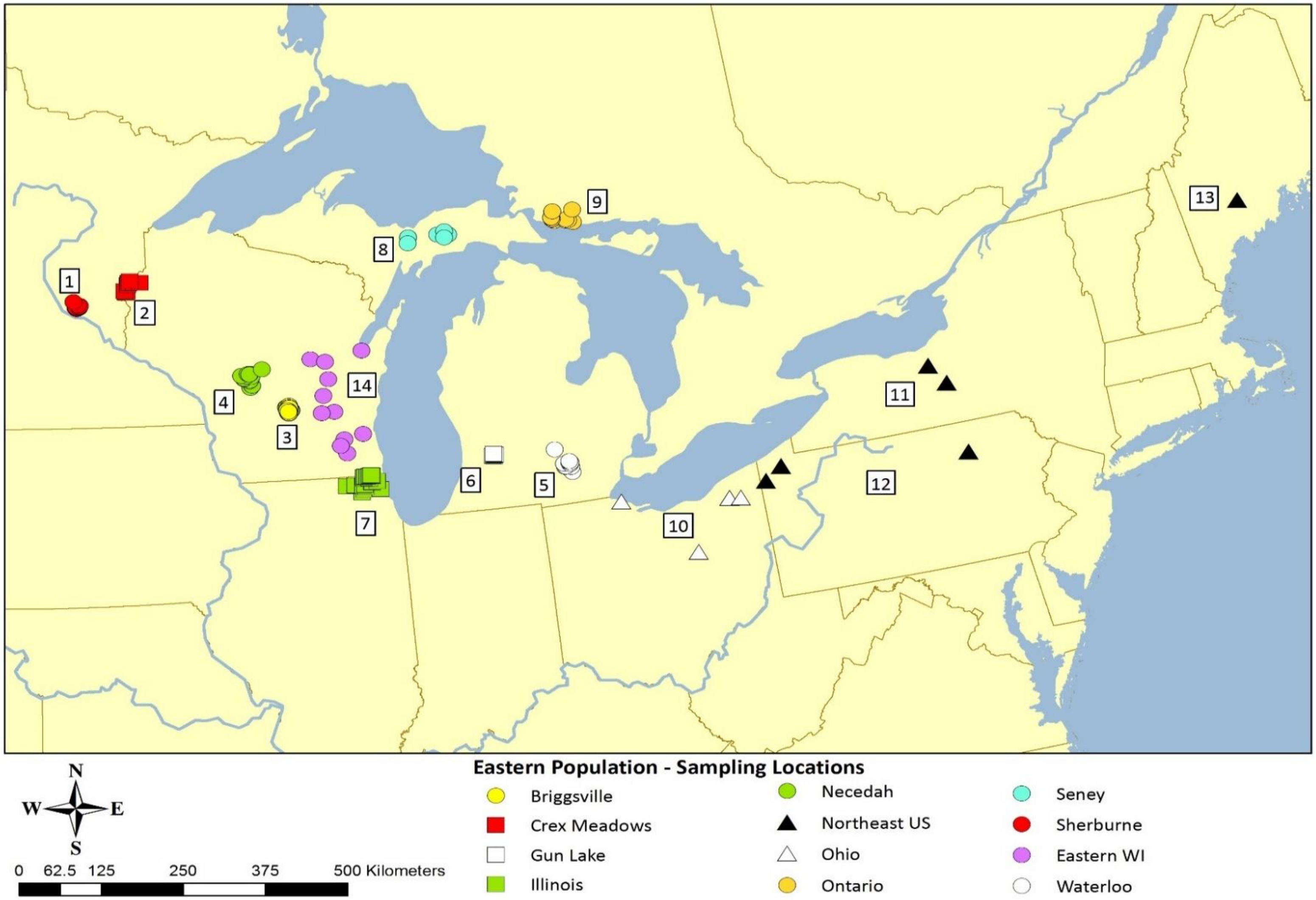

1
2
3
4
5
6
7
8
9
10
11
12
13
14
N
W
E
S
0
62.5
125
250
375
500 Kilometers
Eastern Population - Sampling Locations
Briggsville
Crex Meadows
Gun Lake
Illinois
Necedah
Northeast US
Ohio
Ontario
Seney
Sherburne
Eastern WI
Waterloo

Figure 6.3. Banding and sampling locations of Sandhill Cranes in the Eastern Population. Number at each sampling location corresponds with the numbered location in Table 6.1.

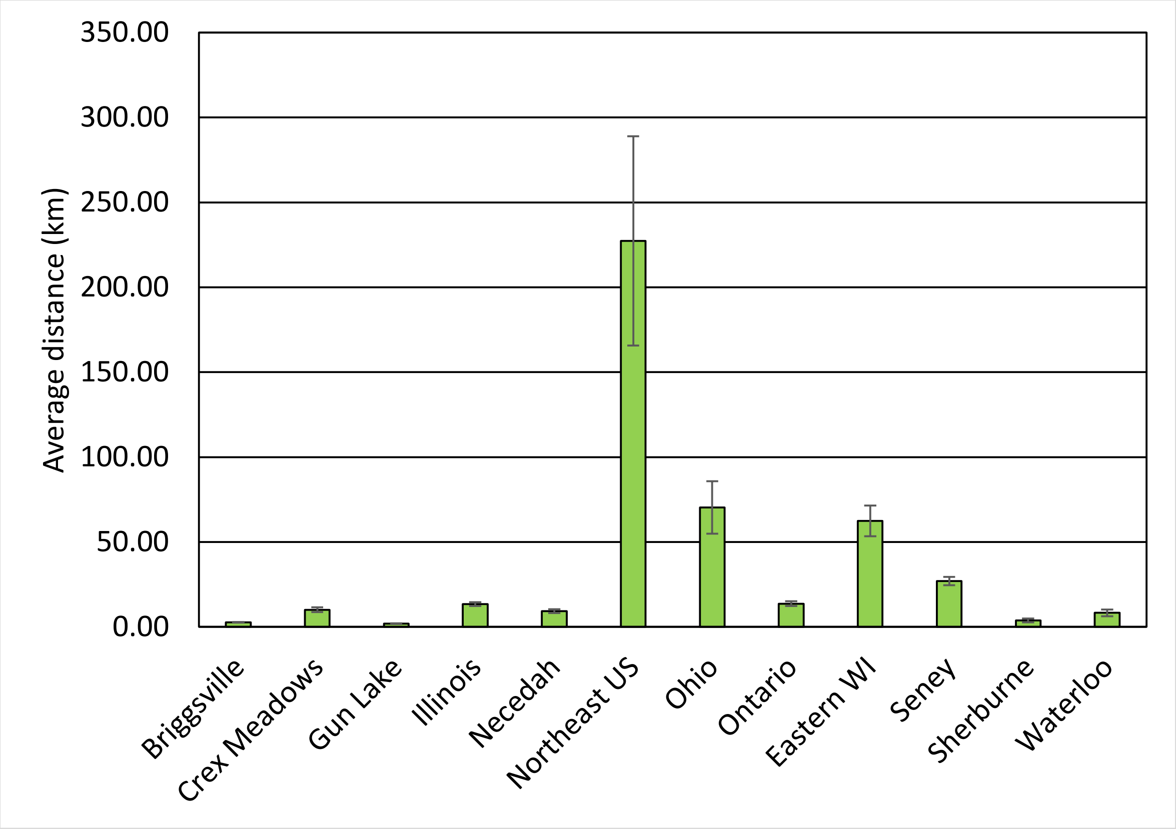


Figure 6.4. Average distance (±SE, km) between the mean center of a sampling area and each capture location in that same sampling area.

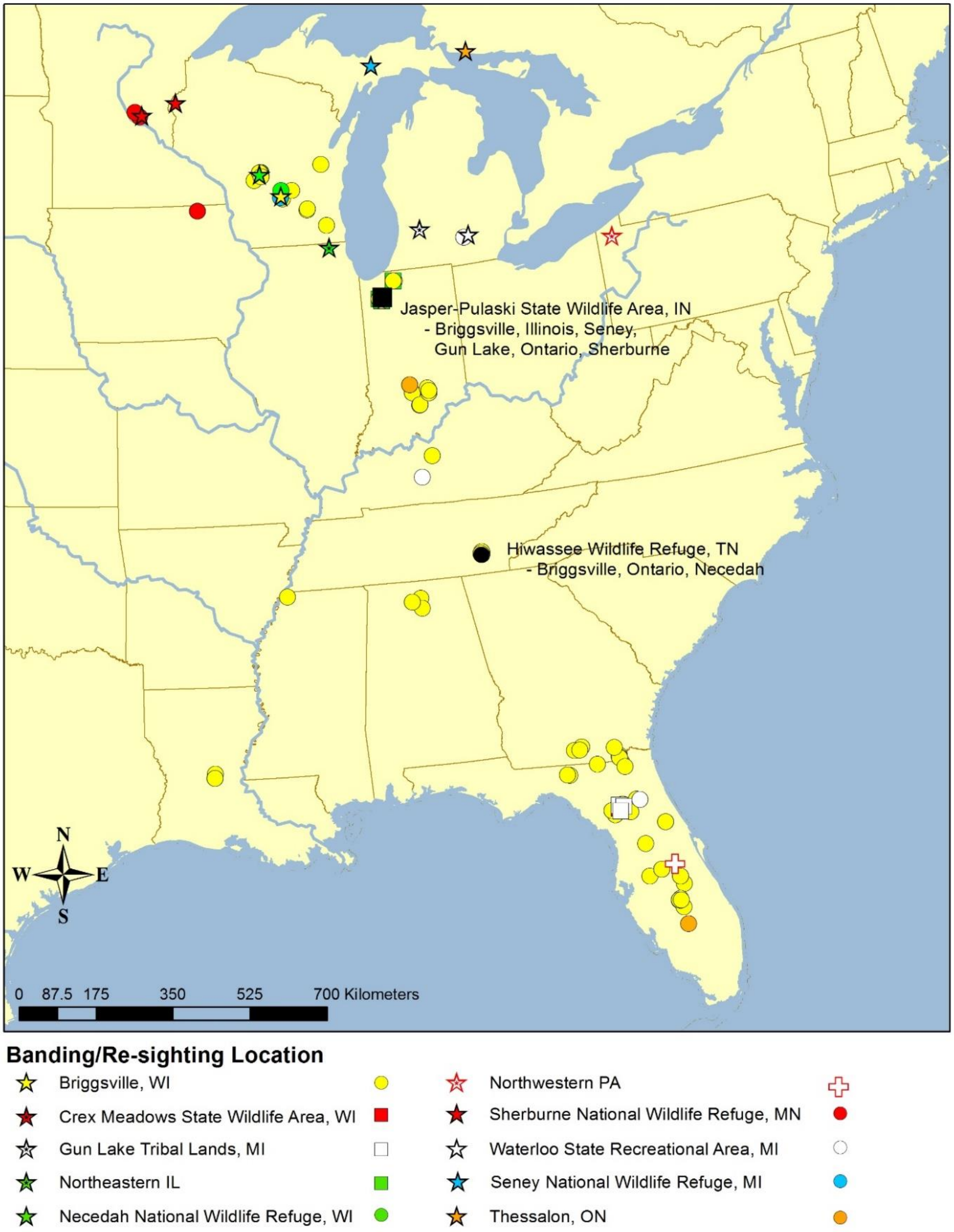


Figure 6.5. Re-sightings of color-banded Sandhill Cranes at migratory stopovers (fall and spring) and wintering areas in the Eastern Population.

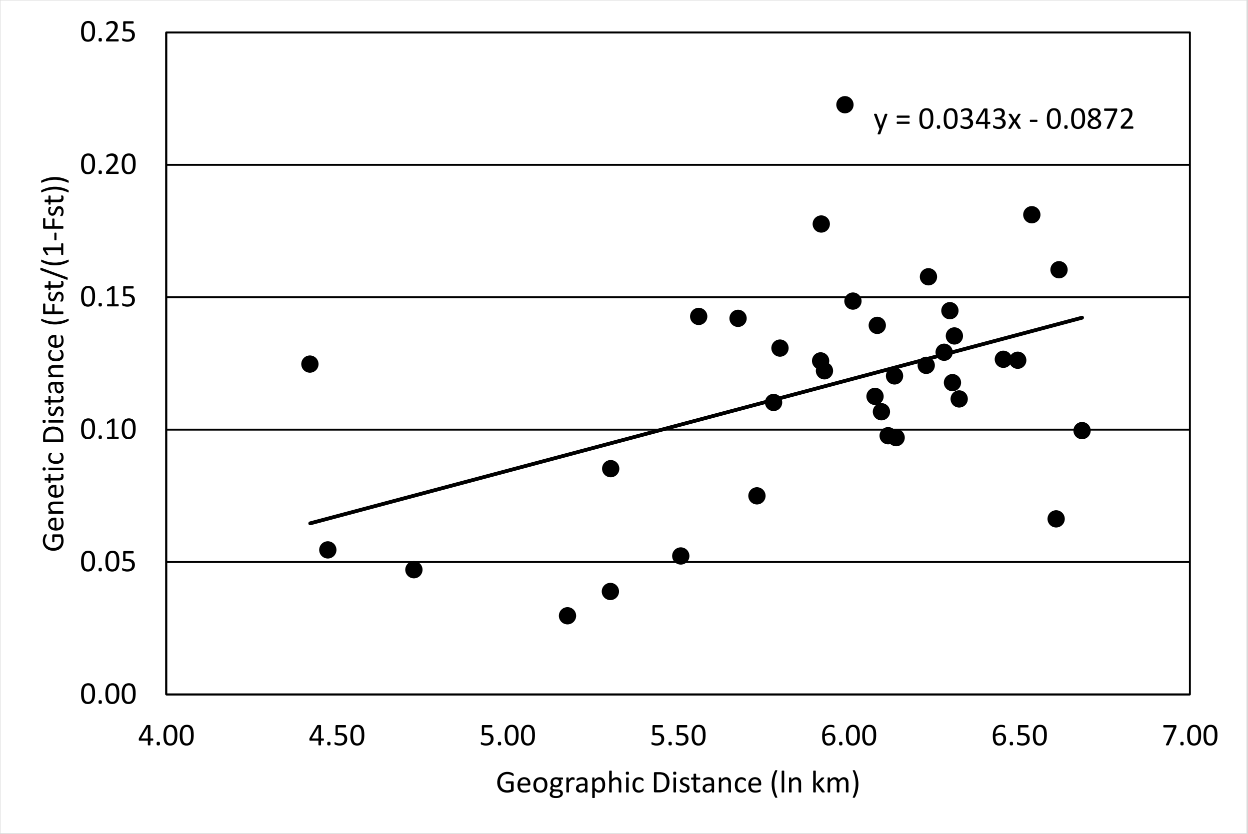


Figure 6.6. Plot of genetic distance against geographic distance for most sampling locations in the EP of Sandhill Cranes. The observed correlation was 0.48 (p = 0.007).

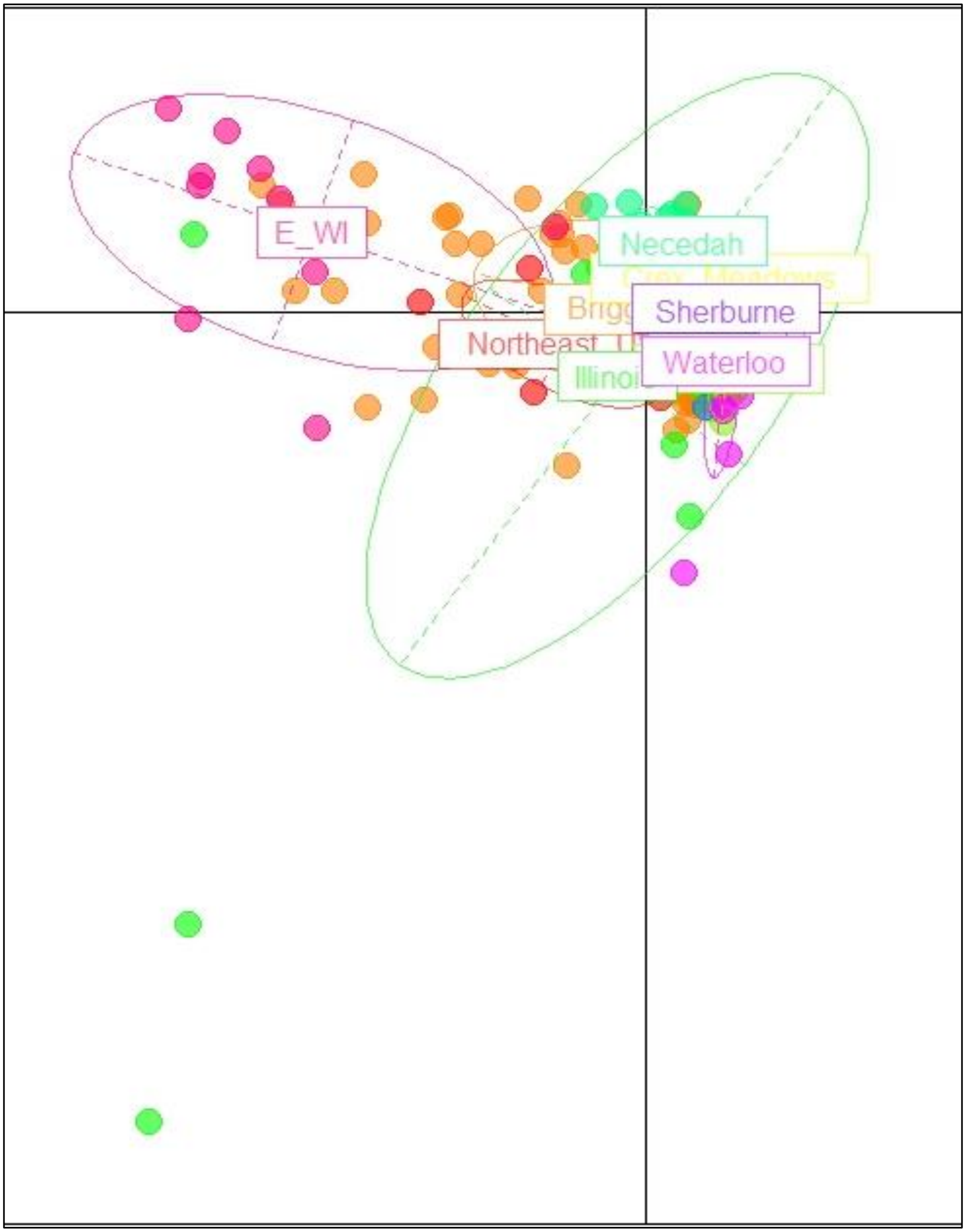


Figure 6.7. Two-dimensional plot of the first two principal components for all 251 Sandhill Crane chicks sampled from the Eastern Population. Samples are grouped based on sample location.

