NESTING ACTIVITY BUDGETS AND ANTIPREDATOR BEHAVIORS OF MISSISSIPPI SANDHILL CRANES

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Abstract: We studied activity budgets and antipredator behaviors of Mississippi sandhill cranes (*Grus canadensis pulla*) to determine if parental behavior influenced nest outcomes. We used infrared motion-activated cameras to capture behavioral sequences from 21 nests over a 2-year period. Overall activity budgets were similar among crane pairs regardless of nest outcome. Specific activity patterns did predict nest outcomes; pairs at unsuccessful nests spent more time away from the nest and more time manipulating nest contents than successful pairs, while pairs at nests that were lost to predation cooperated poorly and started the nest a month later on average than successful nests. Wild-reared birds gave more agonistic displays toward potential threats than captive-reared birds, but both wild- and captive-reared birds successfully defended nests from potential predators. The results suggest that behavior patterns of nesting pairs can be used to predict likely nest outcome, and that birds differ in their ability to defend nests from predators. We suggest that training in antipredator behavior during captive rearing may increase behavioral competence and reduce losses to nest predators.

The Mississippi sandhill crane, *Grus canadensis pulla*, is a morphologically distinctive, non-migratory population of cranes inhabiting a small area of coastal Mississippi (Aldrich 1972). This population has been protected under the Endangered Species Act since 1973 (Gee and Hereford 1995) and has been the subject of a U.S. Fish and Wildlife Service reintroduction program since 1981, representing one of the largest and longest sustained reintroduction programs ever attempted (Ellis et al. 2000). Despite more than 30 years of supplementation with captive-reared cranes, the wild population on the Mississippi Sandhill Crane National Wildlife Refuge has remained stable at approximately 100 adult individuals over this time period.

While several factors may contribute to the limited success of reintroduction to date, including habitat area and quality (Ellis et al. 2000), low genetic diversity (Henkel et al. 2012), and predator pressure (Butler 2009), we also suspected that behavioral competence of nesting cranes may also be a serious impediment to successful breeding. Some breeding pairs on the refuge consistently produce chicks while others do not, and successful pairs frequently contain 1 member that was wild-reared or parent-reared in captivity. Most birds on the refuge were produced through costume-rearing in the captive breeding program, and a variety of behavioral problems are known to arise from altered social environment and learning opportunities during captive rearing (Curio 1998). Nesting birds must master a variety of behaviors critical to success, including cooperation with the mate during incubation, nest maintenance, and nest defense; data on how these behaviors may vary among birds on the refuge are currently lacking.

In this study we asked how behavior patterns differed across nesting pairs over a 2-year period, and how behaviors were related to nesting success. We first asked if the basic activity budgets of nesting pairs were similar regardless of the nest outcome. We then investigated the details of specific behavior patterns to determine if parental behaviors predicted whether a nest would be successful, unsuccessful, or suffer predation. Finally, we focused on antipredator defense behaviors and quantified the types of agonistic displays seen in the population, the frequency with which cranes performed them, and context in which they were given.

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METHODS

The study was conducted on the Mississippi Sandhill Crane National Wildlife Refuge, located 5 km north of Gautier in Jackson County, Mississippi. The refuge encompasses approximately 8,000 ha of pine savannah and flatwoods habitat, managed primarily to maintain high-quality wildlife habitat for Mississippi sandhill cranes (U.S. Fish and Wildlife Service 2007). The refuge currently supports approximately 100 adult cranes; typically, 20-30 nesting attempts occur annually.

We installed motion-sensitive infrared trail cameras (RM 45 Rapidfire, Reconyx Inc., Holman, WI) on 22 nests during 2009 and 11 nests in 2010. To avoid changing the visual horizon close to the nest, cameras were installed on existing landscape features such as small trees whenever possible. A few cameras were installed on steel fence posts that could be concealed by vegetation. Cameras were placed between 2 and 30 m of the nest with a clear field of view of the nest and surrounding area to reduce the triggering of photos by movements of vegetation in the field of view. Data were recorded on 4-gigabyte compact memory cards. Cameras were visited approximately once per week to change batteries or memory cards until the nest was abandoned.

