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Jeb A. Barzen

Andrew P. Gossens

Anne E. Lacy

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SANDHILL CRANE FORAGING BEHAVIOR AND DAMAGE ESTIMATES IN CORNFIELDS DURING SPRING

JEB A. BARZEN,¹ International Crane Foundation, E-11376 Shady Lane Road, Baraboo, WI 53913, USA

ANDREW P. GOSENS, International Crane Foundation, E-11376 Shady Lane Road, Baraboo, WI 53913, USA

ANNE E. LACY, International Crane Foundation, E-11376 Shady Lane Road, Baraboo, WI 53913, USA

Abstract: Damage to corn in the spring caused by greater sandhill cranes (*Grus canadensis tabida*) has increased concurrent with growth of the Eastern Population of cranes. Our study was designed to: 1) describe foraging rates and food acquisition behavior where damage was likely and 2) estimate damage in cornfields treated and untreated with a taste deterrent: 9,10-anthraquinone (AQ; Avipel®). Our 6,251.6-ha study area was located near Briggsville, Wisconsin, and we sampled 415 ± 13.2 individuals/survey ($\bar{x} \pm SE$), of which $36 \pm 1.7\%$ used cornfields. During 10-30 May 2009, 121 observation bouts of 33 marked cranes that foraged in 20 cornfields were collected. Observation bouts averaged 21 ± 1.32 minutes of which 10.2 ± 0.75 minutes consisted of active foraging by cranes. Individuals swallowed an average of 6.08 ± 0.68 items/active minute. Only 10.4% of 6,445 items consumed were identified and 9.7% of items were corn kernels (93% of identified items). Ingestion rates for all foods in fields treated with AQ (6.44 items/min) and non-treated fields (6.21 items/min) did not differ ($t = -0.15, P = 0.88$), but corn kernels consumed in non-treated fields were ingested at more than 3 times the rate measured from treated fields ($F = 3.84, P = 0.05$). Jab/probe ratios did not differ between treated and untreated fields ($F = 0.12, P = 0.72$), so foraging behaviors were similar even though different foods were consumed. We estimated that all sandhill cranes in this study area consumed 71,245 kernels/day (478 kernels/crane/day) and, over the period that planted corn was potentially vulnerable, consumed a maximum of >2.9 million kernels or 41.0 ha of planted corn (3.8% of all corn planted in the study area). Crane damage could be widely scattered, and thus insignificant, or it could be locally severe as non-territorial individuals congregate in 1 field and concentrate damage, making the distribution of severe damage unpredictable. Though effective at alleviating crane damage, treating planted corn must either be applied uniformly or applied based on previous experience with crane foraging patterns and planting phenology in relationship to other fields.

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Key words: 9,10-anthraquinone, Avipel®, crop damage, deterrents, diet shift, *Grus canadensis tabida*, social status.

By 1936 the Eastern Population (EP) of greater sandhill cranes (*Grus canadensis tabida*) was reduced to perhaps 25 nesting pairs in Wisconsin, 10 nesting pairs at Seney National Wildlife Refuge in Michigan, and an unknown number of nesting pairs located elsewhere in the Upper Peninsula as well as in the Lower Peninsula (Henika 1936). Since this nadir, overall recovery of the EP has been dramatic (Lacy et al. 2015), especially in Wisconsin (Hunt and Gluesing 1976, Su et al. 2004) and Michigan specifically (Walkinshaw 1949, Hoffman 1977). Commensurate with rebounding crane numbers has been an increase in crane-caused crop damage. The first noted evidence of damage in Wisconsin was reported by R. C. Hopkins in 1956 (R. A. Hunt, Wisconsin Department of Natural Resources [WI DNR], unpublished data) even though corn had been identified in the springtime diet of sandhill cranes

since the 1930s (Hamerstrom 1938). Earlier still, germinating corn was noted in the diet of resident whooping cranes (*Grus americana*) in Louisiana during the early 1900s (Allen 1952), so it is probable that sandhill cranes were damaging cornfields in the Midwest well before the 1950s but population numbers were too low to notice any significant loss. Hunt and Gluesing (1976), Bennett (1978), and Melvin (1978) were some of the first biologists to study sandhill crane damage to corn and each evaluated potential solutions for the increasing problem.

