

2016

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Matthew A. Hayes Jeb A. Barzen

Hayes, M. A., and J. A. Barzen. 2016. Timing of family dissociation does not affect long-term survival estimates of sandhill crane chicks. Proceedings of the North American Crane Workshop 13:33-41.

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

MATTHEW A. HAYES,¹ International Crane Foundation, E-11376 Shady Lane Road, Baraboo, WI 53913; and University of Wisconsin, Madison, WI 53706, USA

JEB A. BARZEN,² International Crane Foundation, E-11376 Shady Lane Road, Baraboo, WI 53913, USA

Abstract: Sandhill crane (*Grus canadensis*) chicks depend on their parents beyond fledging, but timing of chick separation from their parents has rarely been quantified and reported. We color-banded and radio-tagged sandhill crane chicks on known natal territories in south-central Wisconsin and monitored family groups to determine age of chick independence. Using a Cormack-Jolly-Seber open population model in program MARK, we estimated survival for chicks that dissociated from their parents prior to fall migration, over winter (including migration), and following spring migration. Of 96 chicks with a known timing of dissociation from their parents, 11 (12%) became independent from their parents in the fall before migration during their hatch year, 76 (79%) became independent over winter, and 9 (9%) returned from spring migration with their parents and then became independent. Mean age (\pm 1 SE) at independence varied from 146 \pm 7 days (fall) to 248 \pm 14 days (off breeding areas) to 335 \pm 11 days (spring). Season of chick dissociation did not affect whether a chick was philopatric or dispersive in its first year. Lifetime survival estimates were high (92%) and did not generally differ based on marking scheme (radio-tagged vs. color-banded), sex (male or female), or timing of dissociation (fall, off breeding areas, or spring). Chicks that did not migrate with their parents likely learned migratory routes and behaviors from conspecifics. More research on interactions between parents, their offspring, and other conspecifics off breeding areas (winter and migratory stopover areas) could provide insight into dissociation patterns and the mechanism of separation.

PROCEEDINGS OF THE NORTH AMERICAN CRANE WORKSHOP 13:33-41

Key words: Chick dissociation, estimated survival, *Grus canadensis*, independence, philopatry, sandhill crane.

Three main phases of the dispersal process (departure, transience, and settlement) have been described in animals (Bowler and Benton 2005, Clobert et al. 2009). 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 growth over 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). In species with cooperative breeding systems such as scrub jays (Aphelocoma coerulescens), however, prolonged dependence can increase subsequent breeding success (McGowan and Woolfenden 1990).

Duration and degree of an offspring's post-fledging dependence on its parents vary widely among avian species. Post-fledging family associations persist approximately as long as the nestling period in most passerines (Skutch 1976) while long-lived avian species often require double the nestling period or longer (Warren et al. 1993, McIntyre and Collopy

Precise stimuli for family dissociation are not well known. Departure behavior may be proximately driven by interactions among family 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 (Weise and Meyer 1979; Bustamante 1994, 1995) or a response to a reduction in feeding by the parents (Holleback 1974, Guo et al. 2010, 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

^{2006,} Jonker et al. 2011). For example, exhibiting a brief post-fledging dependence, glaucous gull chicks (*Larus hyperboreus*) take 45-50 days to fledge but are 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 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).

¹ E-mail: mhayes315@hotmail.com

² Present address: S-12213 Round River Trail, Spring Green, WI 53588, USA

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 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 crane chicks learn an array of foraging behaviors and food preferences from their parents, parental provisioning to offspring declines following chick fledging but does not cease (International Crane Foundation [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, Hayes et al. 2007).

Though cranes are well-studied (Meine and Archibald 1996), 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 quickly even though parents separated from their chicks less than a month prior to nest initiation. In non-migratory red-crowned cranes (G. japonensis) (Kamata 1994, Kamata and Tomioka 1991) and in migratory Eurasian cranes (G. grus) (Alonso et al. 1984, 2004), familial dissociation was prolonged over a 1 to 3-month period during the winter and nonbreeding 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 (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 feeding behavior toward chicks changed from provisioning to displacement (by pecking and harassment) or abandonment of the young by parents on winter and non-breeding areas (Kamata 1994, Kamata and Tomioka 1991).

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 techniques, survival skills, and migratory routes), then chicks should remain with their parents at least until after their first fall migration. We expected chicks that dissociated from their parents in the spring after returning from migration to show higher levels of philopatry as second-year birds than those that dissociated during the previous fall or winter as hatchyear birds. We hypothesized that a chick that returned with its parents to its natal area and was then forced from the territory by its parents would benefit from remaining near its natal area to obtain resources and protection from predators. We also hypothesized that any offspring that dissociated from their parents before fall migration would have lower estimated survival than those that dissociated either over winter or postmigration in spring. We 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, we expected more chicks would dissociate from their parents over winter than postspring migration because a chick's association with its parents through spring may increase energetic cost to the parents, as they prepare for the next nesting event, with minimal benefit to the chick, which is nearly adult size and will likely not breed during their second-year (Radke and Radke 1986).