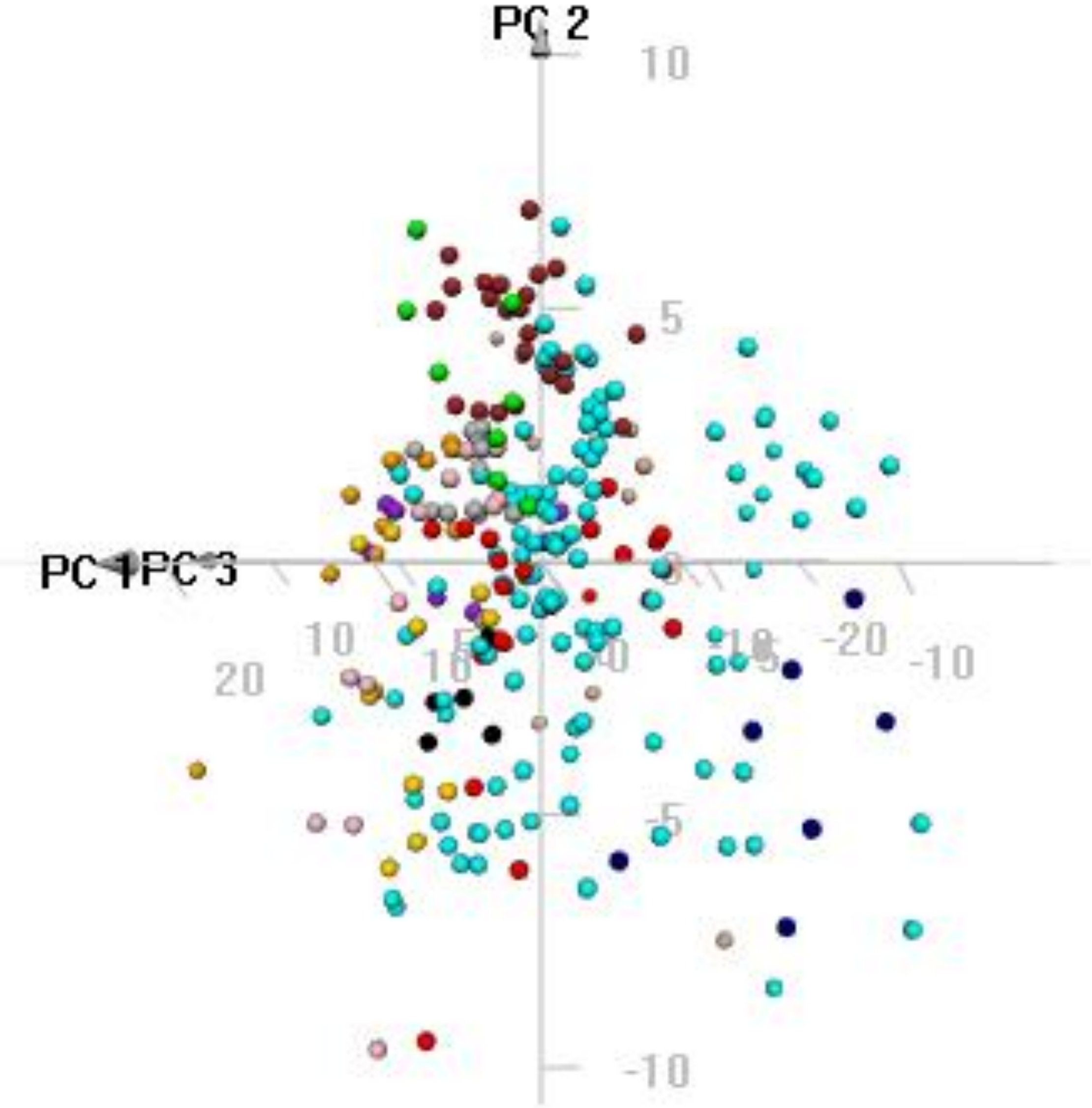


Figure 6.8. Three-dimensional plot of the first three principal components for all 251 Sandhill Crane chicks sampled from the Eastern Population. Groups are organized by sample location. Dark blue spheres = Northeastern U.S., light blue spheres = Briggsville, green spheres = Crex Meadows, yellow spheres = Gun Lake, red spheres = Illinois, maroon spheres = Necedah, black spheres = Ohio, orange spheres = Ontario, purple spheres = Seney, gray spheres = Sherburne, pink spheres = Waterloo, tan spheres = Eastern Wisconsin.

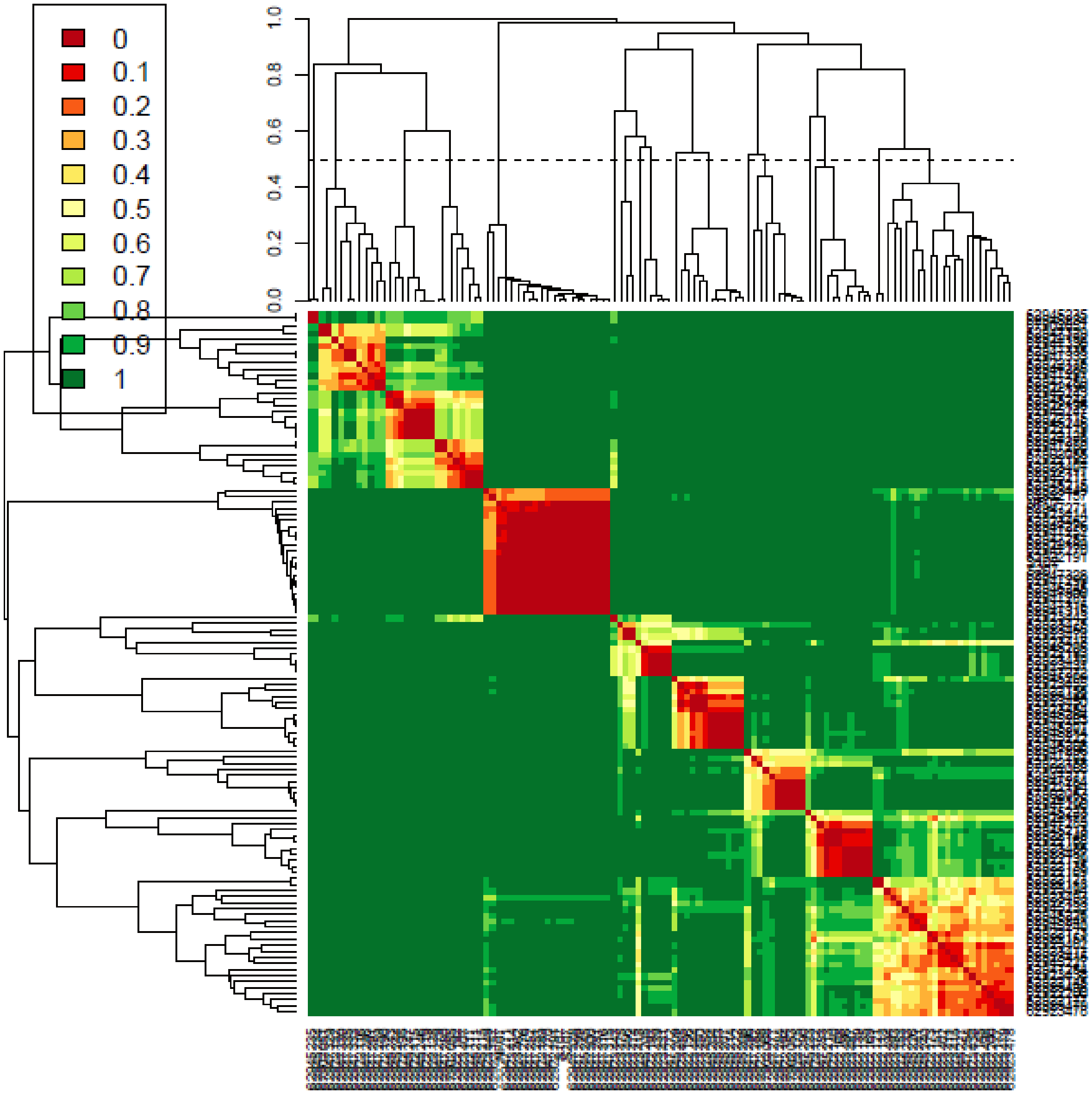


Figure 6.9. Average linkage among 116 chicks from Briggsville, WI in 1,000 MCMC replicates of a non-spatial model. The scale for the heat map is 0 (always placed in the same cluster, colored red) to 1 (never placed in the same cluster, colored green). The dotted line represents a mean posterior probability of cluster membership at 50%.

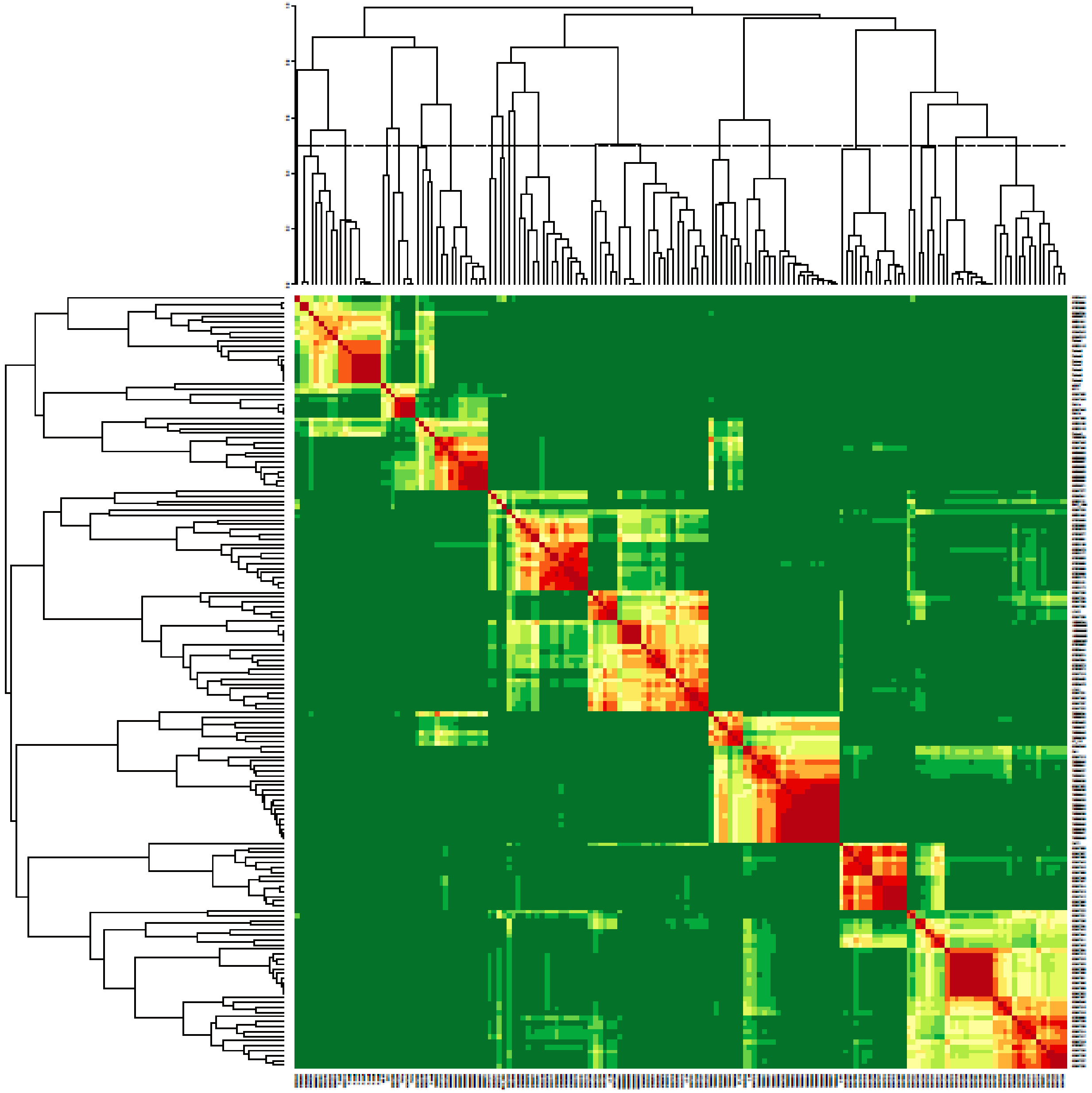


Figure 6.10. Average linkage among 160 birds in the EP during 1,000 MCMC replicates of a non-spatial model. The scale for the heat map is 0 (always placed in the same cluster, colored red) to 1 (never placed in the same cluster, colored green). The dotted line represents a mean posterior probability of cluster membership at 50%.

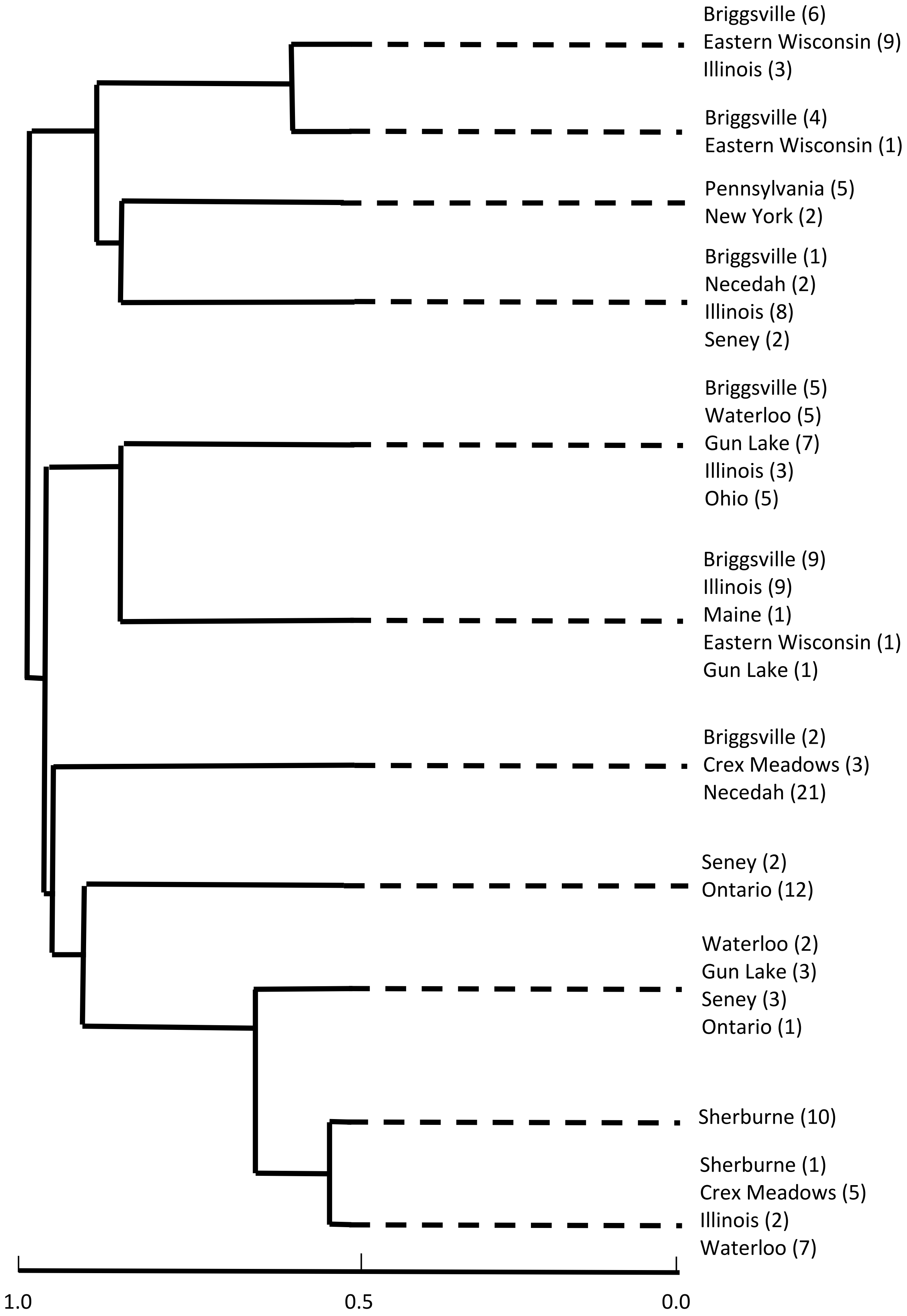

Briggsville (6)
Eastern Wisconsin (9)
Illinois (3)
Briggsville (4)
Eastern Wisconsin (1)
Pennsylvania (5)
New York (2)
Briggsville (1)
Necedah (2)
Illinois (8)
Seney (2)
Briggsville (5)
Waterloo (5)
Gun Lake (7)
Illinois (3)
Ohio (5)
Briggsville (9)
Illinois (9)
Maine (1)
Eastern Wisconsin (1)
Gun Lake (1)
Briggsville (2)
Crex Meadows (3)
Necedah (21)
Seney (2)
Ontario (12)
Waterloo (2)
Gun Lake (3)
Seney (3)
Ontario (1)
Sherburne (10)
Sherburne (1)
Crex Meadows (5)
Illinois (2)
Waterloo (7)
1.0
0.5
0.0

Figure 6.11. Dendrogram based on assignment of 160 Sandhill Crane chicks to genetic clusters using a GENELAND nonspatial model. A value of 1.0 indicates that birds were never placed in the same cluster while a value of 0.0 indicates that birds were always placed in the same cluster. The major seven branches are shown and a dotted line indicates smaller branches that were collapsed for simplicity. The number of individuals from each sampling location are shown in parenthesis.