We first developed a nesting ethogram that we used to calculate time budgets and event rates for each nest. We viewed images sequentially for each nest using Windows Photo Gallery in Windows 2007 (Microsoft Corporation, Redmond, WA) and classified behaviors into 1 of 5 states or 5 events (Table 1). States were defined as behaviors for which a duration could be calculated, and states were mutually exclusive. Events were defined as behaviors that could be tallied, and could occur within a state (e.g., an incubating crane could display alert behaviors without interrupting incubation). We calculated the duration of states using the time stamp on each image, and scored the state as occurring continuously until the crane changed to another state. Because we used black-and-white cameras placed at a distance from the nest, we were often unable to identify individuals by their band colors or numbers, and behavioral rates are presented for the pair as a whole. In pairs where 1 individual was unbanded or bore a transmitter, we were able to record the behavior of individual cranes, and these cases are reported as individual records.

Because a behavioral pattern or single incident may be more critical to nest outcome than the overall time budget, we developed additional behavioral measures to use in fitting models to predict nest outcomes. Since time spent off the nest for any reason may affect egg viability, we calculated total time spent off the nest as the sum of Near Nest and Absent. We calculated the mean duration of each of the behavioral states, and recorded the maximum duration of each state. Finally, we added the Julian date of nest initiation to the list of variables, since there is evidence that nests initiated later in the season may experience greater temperature stress and exposure to predation (Butler 2009).

We examined all images of predator and non-predator interactions in detail to identify the frequency of known threat and attack behaviors (Ellis et al. 1998)

Table 1. Behaviors included in ethogram of nesting cranes at the Mississippi Sandhill Crane National Wildlife Refuge, 2009-2010.

Behavior	Definition
States[a]	
Incubate	Crane sits on the nest, otherwise inactive
Probe	Crane stands and manipulates nest or its contents with bill
Near nest	Crane is off the nest but within the camera's field of view
Preen	Crane grooms feathers
Absent	Neither crane is within the field of view of the camera
Events[b]	
Alert	Crane changes posture to orient head to a stimulus
Exchange crane	One mate takes the place of the other on the nest
Predator interaction	Potential egg predator approaches within field of view of the nest
Non-predator interaction	Non-predator approaches within field of view of the nest
Adjust position	Crane stands briefly and resettles without manipulating nest contents

[a] Percent of total time observed.
[b] Rate per hour of observation.

and their relationship to the outcome of the interaction. The animals encountered were identified whenever possible; if they were not visible or if they were blurred on the image we classified them as unknown. We recorded unambiguous postural threats and movements and classified them into discrete behavioral classes as described in Ellis et al. (1998). Although we relied on still photos, we were able to use photographic sequences to distinguish between static postural threats and agonistic displays involving movement (e.g., wing-spread-hold vs. wing-spread-flap). All statistical analyses were performed in SYSTAT v.13 (SYSTAT Corporation, Redmond, CA). We used 1-way analysis of variance to determine if time budget components and event rates differed among successful, unsuccessful, and predated nests. We classified nests as successful if at least 1 egg hatched, unsuccessful if eggs failed to hatch but were not taken by predators, and predated if eggs were destroyed by predators. To identify behavioral variables that distinguished successful from unsuccessful nests, and successful from predated nests, we fitted models to the data using the expanded set of variables in the General Linear Models module in SYSTAT. The small number of nests available for analysis limited our ability to assess complex models. We first fitted single-variable models and used those with the lowest values of Akaike's Information Criterion (AIC) to further investigate a limited set of models with 2 or 3 variables.

RESULTS

We obtained 14 complete nesting records (cranes re-occupied the nest after camera installation and a definitive outcome was recorded) in 2009 and 7 in 2010. Cranes abandoned the nesting attempt shortly after camera installation in 4 cases, while in 8 others technical problems with cameras resulted in failure of recording before the fate of the nest could be determined. Of the 21 complete records, 3 nests were lost to flooding in 2009 and were excluded from analysis.