Melvin (1978) reviewed and evaluated a variety of damage abatement methods that included chemical seed treatments as well as propane cannons and other devices. Bennett (1978) focused on sandhill crane foraging behavior in relation to damage. At the time, seed treatments (Melvin 1978) and baiting (Bennett 1978) showed some promise for preventing crane damage. Propane cannons were regularly used by WI DNR and appeared to work well if deployed properly (R. A. Hunt, WI DNR, unpublished data). Seed treatments, however, had a much earlier origin. Native

¹ Present address: Private Lands Conservation LLC, S-12213 Round River Trail, Spring Green, WI 53588, USA

Americans were reported to have used taste deterrents to control bird herbivory in the mid-1700s (Benson 1966). The earliest record of taste deterrents being used in North America to prevent ‘corn pulling’ by birds was reported by Dambach (1944) and inconclusive taste aversion trials, including use of ‘anthra-quinone’, were conducted in the 1940s (Dambach and Leedy 1948). Almost 50 years later, Barzen and Ballinger (2017) re-examined conflicts between cranes and people and concluded that seed treatments were the most effective means to diminish crop damage caused by cranes. This positive assessment of taste deterrents was mirrored in other bird species (Werner and Avery 2017) and reviewed for 9,10-anthraquinone (AQ), specifically (Deliberto and Werner 2016).

Since the 1970s much has changed regarding how managers mitigate crane damage to planted corn in Wisconsin and elsewhere. From 1975 to 1977, the first years that payments were made to farmers for crane damage to crops, the WIDNR paid ~\$10,200 per year to reimburse farmers for crane damage on less than 40 ha of planted corn per year (Melvin 1978). In 2017 a seed treatment to abate crane damage to corn was applied to more than 58,000 ha in Wisconsin (K. Ballinger, Arkion Life Sciences LLC, unpublished data). Given the extensive nature of the problem, further research on the ecology of crop damage caused by sandhill cranes in corn, and on the efficacy of abatement strategies, was warranted. In this study we sought to: 1) describe sandhill crane foraging behavior, specifically foraging rates and food acquisition behavior, in cornfields when planted seeds were vulnerable to damage and 2) estimate damage to planted corn that was either treated with a taste deterrent or untreated.

STUDY AREA

The study area, located at the junction of Marquette, Columbia, and Adams counties of Wisconsin (centered on 43°39'04"N, 89°35'10"W), was 6,251.6 ha (Fig. 1). Primary vegetation consisted of sedge-dominated (*Carex* spp.) wetlands (18.4%), many of which were bisected by streams and contained some open water. Forests (25.4%) were located primarily on lateral moraines while row crop fields of corn or soybean (35.2%) were located primarily in valleys as were grassland or alfalfa fields (16.9%) and other types of land use (4.1%). Landscape details were provided by Su (2003) and McKinney et al. (2016).

METHODS

We collected 3 types of data for this study: habitat use data for the entire study area, foraging behavior collected from focal observations of individual cranes, and diurnal radio-tracking data that followed the same individual cranes throughout the day. Habitat use surveys provided estimates of crane abundance while focal observations provided rates of individual behavior and radio-tracking data linked daily habitat use to individual behavior.

Sandhill cranes were captured through both federal and state permits to J. Barzen (master banding permit #22339, Wisconsin Scientific Collectors Permit #SRL-SCR-001-2009), and ACUC supervision through the International Crane Foundation (Application 007, last amended for this study in 2009). All applicable ethical guidelines for the use of birds in research were followed, including those presented in the Ornithological Council’s “Guidelines to the use of wild birds in research” (Fair et al. 2010).

Habitat Use Surveys

To estimate crane abundance, we conducted a roadside survey of cranes. For the entire study area, 3 different routes were traveled 6 times per day, 2 times per week (Fig. 1; McKinney et al. 2016, Wheeler et al. 2018). The first survey for each cycle was chosen randomly, as were starting points within each survey, but each of 6 routes within a survey, used throughout 1 day, started from the same point.

Observers traveled roadways by car and locations of sandhill cranes were plotted on aerial photographs. We recorded location, behavior, number of individuals, and identification of color-marked individuals for each observation. In 2009 the status of cornfields was determined on a daily basis (explained below) while other habitat characteristics were determined once per week. For corn planting dates, growers were interviewed if planting was not directly observed during field work.

We calculated the total number of cranes seen in cornfields and the total number of cranes seen in the entire study area by combining all cranes seen in the designated habitat for all routes and survey areas. The duration of an observation cycle was 3 or 4 days each week. Double-counting of individuals occurred, but our effort was constant, so comparisons between surveys were not biased. In addition, with marked