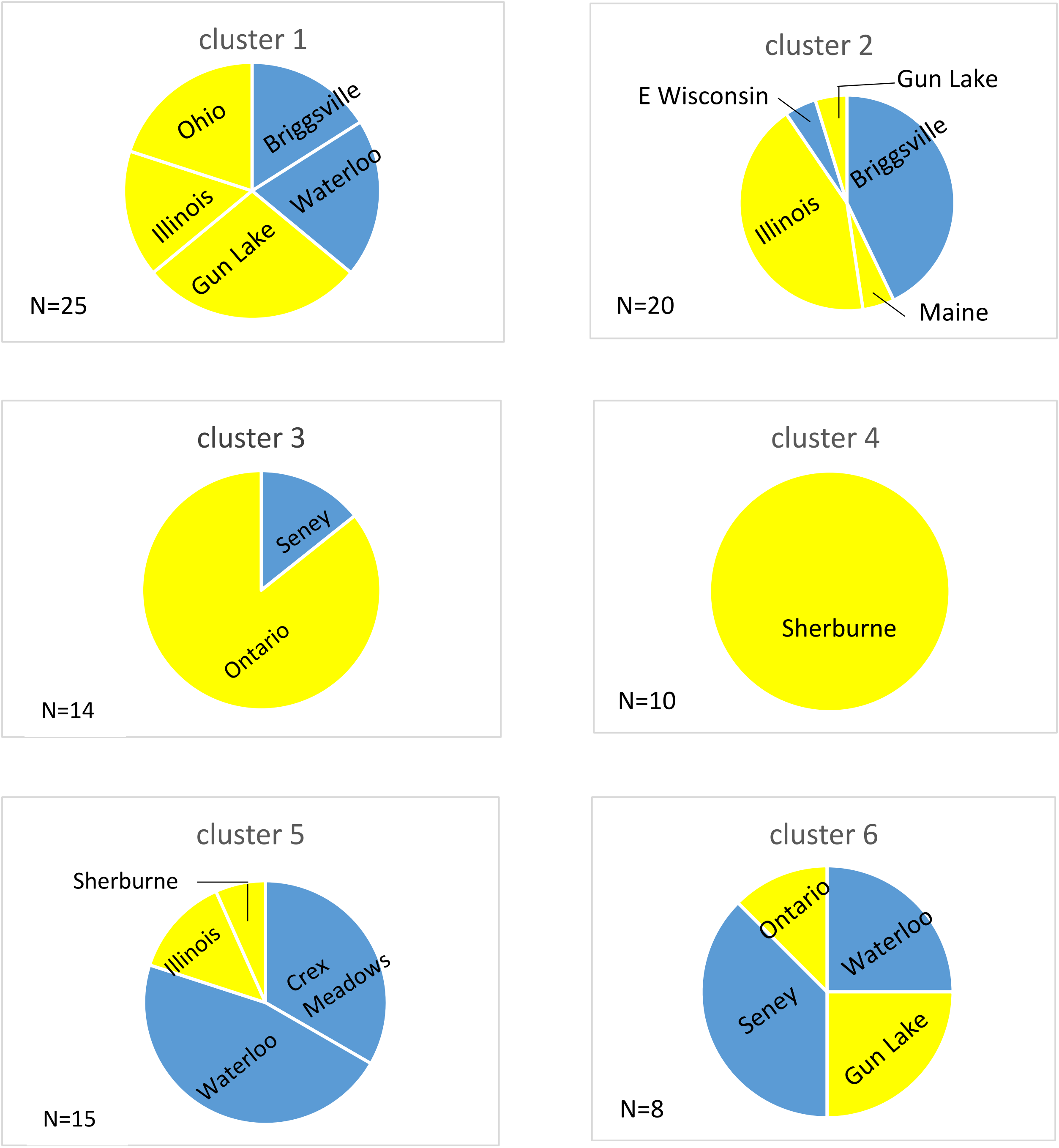
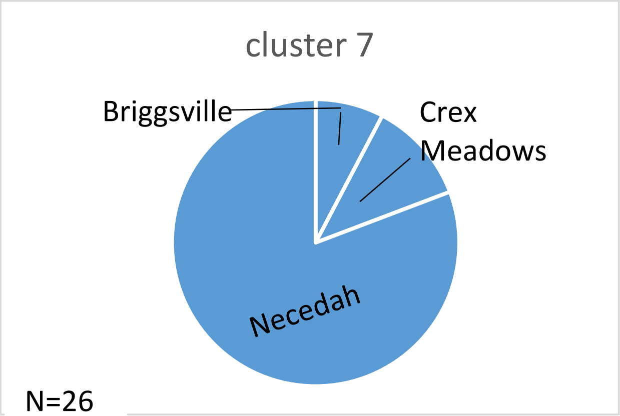
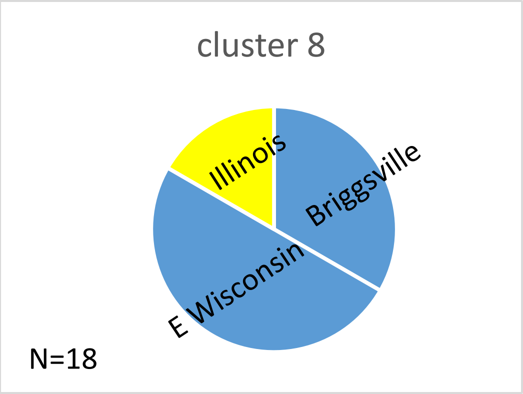
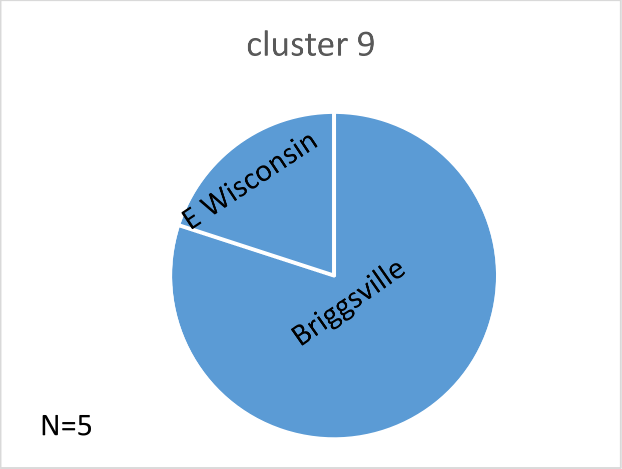
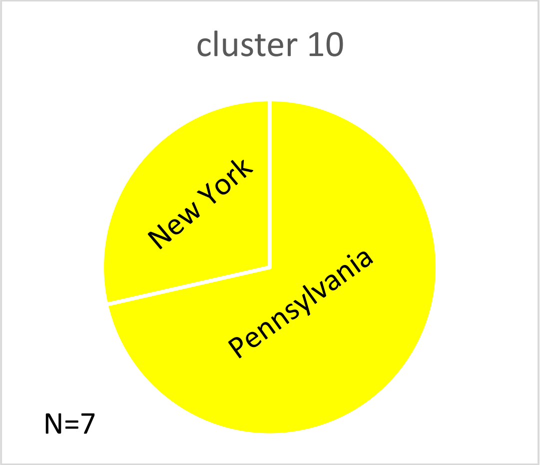


Figure 6.12. Pie charts showing cluster membership for 160 Sandhill Cranes in the EP. Blue sections indicate remnant sample sites. Yellow sections indicate re-colonized sample sites.









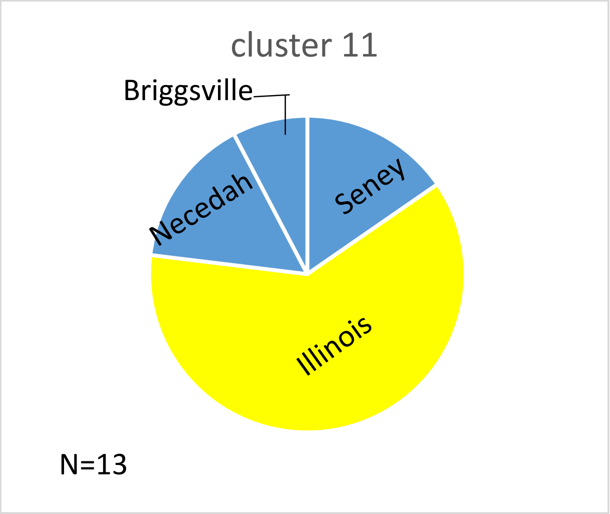


Figure 6.12 (cont.)

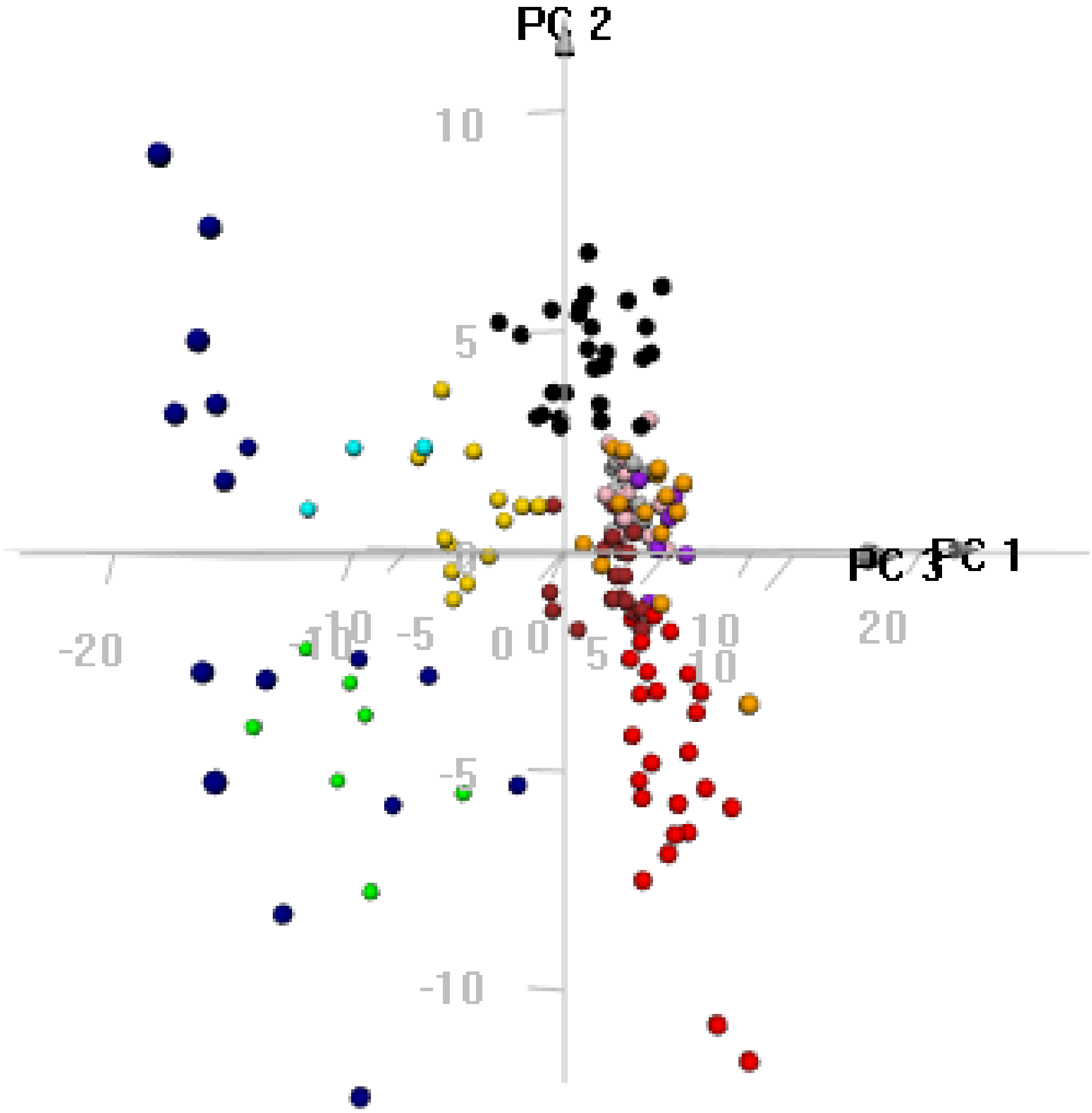


Figure 6.13. Three-dimensional plot of the first three principal components for all 251 Sandhill Crane chicks sampled from the Eastern Population. Groups are organized by GENELAND cluster (Figures 6.10, 6.11). Dark blue spheres =cluster 1, light blue spheres = cluster 2, green spheres = cluster 3, yellow spheres = cluster 4, red spheres = cluster 5, maroon spheres = cluster 6, black spheres = cluster 7, orange spheres = cluster 8, purple spheres = cluster 9, gray spheres = cluster 10, pink spheres = cluster 11.

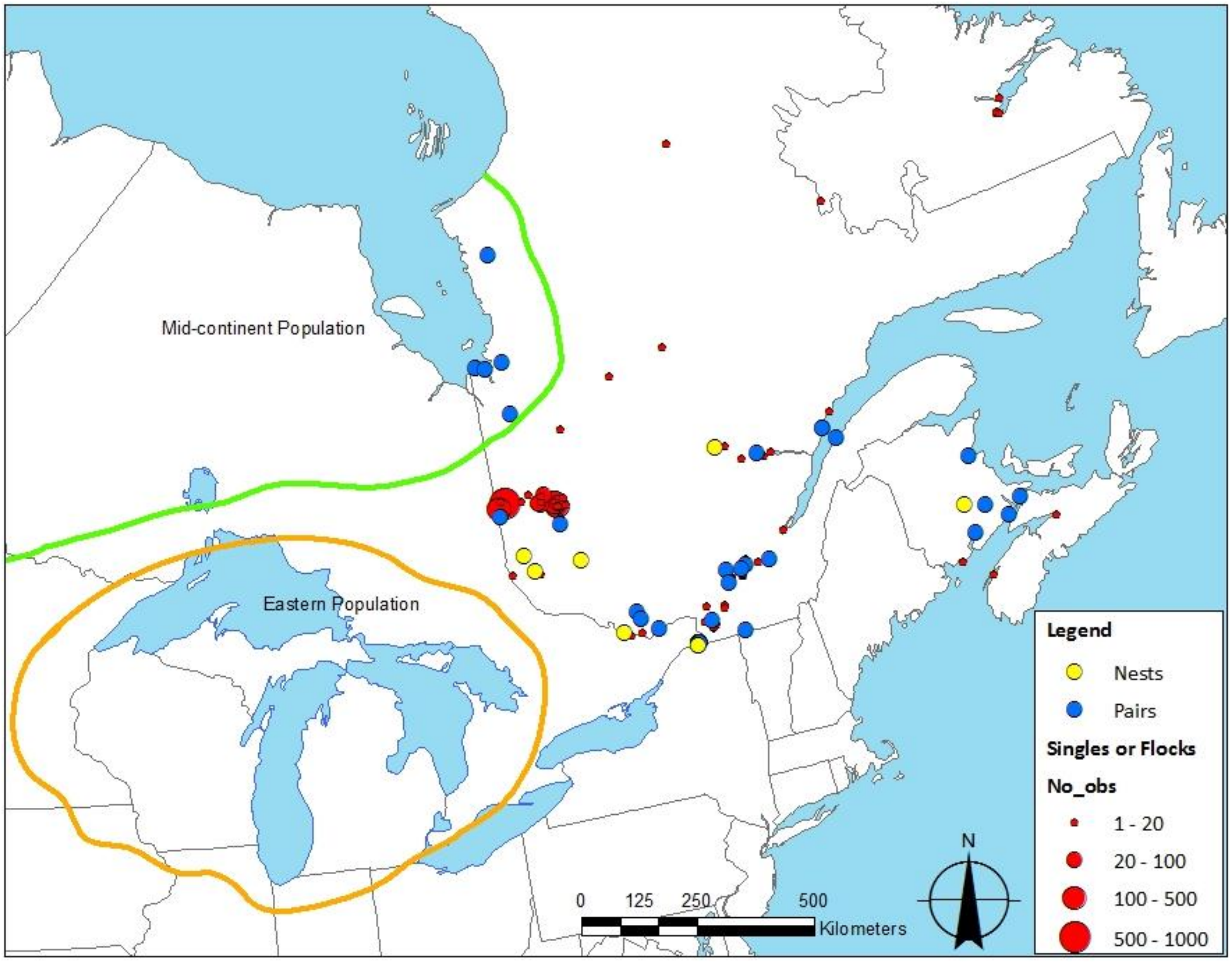


Figure 6.14. Nests and observations of Sandhill Cranes in eastern Canada from 1972 – 2012. Re-drawn from data published in Bannon et al. 2000, 2001, 2002, 2003, 2005; Dalzell 2009, 2010; McTavish 1999, 2002, 2003, 2006, 2007, 2008; Oulette and Bouzet 1975.