We analyzed over 330,000 images acquired over 7,160 hours of recording from all 33 nests at which cameras were installed; mean observation time for the 18 nests included in this study was 278 ± 47 hours (± 1 SE). Of the 18 nests for which an outcome was definitively identified, 10 nests were successful, hatching at least 1 egg, while 3 were unsuccessful and 5 were predated. Not surprisingly, due to nest abandonment, unsuccessful and predated nests were observed for shorter periods of time overall (154 ± 69 hr and 175 ± 53 hr, respectively) than successful nests (367 ± 68 hr). However, this difference was not statistically significant ($F_{2,15} = 2.629$, $P = 0.105$).

None of the 5 states that made up overall time budgets for nesting cranes differed significantly among successful, unsuccessful, and predated nests (Table 2). Similarly, none of the 5 event rates calculated differed significantly among nests. The 2009 Ben Williams pair,

Table 2. Behavior related to nest outcome[a] of sandhill cranes at the Mississippi Sandhill Crane National Wildlife Refuge, 2009-2010.

Behavior	Successful (n = 10)		Unsuccessful (n = 3)		Predated (n = 5)		$F_{2,15}$	P
	Mean	SE	Mean	SE	Mean	SE		
States[b]								
Incubate	92.1	3.0	93.0	2.8	82.7	9.2	0.999	0.392
Probe	4.0	2.6	1.3	0.6	1.9	0.94	0.312	0.737
Near nest	0.6	0.2	0.3	0.2	11.0	8.2	2.213	0.144
Preen	0.9	0.5	0.2	0.1	0.8	0.36	0.335	0.720
Absent	2.4	1.3	5.2	3.2	3.6	1.52	0.577	0.574
Events[c]								
Alert	1.29	0.7	0.15	0.06	7.69	7.04	1.626	0.230
Exchange crane	0.11	0.05	0.01	0.01	0.01	0.01	0.353	0.708
Predator interaction	0.01	0.01	0.01	0.02	0.00	0.00	0.450	0.656
Non-predator interaction	0.15	0.14	0.00	0.01	0.02	0.02	0.318	0.732
Adjust position	0.24	0.15	0.01	0.01	1.95	1.83	3.083	0.078

[a] Successful = Hatched at least 1 egg. Unsuccessful = eggs did not hatch but were not taken by predators. Predated = eggs destroyed by predators.
[b] Percent of total time observed.
[c] Rate per hour of observation.

whose nest was eventually predated, behaved very differently from all other pairs. In particular, this pair spent less time incubating and more time near the nest than other pairs and also had high rates of alert and adjust position. However, the behavior of this single pair was not sufficiently aberrant to produce significant differences between time budgets of predated and other nests (Table 2).

The best fit model predicting successful vs. unsuccessful nests included mean time off the nest and mean time probing the nest (Table 3). Three other models that received some support (δAIC = 2) included some combination of these variables and alert rate and maximum time preening. Pairs on unsuccessful nests averaged 63 minutes off the nest whenever they were not incubating, while those on successful nests averaged only about 9 minutes off the nest when not incubating (Figure 1). Pairs on unsuccessful nests spent an average of 3 minutes at a time probing the nest, while pairs on successful nests spent an average of only 2 minutes at a time probing the nest.

The best fit model predicting successful vs. predated nests included Julian date of initiation and rate at which cranes exchanged position on the nest (Table 3). One other model that received support (δAIC = 2) included Julian date, exchange rate, and percent of the total time spent off the nest. Predated nests were initiated nearly a month later on average (3 May) than successful nests (6 April) (Figure 2). Pairs on predated nests were also observed to exchange incubation duties at much lower rates than pairs on successful nests.

Descriptions of Nest Defense Behaviors

We counted 208 individual agonistic displays during the study (Table 4). The pre-attack droop wing display accounted for 75% of all agonistic displays and wing-spread-hold/wing-spread-flap displays accounted for another 13.5%. Run-flap, tertial elevation, and strut accounted for most of the remainder, and a single jump-rake display was also observed. The distribution of agonistic displays was uneven; 11 pairs used a recognizable threat display or aggressive behavior while 7 never displayed any agonistic behavior during the study. Eight pairs used the pre-attack droop wing display, and 6 of these exhibited at least 1 additional agonistic display.

We recorded 108 interactions between nesting

Table 3. Best-fit models distinguishing successful vs. unsuccessful and successful vs. predated sandhill crane nests[a], Mississippi Sandhill Crane National Wildlife Refuge, 2009-2010.