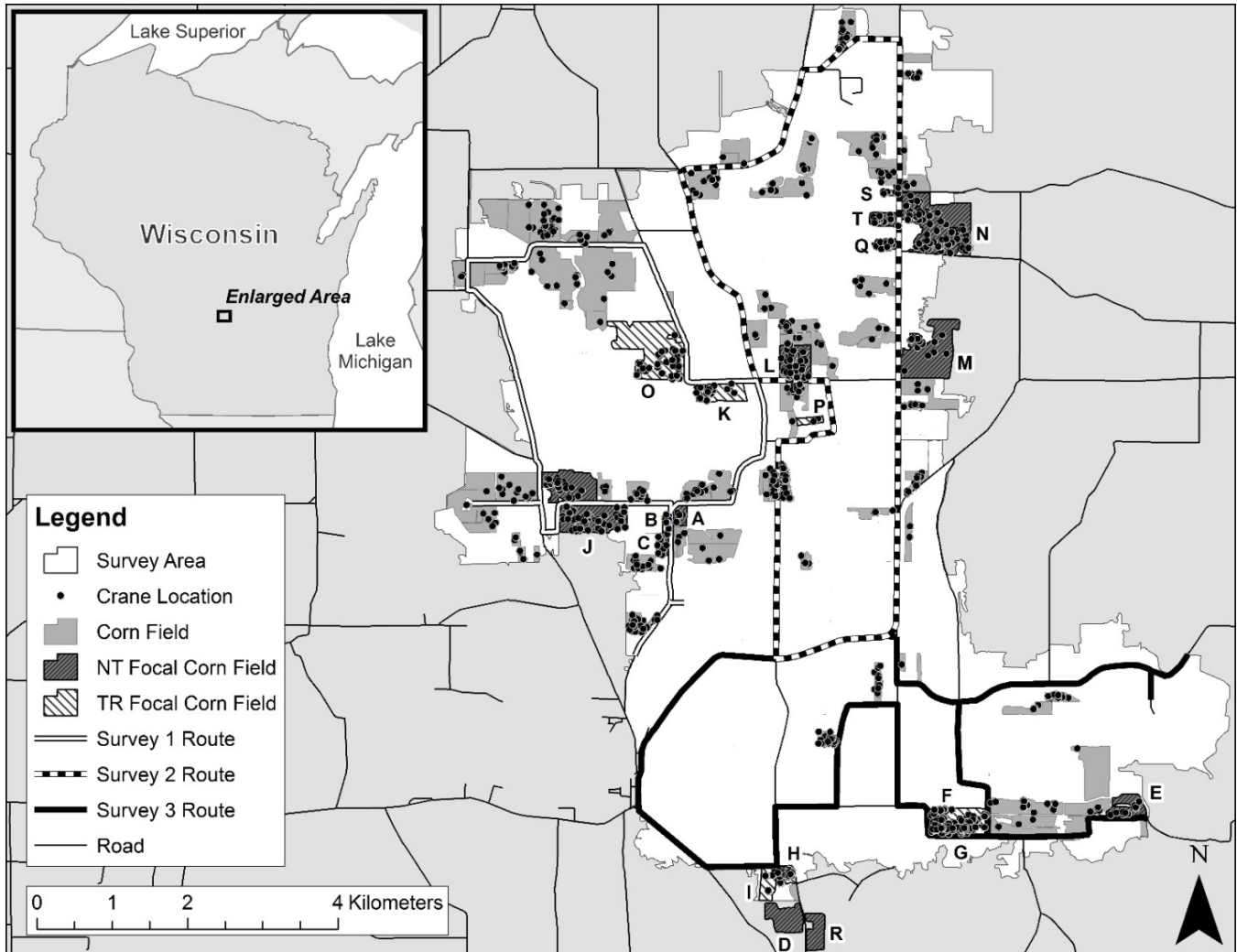


Figure 1. Location of habitat use surveys, all cornfields in the study area near Briggsville, Wisconsin, and crane locations in cornfields during 10-30 May 2009. Letters refer to field identifier (see Table 2). Light gray striped (forward slash) cornfields were treated with a taste deterrent while dark striped fields (backward slash) were untreated. Gray fields (no stripes) were corn in 2009 but had no cranes in them.

birds we know that the turnover rate of individuals within fields was high (McKinney *et al.* 2016, Wheeler *et al.* 2018), so combining route data provided information for a larger number of unique individuals. Our local population estimate (cranes/route) was the total number of cranes seen in all surveys divided by 6 routes per day, whereas our estimate of habitat use by cranes (cranes/survey) was the total number of cranes seen in all 3 surveys combined. Crane population and habitat use metrics for cornfields were calculated similarly for individual habitat types.

Our study focused on cornfields which were characterized by 2 stages: planted (CP) or germinated

(CG). In each stage of field phenology, fields were further characterized by daily development. A cornfield that had been planted 3 days prior to the survey date, for example, was labeled as CP+3. Once the coleoptile was visibly emerged from the soil surface, a cornfield was designated as corn germinated (e.g., CG+5 for corn coleoptile emerged for 5 days).

