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NEST DESERTION IN A REINTRODUCED POPULATION OF MIGRATORY WHOOPING CRANES

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Abstract: Reintroduction of an eastern migratory population of whooping cranes (*Grus americana*) into eastern North America began in 2001. Reproduction first occurred in 2005. Through 2008, eggs were produced in 22 first nests and 2 renests. All first nests failed–50% confirmed due to desertion by the parents and the remaining nest failures also consistent with the pattern of parental desertion. Nest failures were not related to stage of incubation, and they were often synchronous. Temperatures in winter and early spring affected timing of nest failure. An environmental factor such as harassment of incubating cranes by black flies (*Simulium* spp.) may be responsible for widespread nest desertion.

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Key words: black flies, *Grus americana*, incubation, nest desertion, reintroduction, reproduction, *Simulium*, whooping crane, Wisconsin.

The whooping crane (*Grus americana*) is a federally-listed, critically endangered species. The only currently viable population consists of a naturally occurring remnant flock that breeds in Wood Buffalo National Park, Northwest Territories, Canada, and winters on Aransas National Wildlife Refuge (NWR), Texas. Recovery of the species depends on establishment of additional flocks separate from this existing population. Reintroductions begun in the Rocky Mountains in 1975 (migratory) and central Florida in 1993 (non-migratory) have been unsuccessful. In 1998, after considering factors including avoiding the Central Flyway and range of the existing natural population, limited interest elsewhere in Canada, identification of potential wintering areas in the eastern U.S., migration routes of sandhill crane populations, and logistics of reintroduction, the U.S.-Canadian Whooping Crane Recovery Team (WCRT) recommended Wisconsin as the next reintroduction area. The WCRT selected central Wisconsin, with efforts focused on Necedah NWR, as the specific reintroduction site in the following year.

The Whooping Crane Eastern Partnership (WCEP) began reintroduction of this eastern migratory flock of whooping cranes in 2001. Resulting survival, migration, and human avoidance behavior of reintroduced cranes have been adequate to make establishment of a population possible. Likewise, reproductive behavior has progressed with almost all females in the core reintroduction area pairing, occupying established territories, and egg laying as appropriate for their age (Urbanek et al. 2010*a*, 2010*b*; R. Urbanek, unpublished data; WCEP annual reports 2007-08). However, reproductive failure due to nest desertion has appeared as an unanticipated threat to success of the reintroduction. This paper describes this problem during 2005-08.

STUDY AREAS

The core reintroduction area consists of a large shallow wetland complex in central Wisconsin (Urbanek et al. 2010*b*). All breeding territories were located within this area, mainly on Necedah NWR (44°04′N, 90°10′W). Ultralight-training and release sites were on Necedah NWR. Summer, migration, and wintering areas used by the population have been previously described (Urbanek et al. 2005*b*, 2010*a*).

METHODS

General project methodology has been previously described (Urbanek et al. 2005*a*, 2010*a*, 2010*b*). Cranes were costume/isolation-reared (Horwich 1989, Urbanek and Bookhout 1992*a*) as juveniles in 2001-05 and led by ultralight aircraft (Lishman et al. 1997, Duff et al. 2001, Ellis et al. 2003) on their first autumn

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migration from Necedah NWR, central Wisconsin, to Chassahowitzka NWR, central Gulf Coast of Florida. After spending their first winter at a protected release site where they could move freely from a large, open-topped pen (Urbanek 2010*a*), the cranes made the subsequent spring migrations on their own.

In this paper "first nest" refers to the first nest containing eggs of each pair in each year; "renest" refers to any subsequent nest containing eggs. Nest "failure" indicates that no chicks hatched from the subject nest. Nest "desertion" refers to a specific type of nest failure caused by both adults leaving the nest unattended.

We monitored breeding pairs and nest activity daily during each year (2005-08) by standard tracking methods including VHF telemetry with scanner receivers (Advanced Telemetry Systems, Isanti, MN; Telonics, Mesa, AZ) and, where possible, direct visual observation. We tracked cranes mainly from vehicles on the ground and supplemented with aerial surveys from Cessna aircraft. Each ground tracking vehicle was equipped with a through-the-roof, 7-element yagi antenna (Cushcraft Corporation, Manchester, NH). We conducted time-lapse daylight videotape recording at 2 first nests and 1 renest in 2007 and at 3 first nests in 2008. Distance from camera to nest varied from 150 to 450 m.