Model	δAIC
Successful vs. unsuccessful nests	
Mean time off nest + mean time probing	0
Mean time off nest + max. time preening + alert rate	2
Mean time off nest + mean time probing + max. time preening	2
Mean time off nest + mean time probing + alert rate	2
Successful vs. predated nests	
Julian date + Exchange rate	0
Julian date + Exchange rate + percent of total time off nest	2

[a] Successful = Hatched at least 1 egg. Unsuccessful = eggs did not hatch but were not taken by predators. Predated = eggs destroyed by predators.

Table 4. Agonistic behaviors displayed by crane pairs at 18 nests at the Mississippi Sandhill Crane National Wildlife Refuge, 2009-2010. Descriptions after Ellis et al. (1998).

| Behavior	Description	Number of observations	Pairs exhibiting
Pre-attack droop wing	Crane advances with wings spread and primaries lowered to touch vegetation	156	8
Wing-spread-hold	Crane stands with wings lifted and held extended	20	6
Run-flap	Crane rushes at intruder while flapping wings	11	9
Wing-spread-flap	Crane stands with wings extended and flapping	8	3
Tertial elevation	Tertiary feathers are elevated over back	6	2
Strut	Crane turns sideways to intruder and walks in slow, measured steps	6	3
Jump-rake	Crane leaps into the air and slashes with talons	1	1
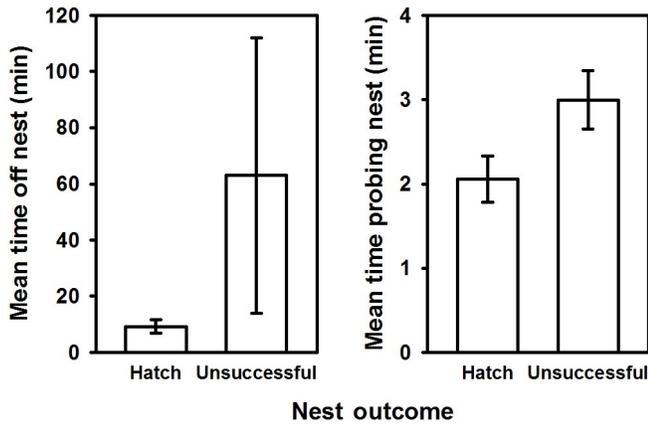
Figure 1: Parental behavior patterns distinguishing sandhill crane nests that produced chicks from nests that were unsuccessful but not predated, Mississippi Sandhill Crane National Wildlife Refuge, 2009-2010. Histogram bars are mean ± SE.
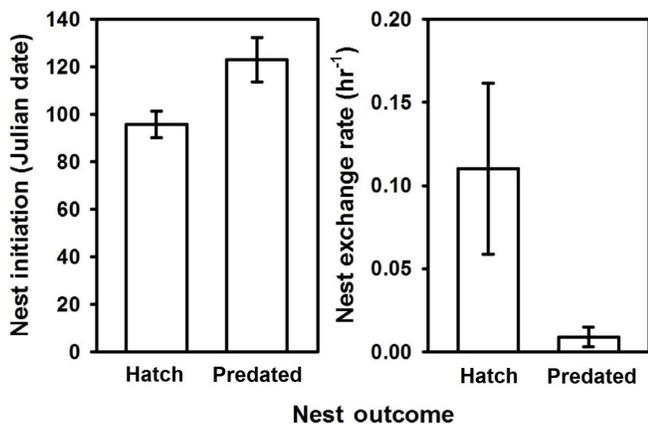

Figure 2: Parental behavior patterns distinguishing sandhill crane nests that produced chicks from nests that were lost to predation, Mississippi Sandhill Crane National Wildlife Refuge, 2009-2010. Histogram bars are mean ± SE.

cranes and other animals; of these, 45 animals were identifiable while 63 were not visible in images. Three nests accounted for 78 of the 108 interactions, while the other 15 accounted for the remaining 30. Cranes encountered humans 8 times, and temporarily abandoned nests to avoid contact; in each case cranes returned to the nest within 4 hours after humans left the vicinity. Cranes encountered non-predatory animals 26 times and ignored them 24 times, giving agonistic displays in only 2 cases. One nesting pair encountered a second crane pair moving through their nest site, and 1 of the resident cranes displayed erect tertial feathers combined with a strut display until the transient pair

moved away.