STUDY AREA

Colored leg bands were deployed on sandhill crane chicks near Briggsville, Wisconsin (43°36′N, 89°36′W; Figure 1). This has been the site of a long-term study on sandhill crane breeding ecology and habitat selection by the ICF since 1991 (Hayes et al. 2003, Su 2003,

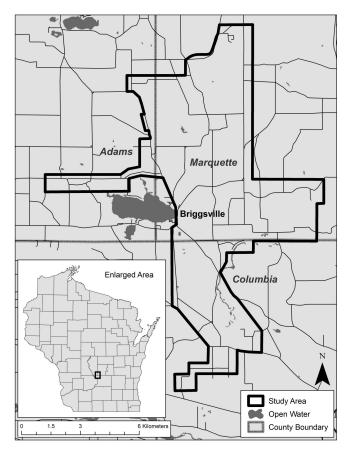


Figure 1. Map of the study area (delineated by the black line) near Briggsville, Wisconsin. This is the site of the long-term sandhill crane research project for the International Crane Foundation, 1991-2012.

Hayes 2015). 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, Hayes 2015).

METHODS

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 1983). Volant adults and chicks (older than 70 days) were captured by using alpha-

chloralose (Bishop 1991), an oral tranquilizer (Fisher Scientific Company, Fairlawn, NJ; and Biosynth Ag, Switzerland) according to the methodology described in Hayes et al. (2003), or leg snares (Hereford et al. 2001).

A captured crane was classified as a chick by the absence of red skin on the crown (Lewis 1979). For flightless chicks, age was further classified into the approximate number of weeks using growth criteria (Hayes 2015). Blood samples were collected from 198 of 204 (97%) chicks banded 1996-2012. Sex was determined from blood using molecular techniques (Griffiths et al. 1998, Duan and Fuerst 2001); otherwise, sex was determined through morphological or behavioral characteristics, i.e., males are larger than females (Nesbitt et al. 1992; ICF, unpublished data), and mature males and females have different pitches to their voices and exhibit different postures during unison call (Archibald 1976). Chicks for which this information was unavailable were considered of "unknown" sex.

Each crane received a size 9 rivet Bird Banding Laboratory (U.S. Geological Survey) band and a unique combination of colored plastic leg bands to allow resightings in the field using binoculars or spotting scope (Dickerson and Hayes 2014). Additionally, randomly chosen adults and chicks received leg band-mounted transmitters or backpack harness transmitters to allow identification and provide non-biased locations at any time (Miller and Barzen 2016, Hayes and Barzen 2016).

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 1 of 2 ways. If a chick was banded while flightless, its hatch date was calculated by subtracting its approximate age in days at capture from the date of capture. Fledged chicks are more difficult to age 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), a mean hatch date was calculated from chicks caught while flightless in that same year. For post-fledged chicks with banded parents (n = 18), we then verified this estimate using previous sightings of the family that had occurred while the

chick was flightless. From these dates, an approximate maximum age (days) of independence for each chick was obtained by subtracting the date when the family unit 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, observations within the study area were regularly monitored from March through November annually. Outside Wisconsin, monitoring was more sporadic in some 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). Resightings outside breeding areas were sent to the ICF or Bird Banding Laboratory by other researchers or the general public, often by dedicated volunteers, after observing a banded bird. Re-sightings reported by non-ICF personnel were only accepted as high confidence in accuracy when they were accompanied by a digital photograph or if all of the bands were reported exactly as they were placed on the bird at the time of capture. All re-sighting and telemetry data were stored in a Microsoft Access or on-line Mapfeeder database.

Statistical Analyses

A deviation from normality was verified using a Q-Q plot in R. We used non-parametric tests for statistical analyses on all data that were not normally distributed. A Mann-Whitney U test (Sokal and Rohlf 2001) was used to determine if males and females differed in the approximate ages when chicks dissociated from their parents and if there was a difference in age for chicks that dissociated from their parents prior to fall migration as a result of capture compared to those that were not directly related to capture. Mean values are \pm 1 SE. All data sets were tested for normality using a Shapiro-Wilk test (Shapiro and Wilk 1965), and significance was set at $P \le 0.05$.