We positioned cameras on the tops of 3-m-high poles set along roads or dikes where birds were accustomed to viewing limited refuge traffic. We used a vehicle or topographic relief to block visibility of activity related to servicing the recording equipment. No cranes ever rose from a nest or exhibited any other significant disturbance as a result of these activities.

To avoid disturbance of incubating pairs, we did not approach attended nests during the course of study. The only 2 exceptions to this protocol were to switch an egg (later found to be infertile) of a renesting sibling pair with a viable egg from captivity and to switch an artificial egg with a viable egg recovered from the previously deserted nest. Beginning in 2006, we collected deserted eggs, within 2-6 hours when possible, and replaced them with wooden (2006-07) or plaster-filled (2007-08) artificial eggs.

We were able to determine when incubation was initiated or terminated by either direct observation from distant vantage points on the ground, visual observation or radiotracking of adults, or aerial surveys. Nest initiation was indicated by observation of only 1 crane, e.g., foraging, when earlier both members of the pair had been present. In all instances in which existence of a nest was predicted by this method, a nest was later confirmed by other methods or by direct examination after abandonment. Because whooping and other cranes spend very little time off their nests during incubation (Allen 1952:182, Walkinshaw 1965), radio signals or sightings of both cranes away from the nest for more than 2 hours indicated nest failure or a serious disturbance problem at the nest.

We placed collected viable eggs in a portable incubator and transported them to the International Crane Foundation, Baraboo, Wisconsin, for continued incubation. They were next transferred to USGS Patuxent Wildlife Research Center, Laurel, Maryland, to provide additional chicks for reintroduction. Egg manipulations have previously been used as a management tool at Wood Buffalo National Park (Kuyt 1996). In 2008, in an effort to investigate egg manipulations as a management tool to promote hatching, we replaced artificial eggs with a viable egg in 1 nest.

We used pooled *t*-tests to compare differences in incubation length between the nesting season following a cold winter (2008) and nesting seasons of earlier (warmer winter) years as well as temperature differences between days of successful incubation and nest failure. We used multinomial chi-square tests to determine if nest failure was associated with stage of incubation as well as describe temporal distribution of nest failures. In the former test, nests for which initiation or termination of incubation was not known within 1 day were not included in analysis. In the latter test, the first certain date of incubation was used as initiation of incubation; if termination of incubation occurred during a range of 2 possible days, the second date was used. Nests without known termination dates within specific 5-day intervals during the incubation period were omitted. As above, it was assumed that a nest found with an intact egg had been deserted within the preceding 2 days.

RESULTS

Pairs and Egg Production

Production of the first eggs in the reintroduced

Table 1. Period and duration of incubation in annual first nests of whooping crane pairs in the reintroduced migratory population, central Wisconsin, 2005-08[a].

Year	2005	2006	2007	2008	Total
No. pairs	2	5	4	11	22
Initiation date					
Mean	17 Apr	8 Apr	13 Apr	13 Apr	12 Apr
Minimum	16 Apr	5 Apr	3 Apr	7 Apr	3 Apr
Maximum	19 Apr	13 Apr	19 Apr	23 Apr	23 Apr
Termination date					
Mean	18 Apr	20 Apr	21 Apr	4 May	27 Apr
Minimum	17 Apr	15 Apr	20 Apr	30 Apr	17 Apr
Maximum	19 Apr	27 Apr	21 Apr	6 May	6 May
No. days of incubation					
Mean	0.75	11.9	8.0	21.7	14.4
SE	0.25	1.92	5.03	2.22	2.18
Minimum	1	9	2	12	1
Maximum	1	19	18	29	29

[a] Data conventions: If initiation or termination date was not known within 2 days, then data for that nest were not included in calculations (resulted in omission of 1 nest in 2007 and 3 nests in 2008).