Interactions with known predators were often more complex and protracted than those with non-predators. Cranes at 5 nests interacted with visible predators in 10 instances: 2 owls (*Bubo virginianus*), 3 crows (*Corvus brachyrhynchos*), and 5 raccoons (*Procyon lotor*). Crows were easily intimidated by cranes simply approaching or displaying; crows left after a strut threat by 1 crane, a run-flap threat by another, and a wing-spread-flap threat by the third. One owl left after a single run-flap threat by the resident crane, but the other persistently attacked the single crane on the nest and was driven off after 22 minutes, during which the defending crane gave multiple pre-attack droop-wing and wing-spread-flap displays and knocked the owl into the surrounding pond during a jump-rake attack. Raccoons were both persistent and opportunistic; 1 nest was attacked on 3 different nights, during which the raccoon repeatedly approached the nest over periods ranging from 3 to 11 hours. The crane on this nest successfully defended on each of the 3 nights, displaying numerous pre-attack droop wing displays each time. However, raccoons destroyed 2 other nests with no effective defense from nesting cranes; at 1 the crane left the nest when the raccoon approached and at the other the crane stood nearby showing alarm but no defensive behavior. The successful defense was by an unbanded, presumably wild-reared crane, while the 2 ineffective defenders were both known costume-reared birds.

Cranes at 10 nests reacted in some way at least once to unidentified intruders. Cranes gave recognizable agonistic displays in all but 1 case, with the pre-attack droop wing displayed 43 times and the wing-spread-flap displayed on 13 occasions. Three nests accounted for 84% (53 of 63) of recorded events. In 2 of these 3 nests, 1 member of the pair was unbanded and wild-reared, and these individuals accounted for 68% of agonistic displays (21 of 31). At the third nest both members of the pair gave threats, but the female of the pair, a known costume-reared bird, accounted for a majority of agonistic displays.

DISCUSSION

Our data suggest that nesting Mississippi sandhill cranes have similar overall time budgets regardless of nest outcome. However, specific behavior patterns varied widely among nesting pairs and individual cranes, and some were predictive of nest outcomes.

The heterogeneity of behavior among members of this population may reflect their diverse origins; while most cranes in the study were costume-reared, some were parent-reared in captivity and still others were produced through natural reproduction on the refuge. The range of behaviors exhibited in this population may provide useful management indicators of prospective nest outcomes, while the diversity of rearing methods and learning opportunities experienced by cranes may allow rearing strategies that promote desirable reproductive outcomes to be identified and more widely implemented.

Detailed behavior patterns distinguished among nests that did not successfully hatch eggs or were predated and nests in which chicks successfully hatched. Cranes at unsuccessful nests spent extended periods of time away from the nest compared to those at successful nests, although it is not clear whether extended absences might have caused eggs to become inviable from insufficient incubation or might instead have resulted from a lack of cues from eggs that might promote attachment. Cranes at unsuccessful nests also spent significantly more time manipulating nest contents, perhaps in response to a lack of expected cues from eggs. The exact biological significance of these behavior patterns was not clear in this study, although they provide clear signs that a nest is likely to be unsuccessful, and that may be useful in managing crane populations.

The low rate of incubation switching among partners was strongly associated with nest predation. The failure of partners to cooperate in incubation may reflect poor attachment within the pair, and this might be a particular problem with young or inexperienced breeders. However, some pairs at predated nests are known to have nested in years prior to the study and were not completely naive. The cumulative stress of incubation for long periods without relief may predispose birds to leave the nest at critical times, and this interpretation is consistent with the inclusion of percent of total time off nest as a factor in the second-best supported model. The later start date of predated nests may be in part due to poorly attached pairs requiring extra time for bonding, or to re-nesting after an initial failure. Late-starting nests may be more vulnerable to predation due to higher predator activity rates or to vegetation growth providing more cover for predators later in the growing season. While the mechanisms underlying these patterns remain to be investigated, the combination of poor coordination among pair members and a late nesting date is a clear indicator of elevated predation risk.