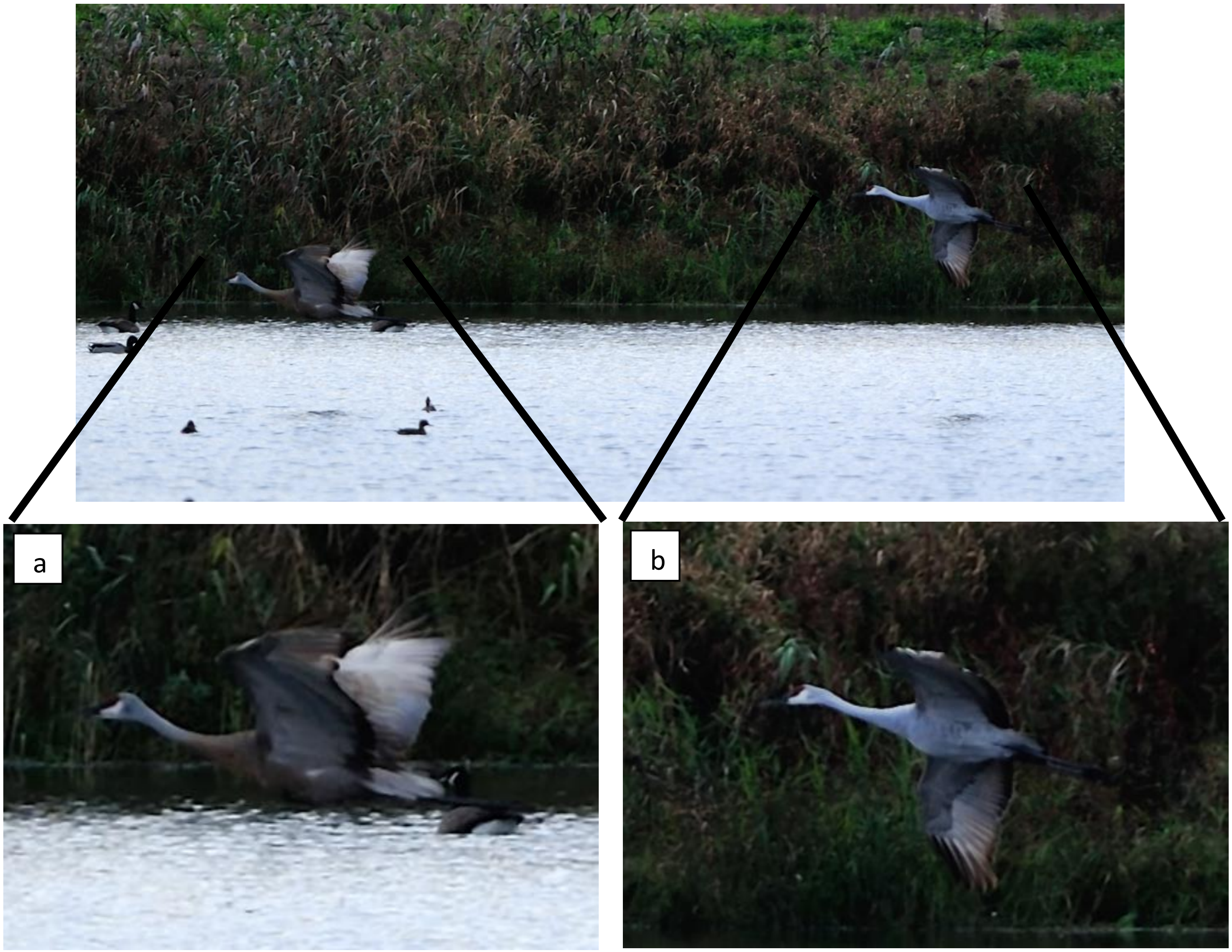


Figure 6.15. Sandhill Cranes observed at Montezuma National Wildlife Refuge, NY on October 28, 2011. (a) The “brown” bird is larger with relatively long bill and wings compared to overall body size suggesting *G. c. tabida*. (b) The “gray” bird is smaller with shorter bill and wings compared to overall body size which could suggest *G. c. rowani*. Photograph courtesy of Douglas Racine.

Chapter 7

POPULATION GENETIC STRUCTURE OF SANDHILL CRANES IN THE PACIFIC FLYWAY OF NORTH AMERICA

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ABSTRACT

We evaluated relationships among three migratory populations (PFP Lessers, CVP Greaters, BC coast Canadians) of Sandhill Crane (*Grus canadensis*) in the Pacific Flyway of North America using breeding location, mitochondrial DNA (mtDNA) haplotypes, and nuclear (281 Amplified Fragment Length Polymorphism (AFLP) fragments) DNA markers. Breeding grounds of all three populations were geographically segregated with PFP birds in high-arctic areas, CVP birds in temperate grasslands, and BC coast Birds in coastal areas inbetween. Most PFP birds showed Type I mtDNA haplotype while CVP birds and BC coast birds showed Type II haplotype. A principal components analysis of AFLP genotypes partitioned 76 birds into six groups. These groups were supported by results of a non-spatial mixture model in GENELAND grouping birds in K=5 clusters. PFP birds formed two clusters and both were differentiated from CVP birds and BC coast birds. CVP birds also formed two clusters which were not directly related. One of these CVP clusters comprised BC coast birds, but each group was placed on separate branches of a topology. These results, combined with mtDNA haplotype, suggest a recent common origin between CVP birds and BC coast birds in the Pacific Flyway. Current gene flow between these populations is debatable.

INTRODUCTION

Following a population bottleneck, there is typically a reduction in heterozygosity and allelic richness compared to non-bottlenecked populations (e.g., Bouzat et al. 1998, Nyström, et al. 2006, Whitehouse and Harley 2001). The effects of a population bottleneck on population genetic structure are not well documented. If habitat loss is the cause of a population bottleneck, then increased population differentiation could occur as a result of increased fragmentation of once contiguous habitat. For example, Golden-cheeked Warblers (*Setophaga chrysoparia*) that were sampled 1890-1915 throughout the range showed no significant population genetic structure (Athrey et al. 2011). A century later, the range had been reduced and heavily fragmented and contemporary samples collected in 2005 showed significant differentiation among sample sites (Lindsay et al. 2008, Athrey et al. 2011). As breeding sites become extirpated, the occurrence of a bottleneck may cause the loss of genetic clusters as private alleles are lost.

Of the 15 extant cranes, Sandhill Cranes (*Grus canadensis*) are the most populous and have the widest known breeding distribution, ranging from Siberia to Cuba (Meine and Archibald 1996). Most Sandhill Crane populations, however, likely experienced a reduction in population size in the 1800’s as suitable breeding habitat was converted to agriculture and human residential use (Walkinshaw 1949). This reduction in available habitat likely resulted in population bottlenecks for most populations, however, the severity of any bottlenecks that likely occurred in each population was not well documented. This lack of documentation is primarily due to the remoteness of the nesting sites for most populations and multiple populations congregate together during migration and the winter (Meine and Archibald 1996).

Six subspecies of Sandhill Cranes have been described based on differences in morphology and geographic distribution (Meine and Archibald 1996). Differentiation between the three migratory subspecies (*G. c. canadensis*, hereafter "Lesser"; *G. c. rowani*, hereafter "Canadian"; and *G. c. tabida*, hereafter "Greater") has been primarily established based on two factors: geography and morphology. The smallest Lessers breed in arctic and sub-arctic regions, largest Greaters breed in temperate regions, and mid-sized Canadians breed in tundra regions between the range limits of Lessers and Greaters. Several studies have investigated the validity of using morphometrics to delineate Sandhill Crane subspecies (Johnson and Stewart 1973, Tacha et al. 1985, Johnson et al. 2005, Jones et al. 2005). The results of these studies suggest that using morphometrics to delineate subspecies is difficult and unreliable unless differentiating the smallest of the Lessers from the largest of the Greaters. Because Canadians are morphologically intermediate between Lessers and Greaters (Walkinshaw 1965), this invalidates using morphology to consistently separate Canadians from Lessers and Greaters.

Similarly, results of genetic studies suggest that Lessers can be differentiated from other Sandhill Crane subspecies as they have a unique haplotype (Type I) in the control region of their mitochondrial DNA (mtDNA) compared to all other recognized morphological subspecies, which express Type II (Rhymer et al. 2001). The Canadian is currently considered a hybrid between Lessers and Greaters as individuals that are morphologically/geographically considered Canadians expressed both Type I and Type II mtDNA haplotypes in mtDNA D-Loop region (Peterson et al. 2003) and contained microsatellite DNA alleles that were shared with both Lessers and Greaters (Jones et al. 2005). The mixing of lineage I and lineage II likely occurred during secondary contact after Pleistocene glacial recession (Jones et al. 2005).

The Pacific Flyway on the west coast of North America contains three recognized populations of Sandhill Cranes (Pogson and Lindstedt 1991). First, the Pacific Flyway Population (PFP), comprised primarily of Lessers, breeds in southern Alaska west of Anchorage and on the Kenai Peninsula (Littlefield and Thompson 1982, Pacific Flyway Council 1983, Petrula and Rothe 2005). Second, the Lower Colorado River Valley Population (LCRVP), comprised primarily of Greaters, breeds in the central Great Basin in Nevada, Idaho, and Utah (Pacific Flyway Council 1995). Third, the Central Valley Population (CVP), comprised primarily of Greaters, breeds from south-central British Columbia south to northern California (Littlefield and Thompson 1979, Pacific Flyway Council 1997, Littlefield and Ivey 2002). A probable fourth, unnamed population containing birds, thought to be Canadians, has been described breeding on the islands off the coast of British Columbia (Littlefield and Thompson 1979, Littlefield and Ivey 2002), however whether these birds belong to the PFP or CVP has been debated (Pogson and Lindstedt 1991; Cooper 1996; Jones et al. 2005; Cooper 2006). Ivey et al. (2005) suggested this group be considered a separate population because of their unique breeding range, migration route, and wintering area (Littlefield and Ivey 2002). While all Sandhill Cranes in the Pacific Flyway share common wintering grounds and staging areas in California (Ivey, unpublished data), only BC coast birds winter in the Lower Columbia River area between Washington and Oregon (Ivey et al. 2005). If and how these coastal breeding cranes interact with other populations of Sandhill Cranes in the Pacific Flyway remains unknown.

Historically, the CVP had a wide distribution, but the population suffered a population bottleneck in the 1930’s and was reduced to 150-200 birds (Walkinshaw 1949). While the CVP currently contains 6,000 – 7,000 Greaters (Meine and Archibald 1996), recovery has been slow and is likely hindered by low availability of suitable habitat (Ivey, unpublished data). The PFP currently has 25,000 birds and while this population also likely was reduced in the early 1900's (Littlefield 2008), it is unknown if this population also suffered a bottleneck as the extent of population size and range reduction was not well documented. Lastly, the BC coast population currently exists in small numbers compared to the PFP and CVP (Littlefield and Ivey 2002). Similar to the PFP, any reduction in population size and range of these birds is not well documented due to the remoteness of the breeding areas (Ivey et al. 2005). Current growth of this BC coast population may also be limited by specific habitat associations such as breeding in forested wetlands and bogs and foraging in shallow estuaries and on beaches (Campbell et al. 1990, Cooper 2006, Roessingh and Penn 2010) which are not observed in other Sandhill Crane populations.

To date, no study has conducted a comprehensive genetic analysis of Sandhill Cranes using the Pacific Flyway of western North America. The goal of our research was to first determine if the Sandhill Crane populations utilizing the Pacific Flyway exhibited any genetic differentiation and population genetic structure. Specifically, we sought to determine what patterns of mtDNA haplotype and the magnitude of nuclear gene flow occurred between the CVP, PFP, and BC coast populations of Sandhill Cranes. If a population bottleneck reduced the size of each of these population, we hypothesized there would be only a few genetic clusters, possibly only one genetic cluster per population.

METHODS

Capture, Sampling Areas, and Telemetry

We captured 72 Sandhill Cranes (37 males, 35 females) with rocket nets (Wheeler and Lewis 1972, Urbanek et al. 1991) and toe snares (Hereford et al. 2001) over a broad geographic range at wintering and migratory staging areas. Capture of these 72 birds was conducted by four institutions (Oregon State University, International Crane Foundation, Hemmera, and U.S. Geological Survey) over 11 years (2001-2011). Sites sampled included northwest and northeast Oregon, central California, southwestern British Columbia, and Alaska (Figure 7.1). All birds, except for four Lessers (hatched the previous spring), had adult plumage (Lewis 1979, Nesbitt and Schwikert 2005). Plastic leg bands were placed above the tarsal joint along with U.S. Geological Survey or Canadian Wildlife Service aluminum bands for long-term visual identification. Cranes banded in California and Oregon (2009-2011) were fitted with very high frequency (VHF) radio transmitters (Sirtrack AVL6171) to enable tracking of individual movements while on breeding and wintering grounds. Cranes captured on the border of Washington and Oregon (2001-2002) and all Alaska and British Columbia cranes were fitted with platform terminal/satellite transmitters (PTT; North Star Science and Technology) to determine summer breeding locations (Figure 7.2; Ivey et al. 2005, Ministry of Transportation 2009, 2010). For each bird, a transmitter was fitted to an 8 cm tall color plastic leg band (Krapu et al. 2011) that was coded on one side with a unique alphanumeric identifier. The other leg of each bird was marked with two 3 cm tall colored plastic bands in a unique color combination. The transmitters received by Alaska and British Columbia cranes had duty cycles to transmit data every 72 hours to increase the probability of determining a breeding location. On wintering areas, cycling time was reduced (192 hours) to maximize lifespan of the transmitter.

Morphological classification of subspecies

Morphological measurements including exposed culmen (mm; n=33), post-nare culmen (n=8), tarsus (mm; n=34), and wing chord (mm; n=34) were collected when possible. Following Johnson et al. (2005), a discriminant function (Lachenbruch 1975) was used to categorize an individual bird as a Greater, Canadian, or Lesser based on measurements collected previously from Sandhill Cranes throughout their geographical range. For those birds without recorded post-nare culmen measurements, an estimate was made from post-nare culmen = 0.663 × exposed culmen + 12.95, a regression calculated using measurements from 102 specimens of all subspecies (Walkinshaw 1949).

Sample Collection, DNA Isolation and Purification

A blood sample was collected from 72 birds described above. Blood was unavailable for four other birds but various tissue types were collected as follows: a) muscle from three dead Sandhill Cranes (two wintering adults [1 M, 1 F] in March 2003 and a one-week-old male chick from British Columbia in 2010), and b) feather pulp extracted from the calamus of a secondary flight feather removed from a hatch-year male chick in British Columbia. All tissue samples were stored in lysis buffer (Longmire et al. 1991) until DNA was extracted. Previous analyses of four different tissue types (blood, liver, muscle, and feather pulp) from domestic chickens (*Gallus gallus*) indicate that identical AFLP fingerprints are produced from these different tissue types from the same individual (Hayes and Berres, unpublished data).

A Promega Wizard Genomic DNA Isolation kit (Promega Corp., Madison, WI, USA) was used to purify DNA from all tissue samples. Muscle and feather samples received treatment with 1.5 µl RNAse A (4 mg/ml; Promega) heated at 37°C for 30 minutes prior to DNA extraction. Pelleted DNA was re-hydrated in 10 mM Tris pH 8.0 and solubilized by heating at 65°C for up to 48 hours. DNA quality and degree of solubilization were checked qualitatively by agarose gel electrophoresis. DNA concentration was estimated on a BioRad SmartSpec Plus spectrophotometer (BioRad Laboratories, Hercules, CA, USA). Each DNA sample was diluted to 50 ng/µl in Tris buffer (pH 8.0) and electrophoresed a second time on a 1% agarose gel to confirm visually the uniformity of each dilution. The sex of each crane was determined by results of PCR electrophoresed on a 1.5% agarose gel (Duan and Fuerst 2001).

Mitochondrial DNA Haplotype

Mitochondrial DNA haplotypes (Type I or Type II; Rhymer et al. 2001) were determined by genetic analysis of tissue samples (see below). A 437 bp portion of the control region of mtDNA was amplified following the protocol of Glenn et al. (2002). PCR products were digested with 5 U restriction enzyme *HaeIII* (New England Biolabs, Ipswich, MA, USA) following manufacturer's recommendations and then electrophoresed on a 1.5% agarose gel. Haplotypes were assigned by mobility differences in amplified bands on the gel (Glenn et al. 2002).

Bayesian Clustering Assignment in GENELAND

Genetic fingerprints were generated with amplified fragment-length polymorphism (AFLP; Vos et al. 1995) following modified protocols described in Berres (2003). While AFLPs are dominant markers, they have a proven history for assessing population genetic structure (Bensch and Akesson 2005, Bonin et al. 2007). The AFLP technique generates hundreds of markers without the need for development of species specific primers to amplify segments of DNA. Because of their dominant nature, less information is available per marker when compared to co-dominant markers such as microsatellites (Yu and Guo 2005). Reduced information content is balanced, however, by the generation of a high numbers of markers with fewer primer sets. Thus, identification of population differentiation and assignment of individuals to genetic clusters is similar to microsatellites (Campbell et al. 2003, Sonstebo et al. 2007). Additionally, sampling from five to ten individuals is sufficient for accurate estimates of genetic diversity (Singh et al. 2006) and differentiation within and among populations and genetic clusters (Fogelqvist et al. 2010, Nelson and Anderson 2013).

To generate AFLP fragments, 200 ng of DNA was digested to completion with 20 U restriction enzyme *EcoRI* and 5 U restriction enzyme *BfaI* at 37^{o}C for 16 hours and followed by a 20-minute deactivation at 65^{o}C. *EcoRI*/*BfaI* adaptors were ligated to the digested DNA ends with T4 ligase at 16^{o}C for 16 hours and diluted with 160 μl 10 mM Tris, pH 8.0. Ligated fragments were pre-selectively amplified with primers *EcoRI*+G and *BfaI*+T. Ten μl of each PCR product was electrophoresed on a 1% agarose gel to evaluate if complete digestion of DNA and sufficient amplification occurred. The remaining 40 μl of each PCR product was diluted 1:9 to 1:18 with 10 mM Tris, pH 8.0, depending on amplification efficiency based on visual scrutiny of the electrophoresed amplicons. Selective amplification was performed with two different primer combinations, *EcoRI*+GG/*BfaI*+TAT and *EcoRI*+GC/*BfaI*+TCT. PCR products were purified over columns of Sephadex G-75 (Sigma-Aldrich, St. Louis, MO) to remove salts and unincorporated primers. Between 1-2 μl of purified PCR products were mixed with 0.5 μl lane standard (Geneflo 625; CHIMERx, Molecular Biology Products, Milwaukee, WI) and diluted to a final volume of 15 μl with fresh, deionized formamide. Automated electrophoresis was performed on an Applied Biosystems, Inc. (Life Technologies, Grand Island, NY) 3730 capillary sequencer.