Chicks were considered philopatric if they were observed within the study area during pre- or postnesting periods (Feb-Aug) following their hatch or dispersive if not seen in the study area during this period but seen alive elsewhere. Any point within the study area was within a distance 10 times the diameter of an average territory (Shields 1982). We did not consider birds seen in the study area only during September-November as philopatric because birds nesting outside the study area often stage (Melvin and Temple 1982)

within our study area during this time (ICF, unpublished data). We evaluated radio-tagged and color-banded birds for philopatric or dispersive behaviors based on our detection method using a Fisher's exact test (Sokal and Rohlf 2001).

For birds with a known season of dissociation from their parents, long-term (lifetime) survival (φ) and encounter (ρ) rates were estimated using a Cormack-Jolly-Seber open population model (Cormack 1964, Jolly 1965, Seber 1965) in Program MARK (White and Burnham 1999). Because radio-tagged birds have increased detectability, especially on areas outside of breeding areas that were monitored, we separated radiotagged 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, off breeding areas, post-spring migration). Program MARK was run 3 times for both radio-tagged and non-radiotagged 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 time and season, and 3) time, combined sex and season, and the interaction between time, sex and season. Model fit was evaluated by AIC and any model ≤ 2 AIC, from the theoretically best model was 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 1 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 prior to fledging while 9 died and 6 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. Five of 176 birds had unbanded parents, so timing of dissociation could not be accurately determined. For the remaining 171 chicks with at least 1 banded parent, dissociation timing was unknown for 75 chicks (44%; 29 M: 41 F: 5 U) because neither the chicks nor their parents were observed prior to the parents' nesting season following their hatch year.

Remaining were 96 (56%; 39 M: 53 F: 4 U) chicks with a known timing of dissociation. Eleven of these birds (12%) dissociated from their parents prior to fall migration. This dissociation occurred approximately 3 weeks after being last observed with their parents (Table 1). Two of these chicks had radio transmitters and were never recorded in the same vicinity as their parents following dissociation. Seven of 11 chicks that dissociated in fall were members of 2-chick broods. The mean age of chicks that departed from their parents before fall migration was similar for males (n = 6; 143) \pm 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. Mean age when chicks dissociated from their parents was lower for dissociations resulting from capture (126 ± 4 days, range = 116-134 days, n = 6) compared to those that were not capture-caused (157 \pm 5 days, range = 140-170, n = 5; 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 of 96 chicks (8.3%) were observed on wintering grounds without their parents (Table 1). Five of these chicks (2 M: 3 F) had radio transmitters, as did 1 parent of each chick, when observed apart. Each parent varied in the distance from its chick, ranging from being in different flocks (i.e., 1 km apart) to residing in different states (i.e., hundreds of km 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. These separations likely occurred off breeding areas, although there was no confirmation from observations in these areas. Twenty-three (8 M: 15 F) of these 68 chicks had active radio transmitters when they returned the following spring. Each chick's frequency was not detected 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%), 2 of which had active radio transmitters, returned to the breeding grounds with their parents in the spring as second-year birds. Similar to chicks that dissociated from their parents in the fall, these birds dissociated from their parents approximately 3 weeks later. Mean age at familial dissociation post-migration in the spring did not differ between males (mean = 334 ± 18 days, range = 307-385 days, n = 4) and females (mean = 344 ± 14 days, range = 304-378 days; Mann-Whitney U = 10.5, P = 1.00, n = 5).

Overall, the season of family dissociation did not affect whether a bird was classified as philopatric or dispersive during their first year (Table 2). For each dissociation timing group, 50% of chicks were philopatric and 50% of chicks were dispersive in their first year. For chicks that separated from their parents away from breeding areas, second-year males tended to be more philopatric while second-year females tended to be more dispersive.

When sex and time were allowed to vary, 4 models were considered valid for radio-tagged birds and 3 models for non-radio-tagged birds (see Hayes 2015:81). For both radio-tagged and non-radio-tagged birds, estimated annual survival (φ) was consistent

Table 1. Summary of timing and age (days) when sandhill crane chicks dissociated from their parents in the population breeding near Briggsville, Wisconsin, 1991-2012.

Age at dispersion	n	Sex ratio (M:F:U)	Age (days) when last dependent			Age (days) when independent		
			Mean	SE	Range	Mean	SE	Range
Pre-fall migration	11	6:5:0	123	7	73-176	146	7	116-191
Off breeding areasa (known)	8	3:4:1	169 ^b	9	136-207	248	14	198-295
Off breeding areas ^a (likely)	68	26:40:2	163 ^b	3	51-201	unknown		
Post-spring migration	9	4:5:0	316	7	301-365	335	11	304-385

^a Includes fall migration, winter, and spring migration.