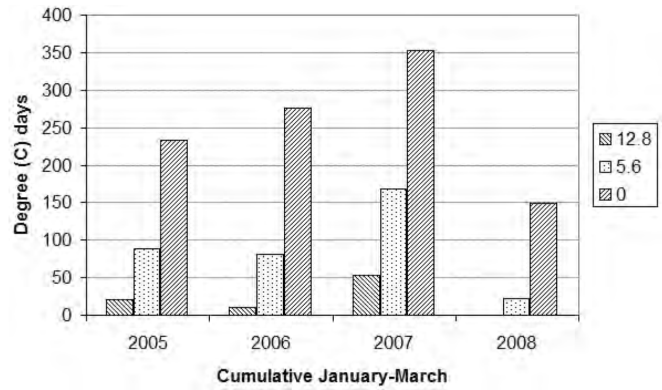

Figure 1. Number of accumulated degree-days above 12.8, 5.6, and 0°C (55, 42, and 32°F) during January-March in years of whooping crane egg production in central Wisconsin, 2005-08 (data from NOAA weather station, Necedah NWR). Note: There were no days with temperatures above 12.8°C during January-March 2008.

population occurred in 2005, and through 2008 there were 24 nesting attempts (i.e., with eggs laid) by 14 different pairs. Date of initiation of first nesting varied from 3 to 23 April. All 22 first nesting attempts during these 4 years failed. Termination of incubation varied from 17 April to 6 May, and incubation ranged from 1 to 29 days (Table 1). Duration of incubation was significantly longer in 2008 (mean = 21.7 days, SE = 2.2, n = 8) than in 2005-07 (mean = 8.5 days, SE = 2.1, n = 10) ($t = -4.26$, df = 16, $P < 0.001$) and was associated with an unusually cold winter with fewer accumulated degree-days through March in 2008 (Fig. 1).

There were only 2 renesting attempts. One in 2006 was initiated on 23 May, 33 days after failure of the first nest, and 2 chicks successfully hatched on 22 June. The other in 2007 was initiated on 14 May, 25 days after failure of the first nest. This was the nest of a sibling pair and was abandoned after an attempted replacement of the single natural egg, later found to be infertile, by 2 non-costumed humans 26 days after initiation of incubation.

Fate of Eggs

In 2005, 1 nest was found deserted while the adult pair was 6 km away and off the refuge. No salvage protocol had been approved for that year; therefore, the egg was not collected. The egg was absent by the following morning, possibly taken by raccoons (*Procyon lotor*), which are common in the area. Of the remaining 21 first nests during 2005-08, 11 contained no intact eggs by the time they were examined, and 1 contained 2 eggs that were found broken on a nearby dike, apparently carried there by a raven (*Corvus corax*) or crow (*C. brachyrhynchos*), between time of desertion and opportunity for collection. Collections at the remaining 9 nests yielded the following eggs (intact unless indicated otherwise): 2 fertile (2 nests), 1 fertile broken and 1 infertile, 1 fertile and 1 infertile, 1 destroyed and 1 late dead embryo, 1 late dead embryo, 1 fertile (2 nests), and 1 infertile.

When we approached deserted nests, no adults were in the nesting marsh, and many were off territory and off refuge, sometimes as far as 16 km away. Although our intention was to collect eggs within 2-6 hours of desertion, the exact time of desertion was usually not known in real time. In addition, multiple nest failures often occurred nearly simultaneously. Therefore, the actual retrieval interval was usually longer and resulted in some eggs lost to scavengers or in dead embryos. The 7 fertile eggs viable at time of collection (2 in 2006, 1 in 2007, 4 in 2008) later hatched in captivity.

Nest Desertion

Results of video surveillance showed vigilant nest attentiveness by each monitored pair until near or at the time of nest desertion. Visual observations of foraging mates and telemetry were also consistent with these findings. No evidence was collected that supported either predators or changes in water levels as threatening factors or causes of nest desertion. Likewise, subsequent examination of failed nests and finding of intact eggs in some nests further eliminated the likelihood of these factors as a major cause of nest failure. Of first nests monitored by video (2 in 2007 and 3 in 2008), incubating adults left 3 nests in response to no threatening stimulus visible on the videotape. Another pair was not visible while leaving the nest, but an aerial survey flight later that morning verified the time frame of desertion. Wind-affected camera movement confounded interpretation of crane movements during the remaining desertion, but no predator presence near the nest was detected. All of these critical desertions occurred in the morning, with 1 pair also engaging in sporadic inattention to the nest during the preceding afternoon in each of the 2 years.