Markers in AFLP fingerprints were visualized using DAx v. 9.0 (Van Mierlo Software Consultancy, The Netherlands). Loci with appropriate baseline resolution (Berres 2003) between 50 and 625 bp were used for analysis. Presence (1) or absence (0) of AFLP markers were evaluated with bins constructed automatically using the DAx program. Bin tolerance was set to ±0.5 bp. Visual scrutiny of the fluorescent traces was performed to detect and correct trace alignment errors.

We applied a Voronoi tessellation model with correlated allele frequencies to determine the number of genetic clusters. This procedure, implemented in GENELAND v4.0.3 (Guillot et al. 2005) is based explicitly on a genetic model (Guillot, 2009; Guillot and Santos 2010). We estimated the number of genetic clusters (K) for all 76 birds using 1,000,000 iterations of the algorithm with 1,000 randomly seeded replicates and variable K (1-20). We ran a non-spatial model and a bird was assigned to a genetic cluster when that cluster contained the highest probability of population assignment as estimated by the iterative MCMC calculation. In practice, the MCMC run exhibiting the highest mean log posterior density of typically 10 or so replicates is chosen. While convenient from an analytical perspective, this procedure does not provide sufficient information concerning any variation of K or individual assignment into specific clusters. Estimation of variance from sampling the MCMC chain tends to yield poor approximations and is further complicated by the MCMC “label-switching” problem (Guillot 2009). To objectively evaluate the stability of K and individual assignment to specific clusters, we first performed a diagnostic to accept or reject the null hypothesis that the MCMC chain is from a stationary distribution (Heidelberger and Welch 1981, 1983). For those replicates meeting the statistical stationary criterion, the pairwise cumulative proportion of same-cluster membership for individuals from at least 1,000 independent MCMC runs was calculated. Relationships among individuals were then visualized by a topology created by applying an agglomerative hierarchical clustering procedure to estimate the unweighted average distance among individuals (UPGMA). These topologies do not depict phylogenetic relationships or population genetic structure *per se*, but rather overall relationships among individuals based on shared membership in a common cluster as determined by GENELAND. A heat map was used to visualize the mean posterior probability of cluster membership among individuals. The scale for the map is 0 (always placed in the same cluster, colored red) to 1 (never placed in the same cluster, colored green).

To complement the GENELAND model, we also applied principal components analysis (PCA) using the adegenet package in R 3.0.2 (Jombart 2008). One feature of PCA is that it is a non-genetic model that groups individuals based on shared AFLP markers without imposing assumptions of Hardy-Weinberg Equilibrium or linkage equilibrium among loci (Hannelius et al. 2008, Rutledge et al. 2010). Three-dimensional display of the first three principal components was constructed using the pca3D and rgl packages in R 3.0.2.

To reduce bias associated with use of dominant data, the method of Zhivotovsky (1999), incorporated in the software package AFLP-SURV (Vekemans 2002), was used to estimate indices of genetic variation and differentiation including pairwise and average Fst. To estimate Fst, groups of birds were assembled based on clusters determined with GENELAND. We used

10,000 permutations to estimate a 95% CI for each Fst calculation. Loci with private alleles were determined in Genetic Data Analysis 1.1 (GDA; Lewis and Zaykin 2002).

RESULTS

Our dataset was comprised of nuclear DNA markers obtained from AFLP fingerprints. Two primer pairs, *EcoRI*+GG/*BfaI*+TAT and *EcoRI*+GC/*BfaI*+TCT, produced 167 and 178 loci respectively. Of these, 121 (72%) and 160 (90%) met our scoring criteria. Of the 281 loci, 107 (88%) and 148 (93%) exhibited polymorphism and were combined for all further genetic analyses.

When all 76 birds were analyzed in GENELAND, a modal K=5 genetic clusters was estimated from 1,000 MCMC replicates (Figure 7.3). Groupings based on the average mean posterior probability of cluster membership (Figures 7.3, 7.4) showed significant differentiation among all five groups. These five groups fit well with geographic distribution based on observations of banded birds and VHF or satellite telemetry.

Thirty-nine birds were distributed between two clusters: cluster 4 (n=18) and cluster 5 (n=21). Using VHF or satellite telemetry, 16 of these 39 birds were located during the summer at two general breeding locations within the geographic range of the PFP in Alaska (Figure 7.2): 1) near Homer (n=12) and 2) near Dillingham (n=4). The GENELAND clusters were split among these breeding areas as cluster 4 contained birds primarily breeding in Homer (with one banded in Dillingham) and cluster 5 contained birds primarily breeding in Dillingham (with two banded in Homer; Figure 7.4). One bird grouped in cluster 4 (Z012) had Type II mtDNA haplotype and bred in N. Harney County, Oregon which is within the geographic range of the CVP (see below). Of these 39 birds, 72% showed a Type I mtDNA haplotype while the remaining 28% showed a

Type II mtDNA haplotype. Of the 12 birds located near Homer, 75% showed Type I mtDNA haplotype and 25% showed Type II mtDNA haplotype while all four birds located near Dillingham showed Type I mtDNA haplotype. Eighteen birds assigned to these two clusters had morphological measurements collected. Sixteen of these 18 (89%) were classified as Lesser, one (6%) was classified as Canadian, and one (6%) was classified as Greater (Table 7.1).

Thirty-four other birds were distributed among two other clusters: cluster 2 (n=14) and cluster 3 (n=20). Using VHF telemetry, 16 of these 34 birds were located during the summer at three general breeding locations (Figure 7.2) within the geographic range of the CVP: 1) Modoc County (n=10), California, 2) N. Harney County (Silvies/Burns area; n=3), Oregon, and 3) S. Harney County (Alvord Desert area; n=3), Oregon. CVP birds from all three breeding areas were equally distributed among both GENELAND clusters (Figures 7.2, 7.4). Eight birds from these two clusters had morphological measurements collected and 100% were classified as Greater (Table 7.1)

Each of these CVP clusters contained birds that were part of the BC coast population. In addition to 12 CVP birds, cluster 2 contained an injured fledgling chick and a dead flightless chick that were sampled near the Reifel Refuge in southwestern British Columbia, an area within the range of the BC coast population (Figure 7.1). In addition to 10 CVP birds, cluster 3 included seven birds located with satellite telemetry on coastal breeding areas in southeastern Alaska and western British Columbia, a region also within the range of the BC coast population. While placed together in cluster 3, the BC coast birds, along with three birds from unknown breeding areas, were placed on a separate branch of the topology from the CVP birds (Figure 7.4). All CVP and BC coast birds had Type II mtDNA haplotype. Nine BC coast birds (the fledged chick from cluster 2 and eight adults from cluster 3) had morphological measurements collected. Two of nine birds (22%) were morphologically classified as Lesser, four (44%) were classified as Canadian, and three (33%) were classified as Greater (Table 7.1).

Cluster 1 contained three non-breeding birds banded on Sauvie Island (Figures 7.1, 7.2) during summer 2011. These birds were captured from a group of 10 birds that had wintered on Sauvie Island during 2010/11, but did not migrate north in spring 2011. This cluster had a mean posterior probability of cluster membership (0.93) distinctive from all other clusters. All three Sauvie Island birds had Type II mtDNA haplotype. No morphological measurements were collected from these birds.

In addition to GENELAND, we used PCA on the AFLP data to assign all 76 birds to groups and then plotted the first three principal components, whose combined eigenvalues explained 58% of the variation. Six distinct groups were formed that aligned with GENELAND clusters (Figure 7.5). PCA group 1 contained the three birds from Sauvie Island. PCA group 2 contained the same 12 CVP birds and the two Reifel Refuge chicks, but also contained Z012 which GENELAND placed in cluster 4 with PFP birds from Homer. PCA group 3 contained the remaining 10 CVP birds while PCA group 4 contained the 10 BC coast birds that GENELAND placed on a separate branch of the topology. When PCA groups 3 and 4 were plotted on a separate 3D PCA plot using the same first three principal components, nine of 10 CVP birds were placed above the PC1/PC3 plane while seven of 10 BC coast birds were placed below the PC1/PC3 plane (Figure 7.6). PCA groups 5 and 6 contained PFP birds which corresponded to clusters 4 and 5 in GENELAND and were divided into birds near Homer and Dillingham (Figure 7.5).

We calculated population genetic diversity estimates and private alleles (Table 7.2) and overall and pairwise Fst (Table 7.2) with groups of birds defined by assignment to specific clusters determined with GENELAND and PCA. Expected heterozygosity and frequency of private alleles were highest among the cluster containing Sauvie Island cranes but lowest among Homer and Dillingham PFP birds (Table 7.2). The highest magnitude of inferred gene flow occurred between Homer and Dillingham PFP birds. Moderate genetic differentiation was observed between clusters 2 and 3 (Table 7.3). As expected, the birds captured on Sauvie Island were distantly related to all other clusters. Fst was significantly different from zero both with the overall average and among group estimates (Table 7.3).

DISCUSSION

Our analyses of combined genetic (mtDNA and AFLPs) and geographic data (breeding ground location via telemetry) suggest that significant population genetic structure occurs among Sandhill Cranes in the Pacific Flyway of western North America. Analysis of 1,000 GENELAND MCMC replicates and groups formed by PCA suggests at least 5 distinct genetic clusters exist in a flyway where historically only two or three geographic populations would have been predicted. Application of an agglomerative clustering model to depict mean posterior probability of individual cluster assignment indicates that although these five genetic clusters are stable, there is likely introgression among populations of Sandhill Cranes in the Pacific Flyway.

Type I mtDNA was only found in PFP Lessers while all other birds showed Type II mtDNA haplotype. While these results helped differentiate PFP birds from other populations, mtDNA haplotype was not useful for overall differentiation among Sandhill Crane populations in the

Pacific Flyway because the scale was too coarse. Similar conclusions were reached by Ball and Avise (1992) when they attempted to use restriction enzyme analyses of mtDNA haplotypes to investigate subspecific differentiation in Downy Woodpeckers (*Picoides pubescens*), Mourning Doves (*Zenaida macroaura*), Brown-headed Cowbirds (*Molothrus ater*), Song Sparrows (*Melospiza melodia*), Eastern Towhees (*Pipilo erythropthalmus*), or Common Yellowthroats (*Geothlypis trichas*). Sequencing of mtDNA haplotype data would provide more fine scale analysis and allows the construction of haplotype networks to potentially differentiate among populations (e.g., van Oven et al. 2011).

In our study, PFP birds were separated into two distinct genetic that corresponded with breeding location in Homer, AK or 400 km west in Dillingham, AK. These clusters showed moderate levels of differentiation from each other based on Fst and few individuals shifted among clusters during replicate runs in GENELAND. One CVP bird (Z012) was assigned to the same cluster as birds from Homer. However, the mean posterior probability of cluster membership (0.43) was much lower than observed with PFP birds in either cluster. This indicates a possibility of either mixed ancestry between a pairing of a PFP bird and CVP bird or from a currently unsampled population, perhaps derived from the Rocky Mountain Population (RMP) or LCRVP.

While neither PFP cluster showed large-scale introgression (based on nuclear AFLP markers) with other populations in the Pacific Flyway, over 25% of birds located in (via telemetry) or assigned to (via GENELAND and PCA) the PFP contained Type II mtDNA haplotype. Introgression may thus be a more recent phenomenon as AFLPs generally reflect historic population structure when compared to mtDNA markers (Brown et al. 1979; Alacs et al. 2011).

Dispersal of BC coast females into high-arctic areas is a more realistic explanation than movement of CVP females as evidenced by Fst and abutment of the geographic ranges of the PFP and BC coast population. If true, BC coast females would still need to disperse > 1,200 km to interact with PFP birds on their breeding areas. This would be the largest natal dispersal distance estimated for Sandhill Cranes. Non-breeding adults typically move less than 100 km from their natal area prior to obtaining a breeding territory (Ministry of Transportation 2010, Chapter 4) and these distances reduce when a bird obtains a breeding territory (Chapter 5). Jones et al. (2005) found arctic-nesting birds with Type II mtDNA haplotype as well as temperate-nesting birds with Type I mtDNA haplotype suggesting a two-way northward/southward exchange of females between breeding areas in the Mid-Continent Population of Sandhill Cranes.

Both GENELAND and PCA divided CVP birds into two distinct clusters that showed great differentiation using Fst. Birds from each cluster were located at three geographic breeding areas within the range of the CVP. These two clusters may be indicative of historically structured populations. Because of their longevity, surviving individuals from these populations may have served as genetic reservoirs and retained significant amounts of historical genetic variation, a phenomenon reported in White-tailed Sea Eagles (*Haliaeetus albicilla*; Hailer et al. 2006). Our results suggest that at least two distinctive genetic clusters survived the population bottleneck experienced by birds in the CVP in the early 1900's where the population size was reduced to 150-200 birds (Walkinshaw 1949). The CVP is currently growing at a slow rate perhaps due to limited availability of suitable breeding habitat (Ivey, unpublished data). It is also possible that we are observing secondary contact between these lineages, as non-breeding birds may need to disperse longer distances to acquire a mate and territory. Long-range natal dispersal of individuals between breeding areas, a phenomenon not typically observed in the Eastern Population (EP) of Sandhill Cranes (Chapters 5, 6), could also be reflective of fragmentation of high quality habitat driving birds to disperse greater distances to attempt successful reproduction.

Type II mtDNA haplotypes were found in both CVP birds and BC coast birds in the Pacific Flyway. These results suggest a common ancestry between these populations and are supported by the placement of one group of CVP birds and BC coast birds into a common genetic cluster by GENELAND. However, these populations have diverged on separate evolutionary pathways because these populations were clustered on different sides of a plane using PCA and placement on separate branches of the topology by GENELAND.

Based on geography and morphometrics, we expected the two Reifel Refuge chicks to cluster with BC coast birds, however, these two birds consistently clustered with the other CVP cluster. Two possible hypotheses exist for these results. Littlefield and Ivey (2002) suggested the northern range of the CVP likely extends into interior British Columbia. These birds hatched on Reifel Refuge on Vancouver Island within the BC coast population range. In 1981, 17 hatch-year birds from Grays Lake National Wildlife Refuge, Idaho, part of the RMP, were banded and translocated to Vancouver (Leach 1987). Some of these banded birds were observed for the first few years following release (Harding 2010) but whether or not they were successfully recruited into local breeding populations is unknown. If these chicks are related to birds from the RMP, our results suggest the occurrence of allelic exchange between the CVP and RMP (currently unknown), possibly through the LCRVP or through range expansion of both the CVP and RMP to integrate with BC coast birds. However, it is more likely that these translocated individuals successfully incorporated into the BC coast population. Acquisition of samples from RMP and LCRVP birds would allow us to further to test this hypothesis.

A small group of Sandhill Cranes residing, but not breeding, on Sauvie Island always formed their own unique cluster (1). Aside from showing Type II mtDNA haplotypes, these birds showed no association with any other population in the Pacific Flyway suggesting that they are from a population genetically very different from any other currently sampled. There was a report of a Sandhill Crane nest on Ridgefield National Wildlife Refuge, WA (adjacent to Sauvie Island) prior to 1980 (E. Anderson, Ridgefield National Wildlife Refuge, pers. comm.) as well as a pair of Sandhill Cranes with young chicks on Sauvie Island in 2002 (Ivey et al. 2005). It is possible that this small breeding population is a relict group from the CVP following the bottleneck. But, the large magnitude of genetic differentiation observed between Sauvie Island birds and all other populations would not occur unless these birds were isolated for a long period of time. The Sauvie Island birds could also be from a different migratory population, i.e. MCP in eastern British Columbia/western Alberta (Krapu et al. 2011), LCRVP in Nevada/Arizona (Pacific Flyway Council 1995), or RMP in Idaho/Montana (Meine and Archibald 1996), but we do not have any samples from either of these areas to make these comparisons.

The northward expansion of the geographic ranges of BC coast birds and CVP birds may be reflective of Sandhill Cranes in the Pacific Flyway responding to climate change. Hitch and Leberg (2007) examined 29 avian species with a northern latitude distribution and 26 avian species with a southern latitude distributed throughout North America over the past 26 years. There was a significant northward expansion of southerly distributed species at a rate of 2.4

km/year without a reciprocal shift of northerly species moving southward (Hitch and Leberg 2007). For example, the range expansion of Hooded Warblers (*Setophaga citrina*) north into the northern continental U.S. and southern Canada over the past two decades is a result of warming global temperatures allowing birds to use resources and nest at more northerly latitudes and fostering growth of forest habitat (Melles et al. 2011). With Sandhill Cranes, this northward expansion of population ranges increases the interaction rate which could lead to more introgression between populations.

The results of our genetic analyses, combined with habitat (Campbell et al. 1990; Cooper 2006; Roessingh and Penn 2010), and migratory differences (Ivey et al. 2005; Petrula and Rothe 2005), indicate that Sandhill Cranes in the Pacific Flyway exist in distinct populations. The BC coast Sandhill Cranes in the Pacific Flyway are more than a hybrid between PFP and CVP birds. Although our genetic analyses revealed that BC coast birds share some similarity with a portion of CVP birds, the separation of lineages suggested by our clustering models are indicative of diversification between these populations. While we recommend more data collection from BC coast birds, our results suggest these birds be provided full population status.

Relating West Coast and Eastern Sandhill Crane populations

While all Sandhill Crane populations likely experienced a population bottleneck in the late 1800’s and early 1900’s, documentation of population reduction occurred for the CVP and EP (Henika 1936, Walkinshaw 1949). Both populations were reduced to similar numbers, however, the response of these populations to the bottleneck has been vastly different in terms of population numbers and growth, range recovery, and recolonization. The CVP expanded from a population of 150-200 birds in the 1930's to a current population size of 6,000-7,000 birds (Meine and Archibald 1996). While the population has grown and expanded from core refugia in California and Oregon that survived the bottleneck, re-colonization has been slow with few pairs settling back into Washington (Littlefield and Ivey 2002). The EP has also grown from a population of 200-300 birds in the 1930's to a current population size of over 60,000 birds (Kruse et al. 2012). Growth and re-colonization was slow, but steady, through the 1980's and 1990's (Su et al. 2004). The EP has currently re-colonized portions of the northeastern U.S. where Sandhill Cranes were extirpated by the 1600's (Melvin et al 2002, 2008).