^b Age (days) = When chick was last observed with parents on breeding grounds before fall migration.

Table 2. Number of second-year birds showing philopatric or dispersive dispersal patterns in relation to timing of dissociation from their parents in the population breeding near Briggsville, Wisconsin, 1991-2012.

Dissociation timing						
	Philopatric				Total	
	n	Sex ratio	7	n	Sex ratio	
Fall Off breeding areas ^a Spring	35	3 M: 1 F 18 M:17 F 2 M: 2 F	3	34	2 M: 2 F 6 M: 25 F:3 U 2 M: 2 F	8 69 8

^a Includes fall migration, winter, and spring migration.

(approximately 92%) among data sets, even when φ varied by sex. Estimates of encounter rate (φ) were more variable and tended to be higher for radio-tagged birds compared to non-radio-tagged birds (Hayes 2015:82).

When the season of dissociation (fall, off breeding areas, 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-radiotagged birds. For radio-tagged birds, 2 models were considered valid with ρ always varying based on season of dissociation and ϕ remaining constant or varying based on season (mean = 92%; Hayes 2015:83). For the model estimates when ϕ varied based on season, estimated survival was lower for radio-tagged chicks that dispersed during fall and highest for chicks that dispersed in spring. For non-radio-tagged birds, there was 1 best model with both ϕ and ρ remaining constant (Hayes 2015:84).

When radio-tagged and non-radio-tagged birds were grouped based on time and the combination of sex and season of dissociation from their parents, there was 1 best model for each data set. Estimates of φ remained constant and were identical (approximately 92%) for both data sets (Hayes 2015:85-86). Estimates of φ were constant for radio-tagged birds (84%). Estimates of φ were 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 (Hayes 2015:86).

DISCUSSION

Sandhill crane chicks likely dissociated from their parents and became independent at a continuum of ages, but we measured these separations at only 3 points in their life cycle: before their first fall migration, when they were off breeding areas, and after returning with their parents in the spring as second-year birds. Most chicks stayed with their parents through their first fall migration and the highest frequency of dissociations occurred off breeding areas followed by post-spring migration and then prior to fall migration. Overall survival rates of chicks were high and did not differ from each other, 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 over-winter separation. There may not be an optimal dependence period for post-fledged sandhill cranes.

Season of dissociation from their parents did not affect philopatry rates during the first year. Chicks that dissociated from their parents in the fall were as likely to remain philopatric as those that dissociated off breeding areas or returned with their parents in spring. A chick's philopatric or dispersive behavior as second-year birds may be more reliant on social influence from conspecifics rather than their parents.

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 6 months of age or earlier, why do they remain with their parents for a longer time period? Sandhill crane chicks are 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.), pre-migratory aggregations are not typically observed (D. Racine, personal communication). Separation from parents (either accidental or by choice) in these lowdensity areas could be fatal because there would not be as many conspecifics nearby to learn migration patterns. Familial dissociation patterns of sandhill cranes in the northeastern U.S. are currently unknown. Still, novel migrations can occur in at least adult cranes without learning (Hayes et al. 2007).

Hatch-year sandhill cranes (R. Urbanek, U.S. Fish and Wildlife Service, personal communication) and whooping cranes (*Grus americana*) (T. Stehn, U.S. Fish and Wildlife Service, personal communication) have been observed spending the entire first winter with their parents and then dissociating during spring migration or immediately after returning to breeding grounds. While it should be noted that our resolution of family dissociation off of breeding areas does not allow us to account for chicks that began spring migration with their parents and then dissociated before returning to their natal area, most pairs were re-sighted on breeding areas without a chick from the previous season present.

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 observed on their natal areas with their parents in the spring? This behavior would reinforce migratory routes and behaviors without affecting long-term chick survival. 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, 2004). Winter territoriality is known to occur in sandhill cranes (G. L. Ivey, ICF, personal communication); 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 comparison 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 (by parents) or a reduced dependence by the chick as it ages, is unknown.

More research is needed on dissociation of sandhill crane families, especially on non-breeding areas during the winter. For example, pair members may or may not remain in close proximity during the nonbreeding season (D. Aborn, University of Tennessee at Chattanooga, 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 help address these currently unanswered questions.

ACKNOWLEDGMENTS

We thank many International Crane Foundation research associates, interns, and volunteers for assisting in capture and re-sighting of color-banded sandhill cranes during the study period. A. Lacy and A. Gossens in the Field Ecology Department coordinated field crews each year and were essential in long-term maintenance of the Briggsville Sandhill Crane project. M. Berres, J. Howard, R. P. Urbanek, and J. Langenberg provided useful comments on this manuscript.

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