There was no significant difference in length of incubation (days) between first-year (mean = 13.8, SE = 2.7, n = 3) and older breeders (mean = 9.0, SE = 0.5, n = 2) (t = –1.36, df = 3, P = 0.268) in 2006. In 2008, excluding 4 pairs for which length of incubation was not known to within 1 day, there was a nearly significant difference between first-year (mean = 20.0, SE = 2.2, n = 4) and older breeders (mean = 27.2, SE = 1.2, n = 3) (t = 2.56, df = 5, P = 0.051). Insufficient data were available for comparison in 2005 and 2007.

Patterns of desertion were evident. For 17 nests in which both initiation and termination of incubation were known within 1 day, nest failures were distributed chronologically during the 30-day period of incubation as follows: 1-5 days (n = 4), 6-10 days (n = 3), 11-15 days (n = 3), 16-20 days (n = 2), 21-25 days (n = 3), and 26-30 days (n = 2). Therefore, nest failure was not associated with stage of incubation (χ^2 = 1.00, df = 5, P = 0.963).

During the 16 5-day periods which covered the total periods of incubation during 2005-08, nest failures occurred in a clumped pattern relative to number of active nests (χ^2 = 837.8, df = 15, P < 0.001). Therefore, nest failure was not evenly or randomly distributed through the incubation period, but rather multiple failures occurred within periods of the same few calendar days. Dates of these desertion periods were related to degree-days (Table 2). For 2007 and 2008, years with pronounced peaks affecting most nesting pairs, desertion occurred when 538-636 degree-days had accumulated during the growing season. Note the result of this factor on length of incubation (Table 1) because of the very different weather conditions (Fig. 1) in those 2 years. [Addendum: In 2009 the same pattern recurred. All first nests (n = 12) failed, and peak desertion of 8 nests occurred 23-24 April at 562-592 degree-days above 0°C (S. Zimorski and E. Szyszkoski, unpublished data).] Within the range of the degree-day-related period of desertion, nest failures also seemed to occur on relatively warm, sunny days (R. Urbanek, personal observation).

These patterns indicate that whooping crane nest failure was precipitated by an environmental factor which is temperature related and affects numerous nesting pairs at about the same time. The spring emergence of black flies (Simuliidae) meets these criteria as a possible factor.

Table 2. Relationship between accumulated degree-days above 12.8, 5.6, and 0°C (55, 42, and 32°F) and modal (peak) whooping crane nest desertion, central Wisconsin, 2005-08 (data from NOAA weather station, Necedah NWR).

Year	Peak desertion period	n/total desertions	Degree-days (above °C)		
			12.8	5.6	0
2005	17-19 Apr	2/2	122-144	311-347	550-598
2006	15-16 Apr	2/5	193-202	243-254	522-538
2007	20-21 Apr	3-4/4	85-97	272-292	538-563
2008	4-6 May	6-7/11	103-124	284-319	590-636
Total		13-15/22	85-202	243-347	522-636

Figure 2. Swarming black flies on eggs in nest of whooping crane pair on day of desertion, Necedah National Wildlife Refuge, Wisconsin, 6 May 2008.

Figure 3. Black flies feeding on whooping crane, Necedah National Wildlife Refuge, Wisconsin, May 2008. Note blood in feathers, bleeding wounds, black flies burrowing under feathers, and black flies embedded in papillae of crown. Photo possible at <1 m because this unpaired adult female was atypically imprinted on the costume and could be closely approached (photo by R. Urbanek).

Black Flies and Whooping Cranes

We commonly observed black flies during spring in central Wisconsin. We frequently found them on whooping crane eggs collected from deserted nests (Fig. 2). Specimens collected from 1 egg in 2007 were identified as females of *Simulium annulus* or a closely related species (adult females of some species cannot be distinguished based on external morphology). In 2008, 1 unpaired adult female whooping crane was available that was imprinted on the costume and could therefore be approached at close range by a costumed individual (RPU). Examination of this female revealed large numbers of black flies under the feathers, imbedded in the papillae of the crown, and resulting bleeding wounds (Fig. 3).

In 2008, 2 pairs later resumed incubation of artificial eggs which had been placed in their nests after the original clutches were deserted. In 1 case, a costumed individual (RPU) switched an original live egg back into the nest. The adults defended the nest, but after RPU left the marsh, the cranes entered surrounding willow (*Salix* spp.) thickets and were observed in rapid bursts of running with the head in a recumbent posture. Several opportunities to view the birds at close range were possible from a vantage point in a vehicle (this pair was habituated to this vehicle, which they largely ignored), and RPU noted obvious irritation and pecking at black flies by the male when he was not in the willows. At dusk the female returned to the nest and resumed incubation, but the pair deserted the nest again early the next morning. RPU had also noted this nest desertion pattern and similar movement into willow thickets by the same pair in 2007, but the birds were too distant to discern the role of black flies.