A total of 386 AFLP loci were generated from selective primers *EcoRI*+GG/*BfaI*+TAT and *EcoRI*+GC/*BfaI*+TCT. A total of 170 adult birds were sampled from the EP, near Briggsville, WI (n=78) and Ohio (n=5), the southeast portion of the MCP (n=13, Jones et al. 2005), and compared to 74 birds from the CVP, PFP, BC coast population (the two Reifel Refuge chicks were removed), and Sauvie Island birds. Estimated heterozygosity was highest for Sauvie Island birds and lowest for PFP birds (Table 7.4). Number of private alleles per individuals sampled was highest for Sauvie Island birds and lowest for EP birds from Ohio (Table 7.4). For known bottlenecked populations (EP and CVP), estimated heterozygosity was higher for Briggsville birds compared to CVP birds and the lowest in Ohio (Table 7.4). Similarly, the number of private alleles per number of individuals sampled was highest for Briggsville while CVP and Ohio birds held similar numbers of private alleles per sampled individuals (Table 7.4).

Results of clustering analyses in GENELAND and PCA revealed population genetic structure among Birds were distributed into a modal K=11 clusters by GENELAND. PFP birds were placed in one cluster while CVP birds were allocated to two clusters, one of which also contained BC coast birds. The Briggsville birds were distributed among five clusters. Two CVP birds were placed in a Briggsville cluster (Figures 7.7, 7.8). These two CVP birds were originally placed in cluster 3 with other CVP birds and BC coast birds. The five Ohio birds were always placed in their own cluster, but close to the Briggsville birds. The MCP birds were placed in their own cluster that also contained one Briggsville bird. These 11 clusters were supported by the results of the groups formed by PCA (Figure 7.9).

The strong clustering of these birds to their source populations suggests little gene flow occurs between the CVP and EP, although some exchange of individuals may occur. This exchange is not likely to occur through the MCP as strong differentiation (based on Fst; Table 7.5) was recorded and little introgression based on the results from GENELAND and PCA. More realistically, birds transition through the RMP, which experiences gene flow with the EP based on microsatellite DNA markers (Jones et al. 2005).

More clusters were found in the post-bottleneck EP compared to the post-bottleneck CVP. Caution needs taken with these results as we do not know how many clusters were present in each population prior to the bottleneck. The results of these genetic analyses, combined with population estimates and range expansion, suggest that the EP is recovering from the bottleneck at a faster rate than the CVP. The increased growth rate of the EP may be assisted by exchange of individuals with the MCP, especially in re-colonized areas in the northeastern U.S.

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Table 7.1. Results of the discriminant function analysis assigning morphological subspecies of PFP, CVP, and BC coast Sandhill Cranes based on morphological measurements and sex.

ID	GENELAND cluster	Sex	probability Lesser	probability Canadian	probability Greater
C001	PFP	F	1.000	0.000	0.000
C003	PFP	F	0.971	0.029	0.000
C004	PFP	M	0.997	0.003	0.000
C007	PFP	F	0.997	0.003	0.000
C008	PFP	M	0.999	0.001	0.000
C011	PFP	M	1.000	0.000	0.000
C015	PFP	F	0.317	0.683	0.000
C016	PFP	M	1.000	0.000	0.000
C018	PFP	M	1.000	0.000	0.000
C019	PFP	M	1.000	0.000	0.000
C022	PFP	M	0.989	0.011	0.000
C023	PFP	F	1.000	0.000	0.000
C026	PFP	F	1.000	0.000	0.000
C027	PFP	M	0.935	0.065	0.000
C031	PFP	M	1.000	0.000	0.000
C032	PFP	F	0.973	0.027	0.000
C033	PFP	M	0.999	0.001	0.000
C010	CVP	F	0.000	0.113	0.887

Table 7.1 (cont.)

ID	GENELAND cluster	Sex	probability Lesser	probability Canadian	probability Greater
Z002	CVP	M	0.000	0.001	0.999
Z003	CVP	F	0.000	0.000	1.000
Z004	CVP	F	0.000	0.000	1.000
Z019	CVP	M	0.000	0.334	0.667
Z021	CVP	F	0.000	0.000	1.000
Z031	CVP	M	0.000	0.001	0.999
Z032	CVP	M	0.000	0.000	1.000
8824	BC coast	M	0.000	0.849	0.151
8726	BC coast	M	0.000	0.215	0.784
8725	BC coast	M	0.033	0.965	0.002
8746	BC coast	M	0.823	0.176	0.000
8827	BC coast	F	0.000	0.729	0.271
8737	BC coast	F	1.000	0.000	0.000
C002	BC coast	F	0.000	0.190	0.810
87530	BC coast	F	0.000	0.031	0.969
107878001	BC coast	M	0.092	0.860	0.048

Table 7.2. Genetic diversity estimates from AFLPs for Sandhill Cranes in the Pacific Flyway. Individuals categorized by clusters from 1,000 MCMC replicates in GENELAND (n=76 birds).

GENELAND clusters	N[a]	n[b]	PL[c]	%PL	PA[d]	He[e]	S.E.	Avg. loci/ind[f]	PL/N	PA/N
1 (Sauvie)	3	281	163	58.0	13	0.22	0.01	126.0±11.5	54.3	4.3
2 (CVP/BC chicks)	14	281	150	53.4	19	0.19	0.01	99.0±6.7	10.7	1.4
3 (CVP/Canadian)	20	281	149	53.0	23	0.15	0.01	92.2±4.5	7.5	1.2
4 (PFP - Homer)	18	281	145	51.6	16	0.15	0.01	95.9±5.4	8.1	0.9
5 (PFP - Dillingham)	21	281	138	49.1	9	0.12	0.01	86.7±5.1	6.6	0.4

[a] number of individuals analyzed

[b] number of loci analyzed

[c] polymorphic loci

[d] private alleles (0 = absence of a fragment, 1 = presence of a fragment)

[e] Nei's gene diversity, or expected heterozygosity

[f] average number of loci (±SD) present in each individual

Table 7.3. Pair-wise Fst for Sandhill Cranes categorized by cluster from 1,000 MCMC replicates in GENELAND (n=76 birds).

Cluster	2 (CVP/BC chicks)	3 (CVP/BC coast)	4 (PFP - Homer)	5 (PFP - Dillingham)
1 (Sauvie)	0.230 (0.188, 0.282)**	0.330 (0.295, 0.390)***	0.356 (0.321, 0.425)***	0.379 (0.345, 0.456)***
2 (CVP/BC chicks)	-	0.162 (0.140, 0.175)**	0.224 (0.201, 0.247)**	0.216 (0.193, 0.234)**
3 (CVP/BC coast)		-	0.061 (0.044, 0.070)*	0.086 (0.069, 0.094)*
4 (PFP - Homer)			-	0.055 (0.036, 0.062)*

Overall Fst: 0.239 (0.215, 0.260)**

[a] 0 to 0.05 indicates little genetic differentiation, *0.05 to 0.15 indicates moderate genetic differentiation, **0.15 to 0.25 indicates great genetic differentiation, ***0.25 indicate very great genetic differentiation (Wright 1978).

Table 7.4. Genetic diversity estimates from AFLPs for 170 adult Sandhill Cranes in six populations. Individuals categorized by population of origin.

Population	N[a]	n[b]	PL[c]	%PL	PA[d]	He[e]	S.E.	Avg. loci/ind[f]	PL/N	PA/N
Ohio – EP	5	386	132	0.342	1	0.113	0.008	98+1.4	26.4	0.20
Briggsville – EP	78	386	180	0.466	58	0.149	0.009	106+1.4	2.4	0.76
MCP	13	386	160	0.415	4	0.132	0.008	111+1.9	12.3	0.31
CVP	23	386	144	0.373	6	0.123	0.008	92+1.5	6.3	0.26
BC Coast	10	386	157	0.407	5	0.114	0.008	94+0.9	15.7	0.50
PFP	38	386	133	0.345	16	0.093	0.007	89+1.0	3.5	0.42
Sauvie	3	386	157	0.407	6	0.153	0.009	123+5.8	52.3	2.00

[a] number of individuals analyzed

[b] number of loci analyzed

[c] polymorphic loci

[d] private alleles (0 = absence of a fragment, 1 = presence of a fragment)

[e] Nei's gene diversity, or expected heterozygosity

[f] average number of loci (±SD) present in each individual

Table 7.5. Pair-wise Fst for 170 adult Sandhill Cranes categorized by population of origin.

Population	Ohio – EP	MCP	CVP	BC Coast	PFP	Sauvie
Briggsville – EP	0.124 (0.103, 0.159)*	0.097 (0.086, 0.111)*	0.112 (0.104, 0.121)*	0.166 (0.152, 0.185)**	0.198 (0.192, 0.205)**	0.314 (0.289, 0.386)***
Ohio – EP	-	0.184 (0.143, 0.222)**	0.167 (0.131, 0.206)**	0.147 (0.102, 0.184)*	0.193 (0.161, 0.221)**	0.358 (0.266, 0.478)***
MCP		-	0.230 (0.206, 0.246)**	0.214 (0.183, 0.241)**	0.274 (0.254, 0.294)***	0.373 (0.327, 0.454)***
CVP			-	0.087 (0.061, 0.107)*	0.113 (0.100, 0.123)*	0.293 (0.254, 0.395)***
BC Coast				-	0.073 (0.053, 0.084)*	0.327 (0.266, 0.386)***
PFP					-	0.384 (0.352, 0.458)***
Overall Fst: 0.233 (0.213, 0.255)**						

[a] 0 to 0.05 indicates little genetic differentiation, *0.05 to 0.15 indicates moderate genetic differentiation, **0.15 to 0.25 indicates great genetic differentiation, ***0.25 indicate very great genetic differentiation (Wright 1978).

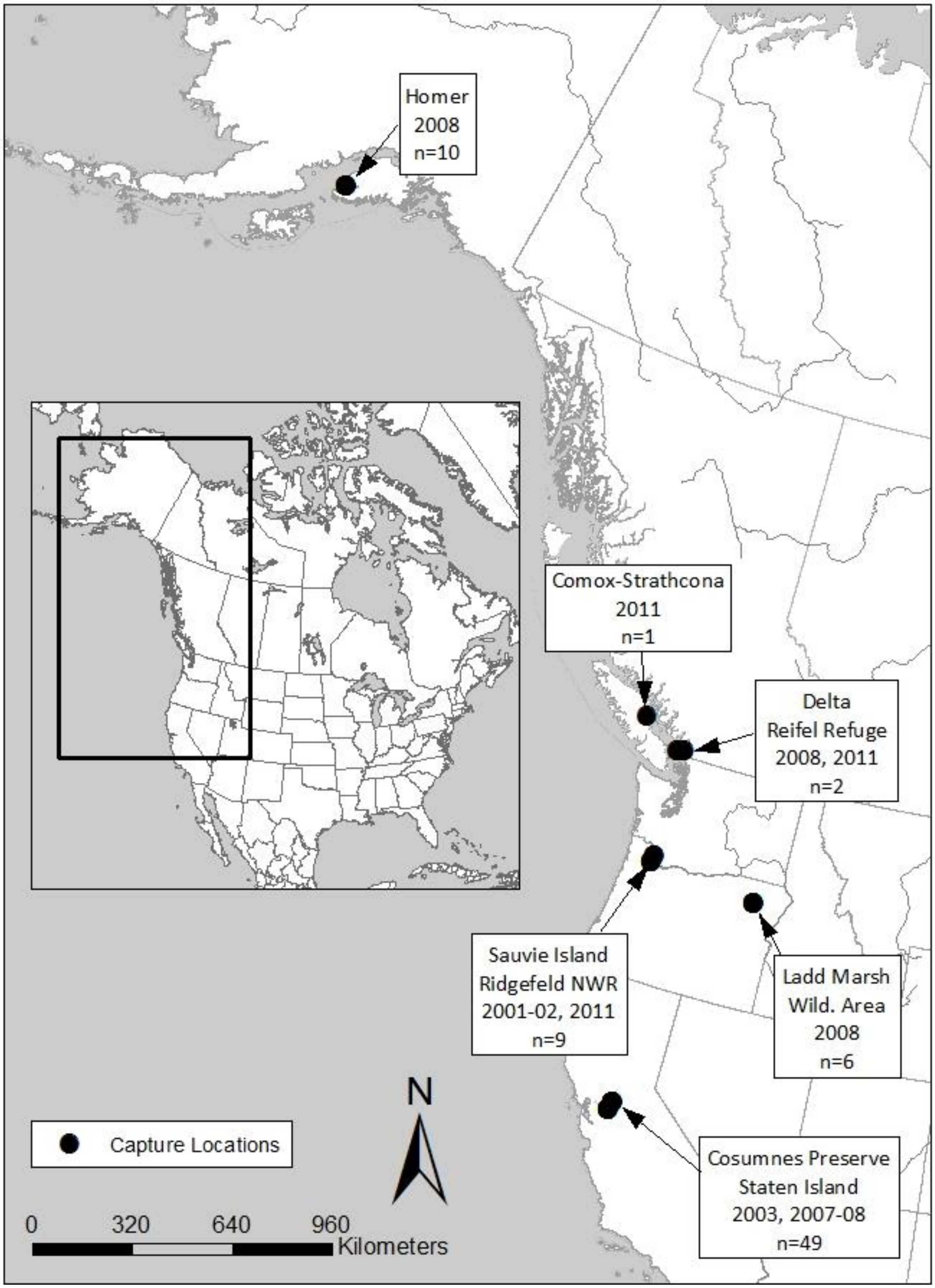

Figure 7.1. Locations, dates, and number of Sandhill Cranes captured and banded in the Pacific Flyway.

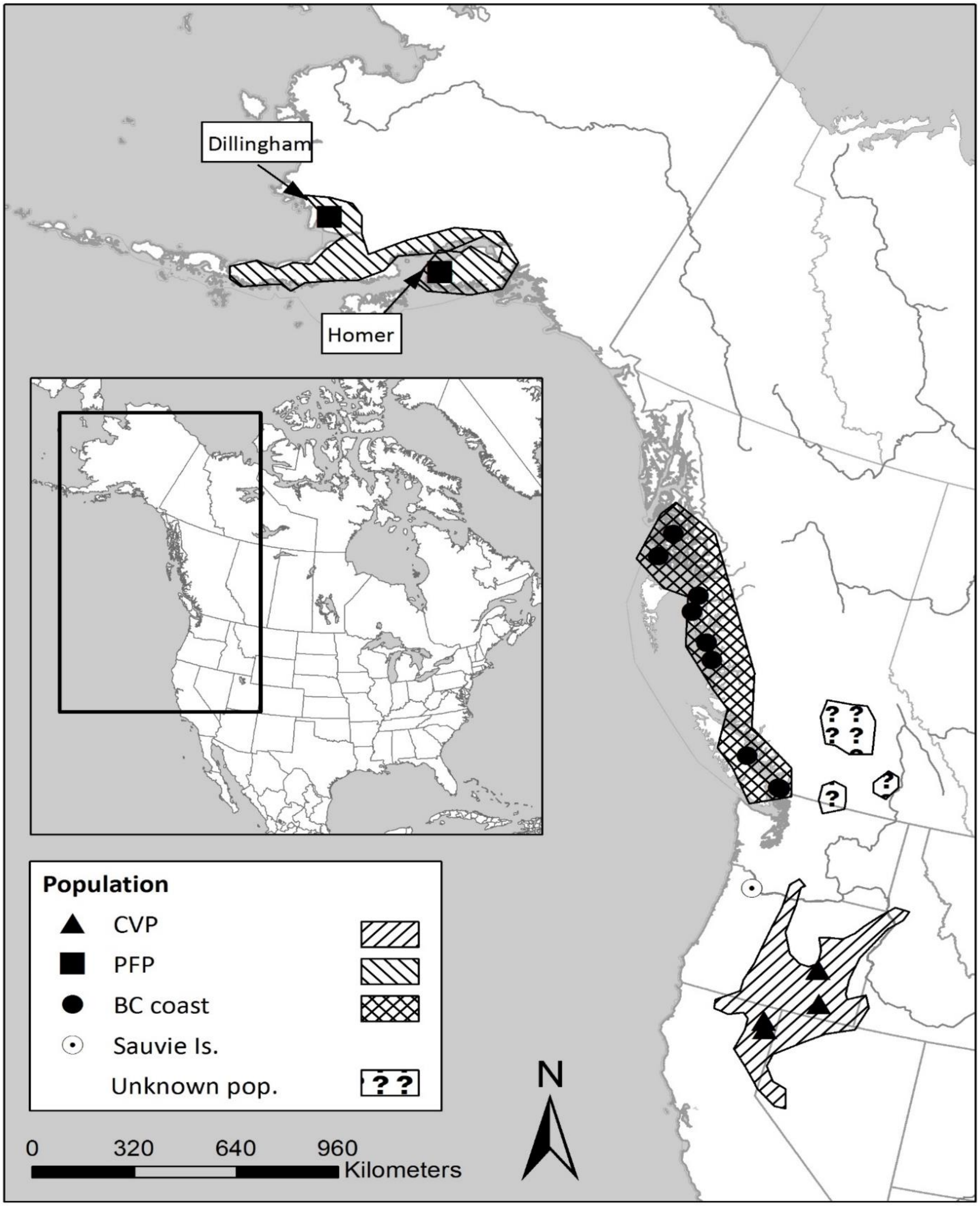

Figure 7.2. Summer, and probable breeding, locations for Sandhill Cranes in the Pacific Flyway determined with satellite and VHF telemetry. Estimated geographic breeding ranges redrawn from Littlefield and Ivey (2002) and Ivey et al. (2005).