Individuals and pairs varied greatly in their display repertoires and competence in defending nests, and the passivity of many birds to potential threats may be an important mechanism underlying poor nesting success in the refuge population. All pairs showed similar rates of alert behavior except for 1 hyper-vigilant pair, but few birds responded to potential danger with agonistic displays or attacks. Over a third of all pairs never made a threat display of any kind in response to any cue, and only 3 pairs accounted for a majority of threats directed at unknown cues. While it is possible that cues perceived by some pairs never indicated a danger requiring a response, observations of interactions with known predators suggest that some pairs did lack the ability to respond competently to threats in defense of the nest. The 2 instances in which cranes were present at the nest but took no action or left in response to egg predation by a raccoon clearly indicate that some birds lack the skills required to defend the nest. It is notable that these 2 pairs gave agonistic displays in other circumstances. Both gave pre-attack displays and run-flap or wing-spread-flap displays to perceived threats that were not captured on camera but failed to use them appropriately when confronted with a potential predator closely approaching the nest. This suggests that in some cases birds can perform appropriate defense behaviors but do not perform them in the proper context.

In contrast, other birds on the refuge did exhibit a large number of known agonistic displays and some employed them effectively in nest defense. Although our sample size is small, wild-reared birds appeared particularly aggressive toward unknown cues and persistent in nest defense. Competence was not limited to wild-reared birds, as costume-reared crane no. 337 was consistently aggressive to cues from perceived threats that were not visible on camera, and 1 member of a costume-reared pair mounted a sustained and effective defense against owl attack.

We suggest that competence in nest defense depends on social learning during development (Griffin 2004) and that the current refuge population has not had equal opportunity to learn appropriate displays or the context in which they must be given. The competence of wild-reared birds suggests that they likely observe the behavior of their parents during the pre-fledging period, learn which animals pose a threat, and learn how to use aggressive displays to deter them.

The fact that some costume-reared birds were highly competent suggests that these behaviors can be learned after fledging and release, but it is not clear whether naive birds must observe competent ones or gain their skills through trial and error, or how much experience may be required to become competent. It also seems likely that poor nest defense is a greater problem when confronting mammalian mesopredators than avian predators. Cranes effectively defended against crows and owls in all cases observed, and lost eggs only to raccoons during the study.

We propose that giving pre-fledging captive-bred chicks greater opportunity to learn common mammalian mesopredators, aggressive displays, and the context in which they are useful will help more birds learn skills required for nest defense after release. A pilot study to teach Mississippi sandhill cranes predator avoidance has been carried out with promising results (Heatley 2002), and although the methods developed in that study were not implemented in the rearing program, they provide a clear path to designing a program to condition nest defense behaviors. A number of captive breeding programs have used instruction in predator recognition and avoidance to improve survivability of released animals (Griffin et al. 2000), although cranes would require the modeling of appropriate aggressive behaviors rather than simple avoidance. Captive parent-reared chicks may be able to observe parental defensive behavior if their parents are themselves competent and are deliberately challenged by an appropriate mesopredator. Costume-reared chicks may benefit from having costumed personnel model threat displays in response to mammalian predators, perhaps adding realism to the relatively shapeless costume by utilizing wings from deceased birds or wings constructed to resemble them.

Some training programs for captive-bred animals have succeeded in teaching predator avoidance behavior using models such as stuffed predators or plush toys (McLean et al. 1999, Griffin and Evans 2003, Shier and Owings 2007) and this may provide a safe way to condition captive chicks without the risk of exposing them to actual danger. However, training programs will have to be carefully designed to promote learning of only appropriate cues and to avoid conditioning birds to irrelevant stimuli that are incidental to the training (e.g., specific movement patterns of models, unnatural noises, objects required to present stimuli). It is currently not known how many trials might be required to learn cues and responses, whether inanimate models would be effective, or whether cranes are capable of generalizing from 1 model to other mesopredators, so the complexity of a training system would have to be established through trial and error. This will present a significant challenge to current rearing methods, but improving viability of captive-reared birds after release would help advance the ultimate goal of creating a self-sustaining wild population.

ACKNOWLEDGMENTS

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