DISCUSSION

Average annual mortality of white-plumaged whooping cranes in the natural Wood Buffalo-Aransas population was 9.7% during 1938-2008 (B. Johns, Canadian Wildlife Service, unpublished data). With the exception of a 1.4-year period of excessive mortality that occurred during drought (Urbanek et al. 2010*b*), the survival of reintroduced eastern migratory whooping cranes has been similar and adequate to provide the foundation for a viable population, as have migration, homing, and pre-incubation reproductive behavior. Widespread nest desertion has, however, occurred as an unanticipated problem that threatens natural recruitment.

Factors Dismissed as Primary Causes of Nest Desertion

Monitoring of nests confirmed that neither predation nor water level fluctuations were the primary cause of these extensive nest failures. Because no first nests were successful and data were limited, evaluating effect of age or nesting experience on nest success was inconclusive. The single successful nest (a renest) was by a pair of second-year breeders; however, they failed during the following 2 years.

Non-optimal nesting phenology, in combination with other factors, might have some effect on nest desertion. Data compiled by Allen (1952:52-53) for 17 whooping crane nests (eggs collected from 15) in Iowa (1866-1894) indicated 14 of the nests active during the first half of May. Although stage of incubation was not available, these dates indicate possibility of later nesting of those whooping cranes than cranes currently in Wisconsin, even at lower latitudes in Iowa.

Poor body condition of returning birds, due to inadequate food resources on the wintering grounds, does not explain the consistent widespread nest failure among all pairs because most pairs winter at different, often widely separate, locations (Urbanek et al. 2010*b*).

Whooping cranes are especially sensitive to human disturbance. In captivity whooping cranes may skip an egg laying season (Mirande et al. 1997) or break their eggs (Puchta et al. 2008). We suspect that a crane frightened from its nest in the field might inadvertently puncture its egg with a toenail. However, in this study we neither approached nor significantly disturbed any incubating birds on active first nests. Areas including nests were closed to other human activity. Therefore, human disturbance was not a factor in these first nest desertions.

Aquatic habitats on Necedah NWR are low in nutrients. This might result in limited availability of food to whooping cranes during the pre-growing season and contribute to nest desertion. However, food shortage, although possibly contributing, does not explain the widespread and largely simultaneous desertion.

Normal territorial establishment and formation of breeding pairs indicated that the problem was probably not related to reintroduction methods. Likewise, most nests of costume-reared non-migratory whooping cranes reintroduced in Florida were incubated full-term, and no differences were noted in reproduction between costume and parent-reared cranes (M. Folk, Florida Fish and Wildlife Conservation Commission, personal communication; Spalding et al. 2010).

Black Flies as the Suspected Cause of Nest Desertion

Duration of incubation was significantly longer after a cold winter with prolonged below-average temperatures continuing into early spring. Because the cranes begin nesting on approximately the same schedule each year, length of incubation before occurrence of desertion was dependent on the preceding weather conditions. The cause of nest desertion appears to be an environmental factor that becomes effective after a developmental period dependent on winter and early spring temperatures. The milder the winter, the shorter was the incubation period before nests were deserted. The colder the winter or greater prevalence of below-average temperatures into spring, the longer incubation progressed before nest desertion.

The pattern of nest failure involved coincidental, often simultaneous, desertion on seasonally warm days. This pattern was primarily related to 1) previous winter temperatures and secondarily to 2) conditions suitable for black fly dispersal from breeding streams to whooping crane nesting sites. These two factors likely resulted in a large initial emergence of black flies that would explain widespread and simultaneous desertion of multiple whooping crane nests. In the Wisconsin reintroduction, black flies were observed directly interfering with incubation duties of 1 whooping crane pair. Black fly outbreaks, related to spring temperatures, offered an explanation of widespread and simultaneous desertion of multiple nests.