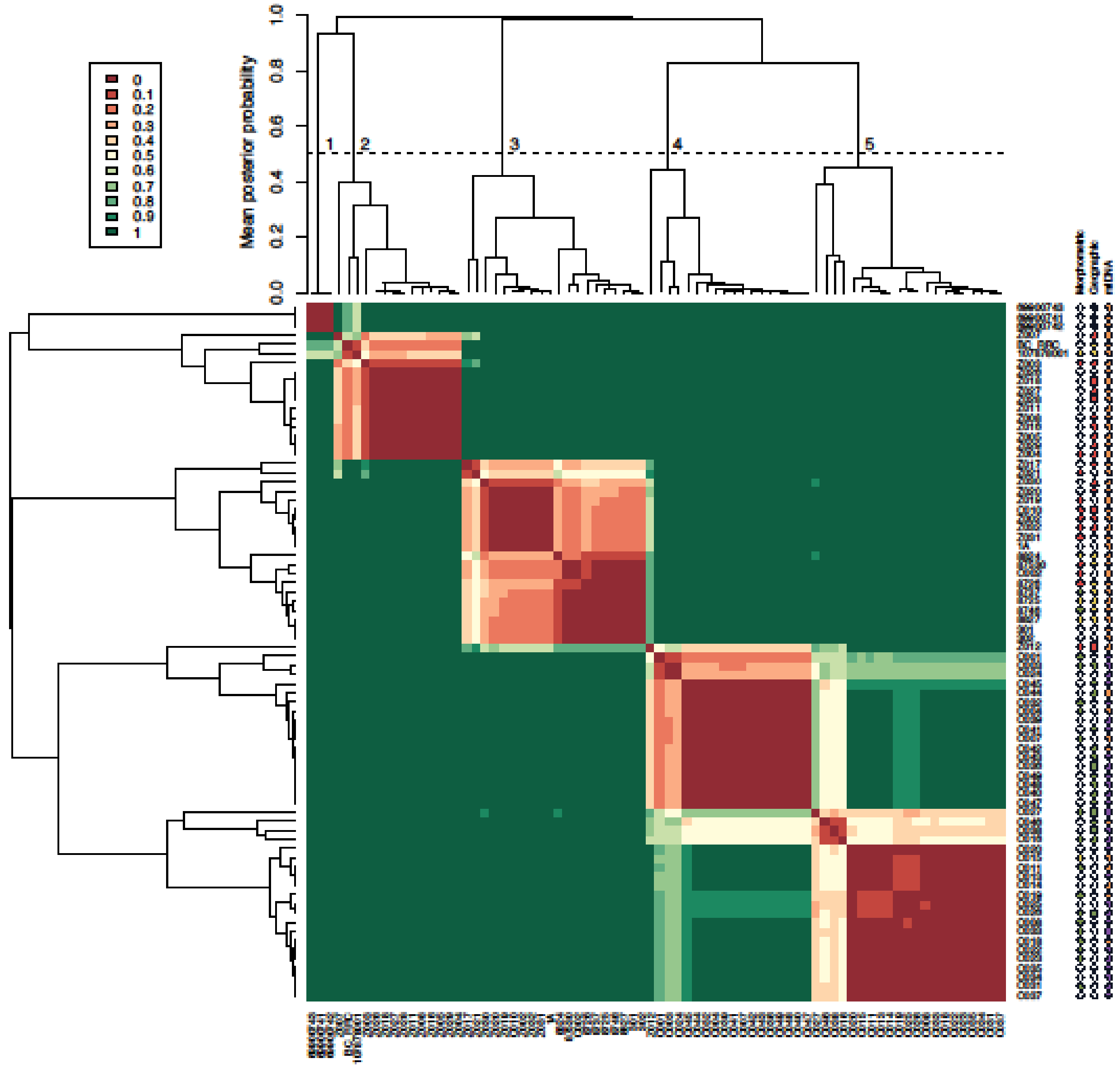

Figure 7.3. Average linkage among 76 individuals in 1,000 MCMC replicates of a non-spatial model. The scale for the heat map is 0 (always placed in the same cluster, colored red) to 1 (never placed in the same cluster, colored green). The dotted line represents a mean posterior probability of cluster membership at 50%. Three columns of varying shapes and colors represent three possible ways each bird was categorized. Open/white circles for all columns show the information for that bird in that category is unknown. Far left-hand column shows

morphometric classification: red circles are Greaters, goldenrod circles are Canadians, and olive circles are Lessers. Middle column shows geographic classification: red circles are Central Valley Population birds in Modoc, red squares are Central Valley Population birds in Silvies/Burns, red triangles are Central Valley birds in Alvord Desert, goldenrod circles are from the BC coast population nesting along the coast of Alaska/British Columbia, olive circles are Pacific Flyway Population birds in Homer, olive squares are Pacific Flyway Population birds in Dillingham, black circles are birds on Sauvie Island. Far right-hand column shows mtDNA haplotype: purple circles are Type I and orange circles are Type II.

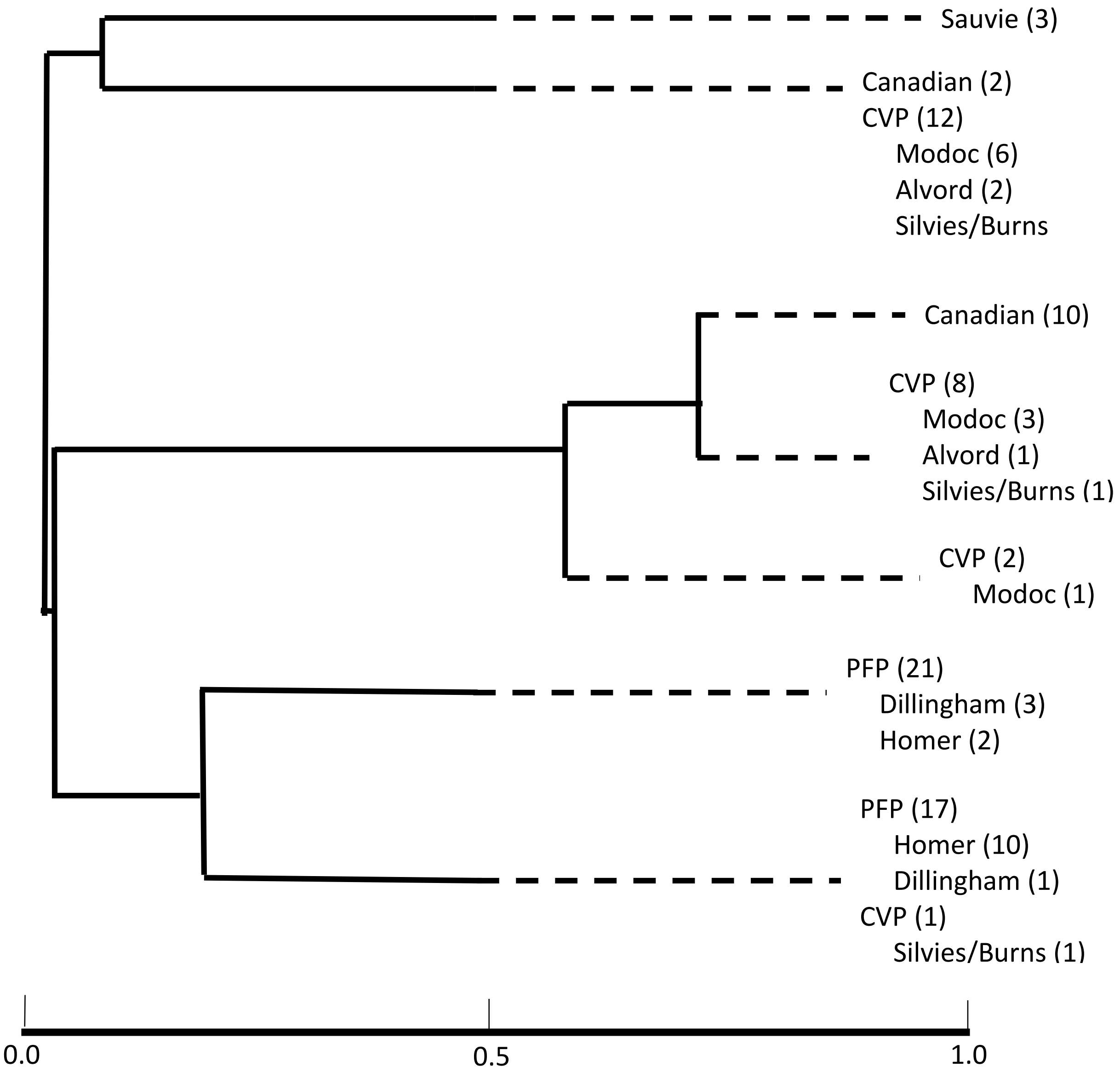

Figure 7.4. Dendrogram based on assignment of 76 Sandhill Cranes to genetic clusters using a GENELAND nonspatial model. A value of 1.0 indicates that birds were never placed in the same cluster while a value of 0.0 indicates that birds were always placed in the same cluster. The major seven branches are shown and a dotted line indicates smaller branches that were collapsed for simplicity. The number of individuals from each subspecies and sampling location (if known) are shown in parenthesis.

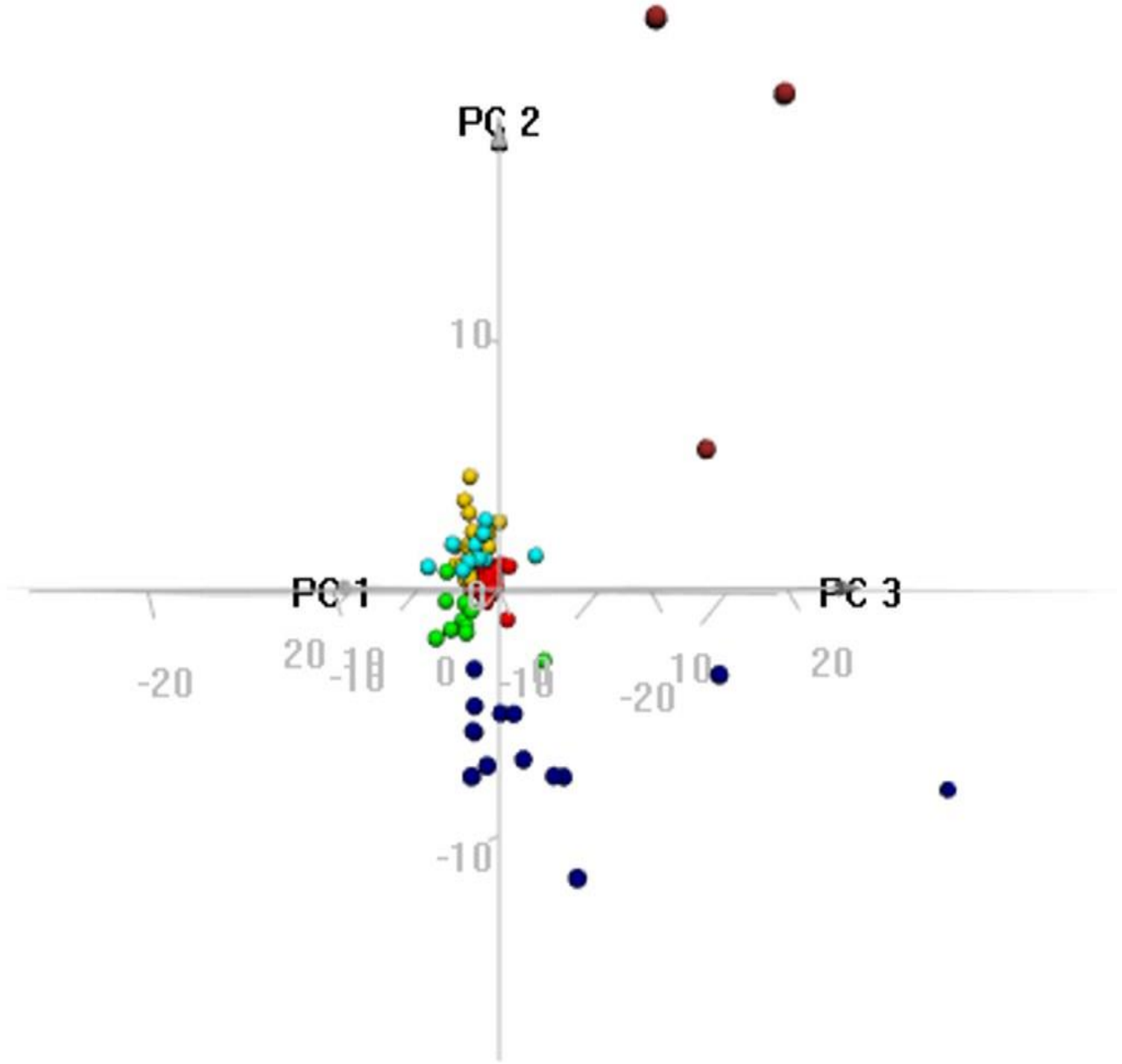

Figure 7.5. Three-dimensional plot of the first three principal components for all 76 Sandhill Cranes. Maroon spheres = Sauvie Island, dark blue spheres = cluster 2, green spheres = CVP birds in GENELAND cluster 3, light blue spheres = BC coast Canadians in GENELAND cluster 3, yellow spheres = PFP birds in GENELAND cluster 4 (most banded in Homer), red spheres = PFP birds in GENELAND cluster 5 (most banded in Dillingham).

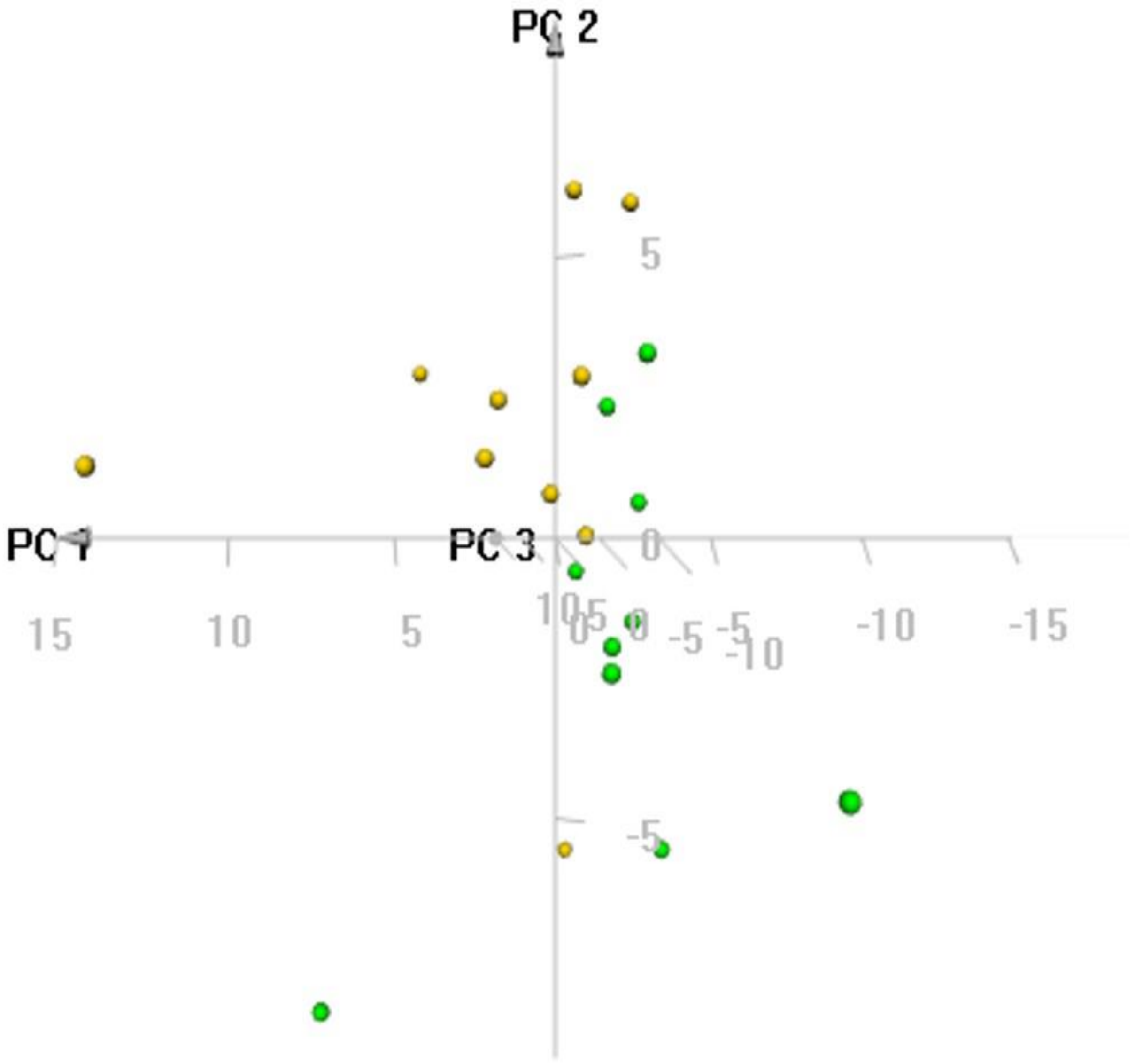

Figure 7.6. Three-dimensional plot of the first three principal components for 20 Sandhill Cranes in GENELAND cluster 3. Green spheres = BC coast Canadians in GENELAND cluster 3, yellow spheres = CVP birds in GENELAND cluster 3.