Nest desertion due to black fly harassment of other avian species has been documented (Smith et al. 1998, Bukacinski and Bukacinska 2000), and swarms of black flies have even killed birds (reviewed by Adler et al. 2004). *Simulium annulus*, the black fly species collected in this study, has been recorded feeding on common loons (*Gavia immer*) in North America (Adler et al. 2004, Weinandt 2006, Currie and Hunter 2008) and on common cranes (*Grus grus*) in Europe (Malmqvist et al. 2004, Hellgren et al. 2008). This species has also been implicated in nest abandonment by common loons in Wisconsin (Meyer 2005) and the Upper Peninsula of Michigan (Rasmussen 2008).

Sandhill cranes (*Grus canadensis*) in the Great Lakes region coexist with black flies and successfully nest (Urbanek and Bookhout 1992*b*, Urbanek et al. 2005*b*). Eggs of sandhill cranes in the Upper Peninsula of Michigan have also frequently been observed covered with black flies (R. Urbanek, personal observation) similar to whooping crane eggs in Wisconsin. Therefore, black flies were not initially suspected as the cause of whooping crane nest desertion. Sandhill cranes, however, nest in more heavily vegetated marshes and in shallower water than do whooping cranes. Perhaps most importantly, sandhill cranes in the Great Lakes region paint their plumage with bog iron. Long thought to be merely camouflage (Walkinshaw 1949), this painting may have an insect repellent or blood-feeding deterrent quality.

Once black flies were suspected as a cause of nest desertion, we questioned biologists in the former core breeding range of whooping cranes (Allen 1952) in Illinois, Iowa, central and western Minnesota, South Dakota, North Dakota, Manitoba, Saskatchewan, and the current breeding area in Wood Buffalo National Park, Northwest Territories, Canada. The 13 respondents indicated few or no records of mass spring emergence of black flies such as commonly occur in Wisconsin and other areas farther east and north. These results were consistent with the known range of *Simulium annulus* (Adler et al. 2004), which abuts the northeastern side of the former core whooping crane range (Allen 1952) with minimal overlap.

Black flies lay eggs only in flowing water, typically in streams and rivers more than 10 m wide, but occasionally in flows as small as 2 m in width. The larvae develop during the winter, pupate from late March into April, and the adults emerge in April or early May. Females have a typical flight range of 2.5 km, although distances of at least 8 km are possible (Bennett and Fallis 1971). Date of emergence depends on development related to late winter and spring temperatures. A late spring would result in later black fly emergence and allow many nests to succeed further into incubation, and this longer period of incubation is what we observed in 2008. Alternatively, much warmer conditions had resulted in significantly shorter incubation and earlier nest failure in 2007. Adults of *Simulium annulus* are active for only a few weeks in early spring during which females feed on blood, reproduce, and then die. Black flies are not active at night, consistent with behavior of the affected cranes, which tended to incubate at night while desertion of nests occurred in daylight.

Black flies were too small to be readily visible on videotape. In addition, severity of black fly infestation on whooping cranes was often not apparent by direct observation of behavioral cues from long distances in the field. An adult crane imprinted on the costume and that could subsequently be observed from close range responded to numerous biting flies by only occasionally rubbing her crown on her back. This bird was not committed to sitting on a nest and could move for relief. Higher-powered viewing optics or video recorders of higher resolution might have improved visibility of black flies affecting some crane pairs. However, nest locations and distances necessary to avoid nest disturbance by observers still limited visibility, and behavioral responses of incubating cranes were not necessarily demonstrative of the severity of infestation. The black fly problem cannot, therefore, be adequately measured and assessed by simple observation of cranes in the field.

MANAGEMENT IMPLICATIONS

The 2 renests in 2006 and 2007 occurred after black fly emergence and proceeded near or full term. However, renesting is not a viable solution to the nest failure problem because renesting frequency, as demonstrated by current nesting records, is too low. In addition, renests occurring while black flies are still abundant, especially if emergence is late due to a prolonged winter, might fail for the same reasons as first nests.

Surveys of adult and larval black flies need to be performed to determine species identity, distribution, and abundance in the whooping crane reintroduction area. To test the nest desertion hypothesis presented in this paper, numbers of emerging black flies could be experimentally suppressed by treatment of streams containing larvae with a target-specific, precisely applied biological control agent in late winter or early spring. Effect on whooping crane reproduction could then be measured. If treatment was successful and reproduction improved, continued control of black flies in future years would likely be necessary to sustain whooping crane reproduction. If black flies are the cause of nest desertion and they are not controlled, the reintroduction may fail.

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