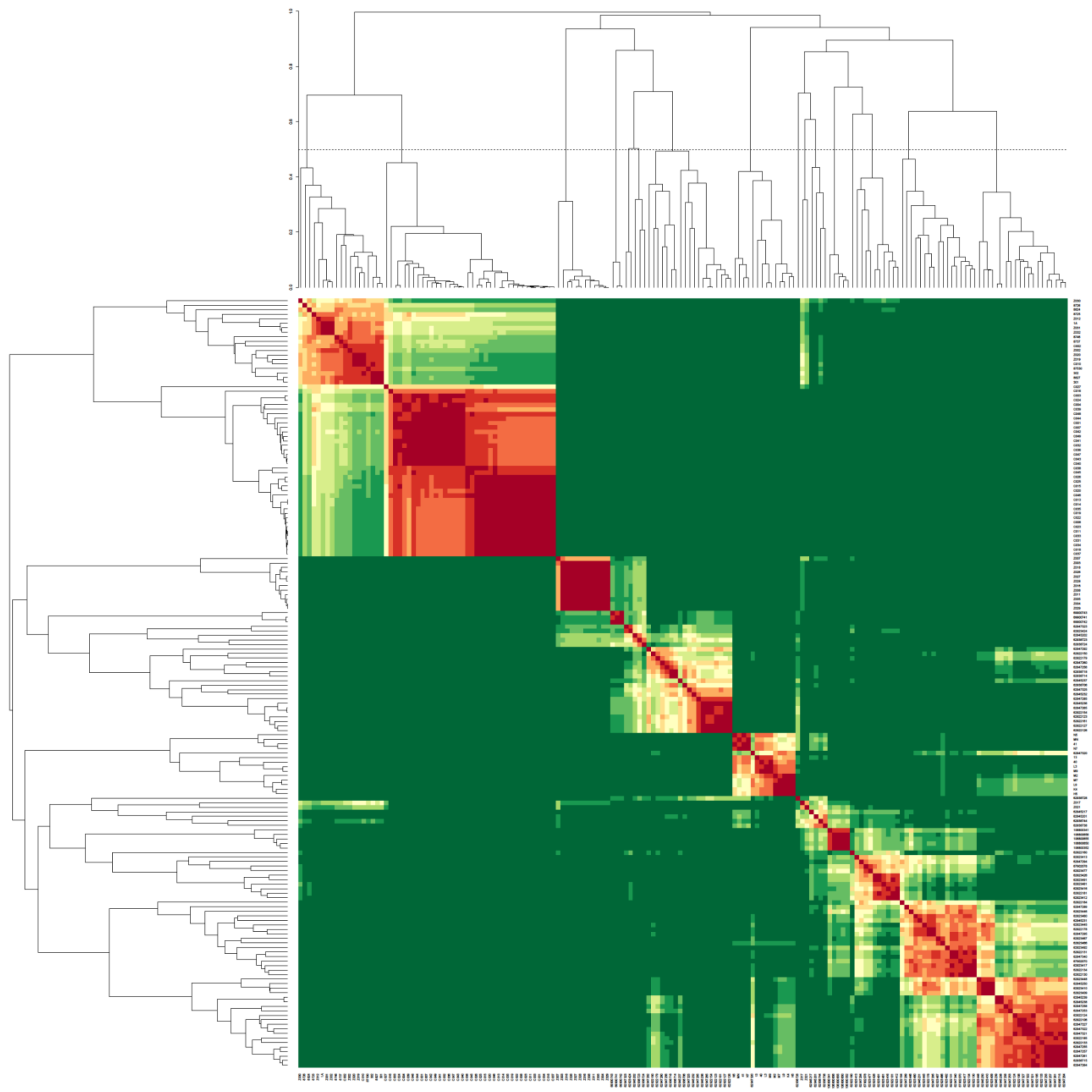

Figure 7.7. Average linkage among 170 individuals in 1,000 MCMC replicates of a non-spatial model. The scale for the heat map is 0 (always placed in the same cluster, colored red) to 1 (never placed in the same cluster, colored green). The dotted line represents a mean posterior probability of cluster membership at 50%.

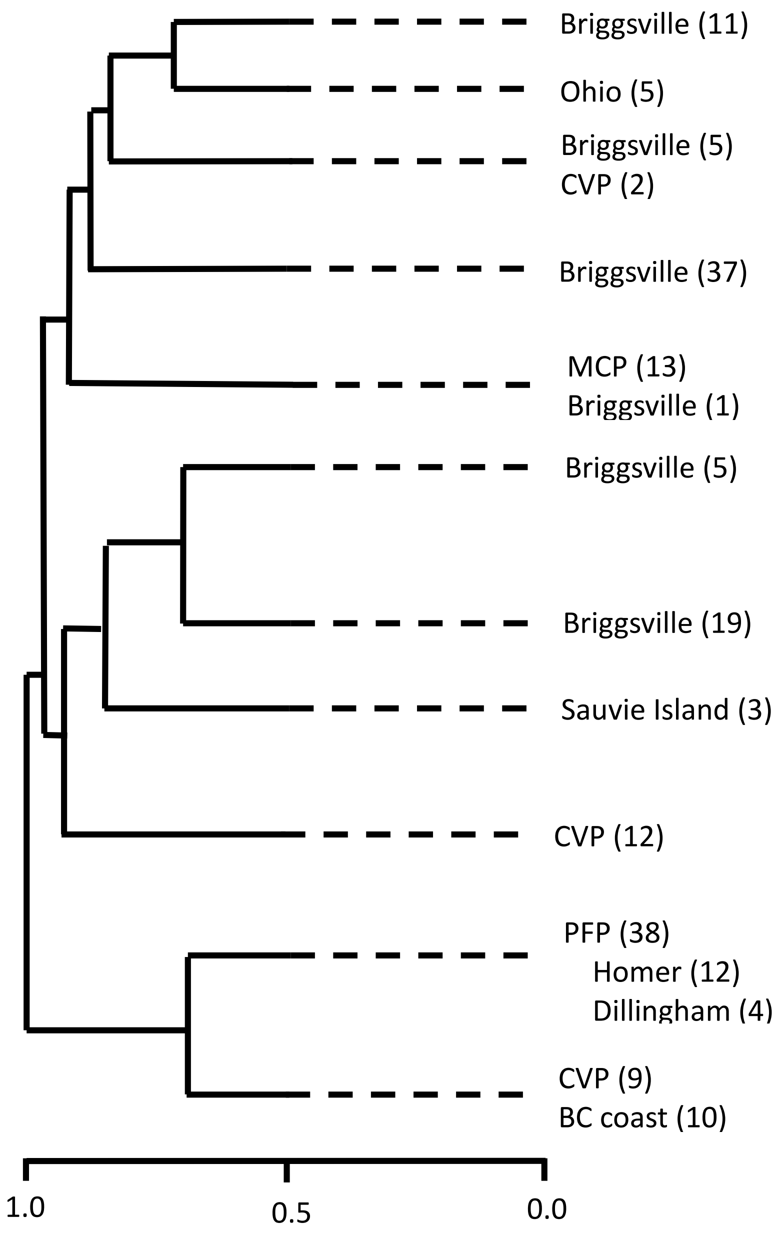

Figure 7.8. Dendrogram based on assignment of 170 Sandhill Cranes to genetic clusters using a GENELAND nonspatial model. A value of 1.0 indicates that birds were never placed in the same cluster while a value of 0.0 indicates that birds were always placed in the same cluster. The major 11 branches are shown and a dotted line indicates smaller branches that were collapsed for simplicity. The number of individuals from each population and sampling location (if known) are shown in parenthesis.

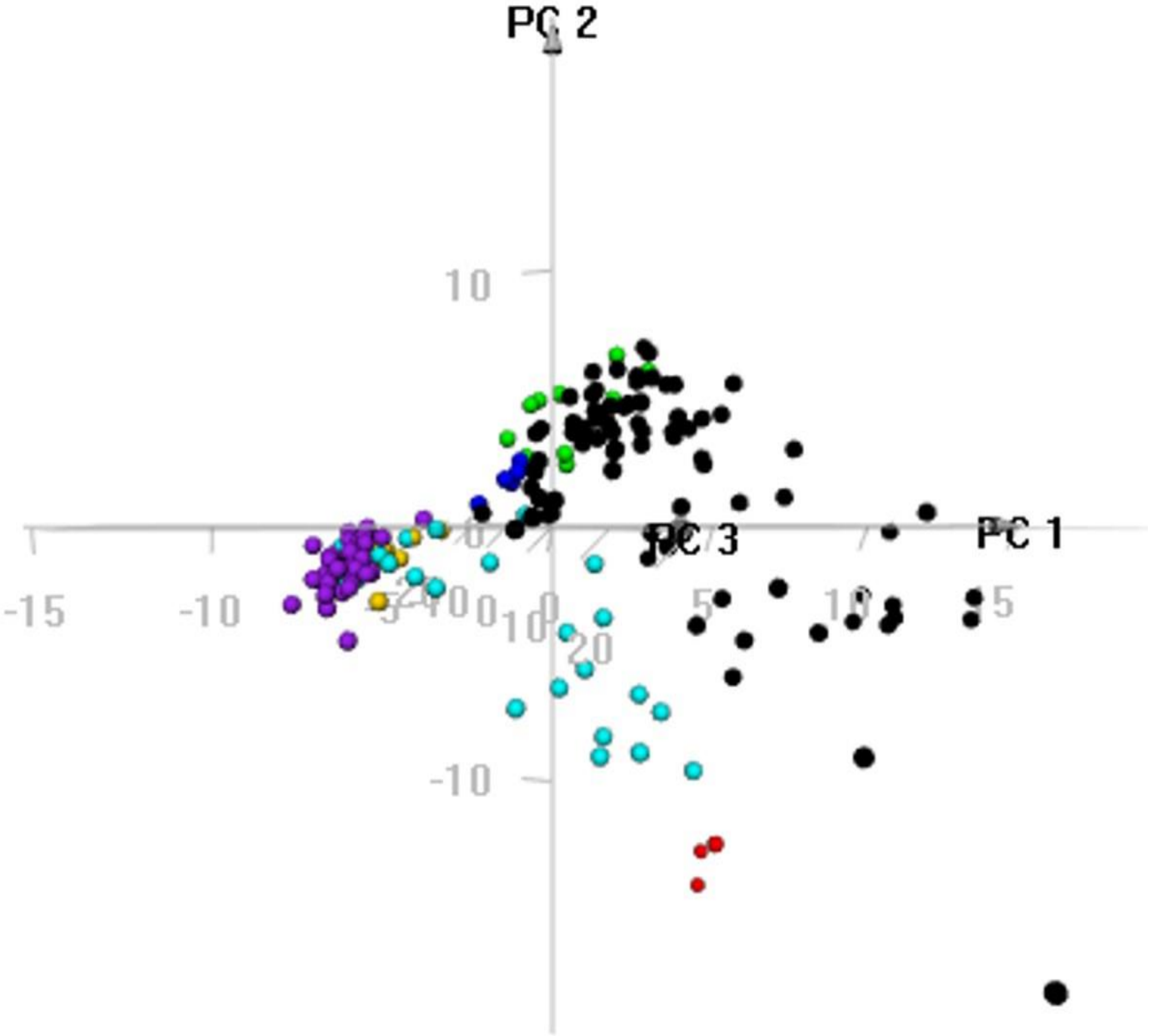

Figure 7.9. Three-dimensional plot of the first three principal components for all 170 adult Sandhill Cranes based on sampling population. Blue spheres = EP – Ohio, light blue spheres = CVP, green spheres = MCP, yellow spheres = BC coast, red spheres = Sauvie Island, purple spheres = PFP, black spheres = EP – Briggsville.

Chapter 8

CONCLUSIONS

Several key results regarding population dynamics of Sandhill Cranes can be emphasized from this dissertation. Breeding, not non-territorial, Sandhill Cranes drive social and population dynamics in the Briggsville study population. As territory holders, they are the only social class capable of attempting reproduction each year. Since experienced birds were typically chosen as new mates following any type of mate switch (divorce or mate death), few non-territorial birds moved from the non-territorial flock to a breeding territory in the study area, even if they were sexually mature. While breeding dispersal occurred following divorce, distances moved by dispersing individuals were short, and typically birds moved to adjacent territories with a widowed or divorced bird.

Because breeding dispersal was rare, gene flow between breeding areas within the Eastern Population resulted from dispersal by non-territorial birds. Dispersal distances from their natal area were greatest for one-year-old birds and these birds returned near their natal area as they approached breeding age. For birds that obtained breeding territories, males nested closer to natal areas than females but both sexes were philopatric. Long-distance dispersal (greater than 25 km) movements were recorded for two females.

These results suggest that non-territorial Sandhill Cranes are not moving to reduce the occurrence of inbreeding. Differences in distances and directions travelled by males and females were not great enough to reduce encounters between siblings or between parent and offspring. Some male offspring nested less than one km from their natal territory, even when both parents were still present on that territory. Because experienced birds were preferred by territory holders to replace mates, this reduced the possibility that offspring would pair with a parent. Non-breeding associations occurred between nest mates after reaching independence, however none of these associations resulted in a breeding pair. The lack of severe inbreeding (in the Briggsville study area) is likely a result of a large pool of available mates. Similar results likely occur in other areas in the Eastern Population as evidenced by low inbreeding estimates for all sample areas.

Alternatively, movements by non-territorial birds are likely the result of resource availability. Young birds prefer to settle near their natal area if possible, but will disperse until they locate an available breeding location. Because few birds obtained a breeding territory as a pair, non-territorial birds are likely obtaining previously established territories and filling gaps left by breeding birds as a result of mate death or divorce. These territories may be low quality (in terms of chick production) compared to openings on high quality territories that are likely filled by experienced birds. More intense observations of reproductive success on possible territories would test this hypothesis.

Patterns of dispersal distances travelled by Sandhill Cranes between natal and breeding territories help explain population genetic structure observed in the Eastern Population. There was significant population genetic structure found based on sampling area. There was a strong correlation between geographic and genetic distance suggesting that most birds preferred to be philopatric near their natal territory. Genetic clusters often contained most birds from a particular breeding area. These results suggest strong natal philopatry in the Eastern Population of Sandhill Cranes.

There was also support for long distance dispersal between breeding areas. Several genetic clusters contained birds from breeding areas that were very geographically distant from each other. For example, it is possible that a bird from southeastern Michigan could pair with a bird from northwestern Wisconsin and one bird (likely the female as they were typically the dispersing sex) follows its mate to its natal area. Typically, the distances between breeding areas were greater than the longest natal dispersal distance recorded by a female Sandhill Crane in this study (103 km). So, either many birds are moving great distances, but these distances have not been recorded. Or, the population bottleneck experienced by the Eastern Population in the early 1900's has affected the population genetic structure and those effects are still observable in the genes of this long-lived species. This has also been observed in White-tailed Eagles (Hailer et al. 2006). It is probable that dispersal patterns were altered during the population bottleneck and birds were willing to travel great distances to locate a mate and available territory. This includes mate following which is common in male waterfowl that follow their female mates to their natal area (Anderson et al. 1992).

Western populations of Sandhill Cranes showed significant population genetic structure. The presence of two distinct genetic clusters among both Lessers and Greaters with little exchange between clusters suggests significant barriers to gene flow within both groups. For Lessers, this barrier could be geographical, or landscape, in nature as the distance between primary breeding areas was 400 km. For Greaters, this barrier was not geographical as birds from each cluster were mixed between three breeding areas. It is possible this barrier is cultural or sociobiological, but more research is needed to investigate this. While Canadians grouped with one cluster of Greaters, they formed their own branch. While gene flow occurs between Canadians and Greaters, each group is likely distinct with limited exchange. There was evidence of gene flow between Lessers and Canadians or Greaters based on the presence of type II mt DNA in Lessers which typically showed type I mt DNA. Sauvie Island birds were genetically distinct from all groups and may be from another unsampled population or from a remnant, unsampled population. More research comparing genetic samples from these birds to other nearby populations would help determine which hypothesis is supported.

Further research opportunities could answer open questions regarding Sandhill Crane family dynamics and behavior of non-territorial birds. More research directed toward wintering grounds would help unravel the family dissociation process and social dynamics between offspring and parent. How do the benefits of remaining together as a family change as a chick is capable of caring for itself? What causes a family to remain intact and return together in the spring? Is there winter site fidelity? Do pair members spend the winter together? If a pair successfully fledges a chick, are they more likely to spend the winter together? Determining the answers to these questions could provide insight into crane family dynamics and the costs and benefits of family group retention. If parents actively displace their chicks, it would suggest that the costs of chick provisioning and defense have outweighed the benefits of chicks staying with their parents. If chicks make the decision to leave their parents, it would suggest that the benefits they are receiving from their parents are outweighed by the chick’s ability to become independent and develop into adulthood.

More information is needed regarding long and short-range movements made while young, independent Sandhill Cranes before they obtain a breeding territory. The results of this dissertation suggest that non-territorial Sandhill Cranes are capable of utilizing a larger home range area and dispersing long distances from their natal area, but few stay far from their natal area for long periods of time. A study that investigates movements of non-territorial cranes that are three to five-years-old would provide insight into the decision-making process with regards to territory choice. Because site fidelity of breeding birds is extremely high, a decision process likely drives territory choice in Sandhill Cranes. It is also possible that young birds will focus on an area where there is a high probability of territory acquisition. Is prospecting for a specific territory a viable option for these birds? Or are they flexible by staying in a general location and observing when a territory becomes available? How does habitat preference play into territory choice? Does a chick consider its natal territory to be high quality habitat? Or does it learn habitat preferences as a non-territorial bird as it wanders throughout the landscape?

There was significant population genetic structure present in the Eastern Population of Sandhill Cranes. While levels of natal philopatry were likely high for most birds during the bottleneck, the reduction of available mates and suitable habitat possibly caused some birds to disperse longer distances to locate those resources. This may have increased mixing of lineages that explains the proportions of birds assigned to genetic clusters. We do not know if social dynamics changed during the bottleneck or if dispersal distances increased. More research is needed in the small, but growing, portion in the northeastern U.S. and Canada. So little is known about this population, and the loss of Scott Melvin from Massachusetts DNR will significantly affect our knowledge about this part of the population. Where do these birds winter? What areas do they use during migration? There is genetic evidence of interaction between the northeastern portion of the Eastern Population and the southeastern portion of the Mid-continent Population. Are birds from southern Canada now migrating through the northeastern U.S.? Are some of these birds staying to reproduce and integrating with northeastern birds?

Our results also show distinct genetic clusters present in west coast populations of Sandhill Cranes that also experienced a population bottleneck. In contrast to the EP, why is there little introgression between the two genetic clusters of CVP birds? Why is there little introgression between the two genetic clusters of PFP birds? More samples from the coast of British Columbia would help determine their relationship with the CVP and PFP. What percent of the population winter on Sauvie Island and what percent winter with other west coast populations? How does winter site location and fidelity influence possible mixing of these lineages?

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