Melvin (1978) and Bennett (1978) both suggested that the stored energy in the sprouted kernel served as valuable food for cranes. Corn kernels contain an embryo, stored energy, and nutrients to provision the seedling until photosynthesis renders the plant self-sufficient (Cooper and MacDonald 1970), so we noted

how many days had occurred following germination. Cooper and MacDonald (1970) demonstrated that most endosperm was consumed by the 2-leaf stage of corn development, which occurred typically at 10 days post germination. Seedling growth and development, however, is dependent upon temperature and moisture, so some endosperm would often remain in the kernel through day 17 post-germination (the 4-leaf stage of the seedling). We defined sprouted kernels as being vulnerable to crane damage for CG+0 to CG+9, possibly vulnerable for CG+10 to CG+17, and not vulnerable >CG+17.

Foraging Observations

We selected CP and CG fields for observation primarily from within the survey area. To increase the number of observations of marked cranes, we also observed foraging cranes in 2 fields that were adjacent to the survey area (Fig. 1), field R (10.45 ha) and D (15.46 ha). Individual fields surveyed were chosen randomly throughout the observation period (10-30 May 2009). Cornfields with greater crane use were observed more frequently than were cornfields with less use. Within a field we observed only color-marked cranes or unmarked cranes that were associated with color-marked cranes (and thus distinguishable). All color-marked cranes had been captured and banded in previous years (Hayes et al. 2003, Dickerson and Hayes 2014, Hartup et al. 2014), so their social status (territorial or non-territorial) and their age, if captured as chicks, were known. Non-territorial status was attributed to sexually immature but independent cranes as well as to paired or unpaired, sexually mature, adults of any age (Hayes and Barzen 2006). Adult, non-territorial cranes could have been territorial previously or not (Barzen and Gossens 2014). Cranes categorized as territorial nested in 2009.

Once we chose a crane for observation, the target individual was observed until the bird left the field or moved out of sight. The entire length of observation, recorded to the nearest minute, was called an observation bout. Within observation bouts, we used a stop watch to calculate active foraging time, defined by measuring how long food acquisition behavior, food manipulation time, or food searching behavior persisted within the observation bout (Barzen et al. 2018). Food searching behavior included walking while peering down, stalking, or scanning for food. Calculation of

active foraging time was stopped during rest, comfort, alert, non-foraging locomotion, or social interaction (Ellis et al. 1991).

The only food acquisition behaviors observed were low jabs and probes. Low jabs secured food at the soil surface with a relatively quick extension of the head and neck to acquire a visible food item. Probes, in contrast, included insertion of the bill into the soil while searching for unseen foods. A single probe was defined as the insertion of the bill into the soil, followed by a recovery of the bill tip to a point at or near the soil surface. Individual probes were often repeated in rapid succession whereas jabs were not. Digging with the bill, the lateral movement of the bill while it was inserted into the soil, was included as probing behavior. Jabs were often associated with probes where birds would expose a subterranean food item by probes but acquire the item prior to swallowing with a jab. Both jabs and probes were tallied. Since planted corn, the sole food item susceptible to crane damage, was obtained primarily through probing behavior, we calculated a jab to probe ratio to infer corn abundance in the diet. When probes were the predominant food acquisition behavior, the jab/probe ratio was <1. Swallows of food items were defined following Ellis et al. (1991) and quantified following Barzen et al. (2018).

We attempted to identify foods swallowed but a rigorous process of determining the identity of food, based on foraging behavior (Barzen et al. 2018), had not yet been established at the time of this study. Instead, we noted the identity of any food item that we could see through spotting scopes using 45-60× objectives.

To assess individual daily habitat use by sandhill cranes in our study population independently from habitat use surveys, we examined data from 11 individuals that were tracked with VHF transmitters (Hayes and Barzen 2016a,b). These cranes often utilized areas that were outside of the survey area but similar in land use composition. Each radio-tracked crane was followed from morning roost location to evening roost location and located once every 1-2 hours throughout the day. Habitat and behavior were recorded with each location. Where crane location was triangulated (Mech 1983), we estimated habitat from the ground observation if possible or used Cropscape 2009 (USDA National Agricultural Statistics Service Cropland Data Layer 2009) to determine habitat type as well as aerial photos from 2009 to confirm habitat types containing perennial cover. Ten individual cranes were tracked

once during 9-29 May and 1 crane was tracked twice, once on 6 May and once on 29 May. All radio-tracked cranes were non-territorial at the time of tracking and were hatched and banded in 2006 ($n = 3$), 2007 ($n = 4$), and 2008 ($n = 4$). Rotation spots for tracking individuals were randomly selected.

Seed Treatment

All planted corn kernels were treated by cooperating growers with insecticides designed to prevent insect damage to the kernel or seedling, resulting in kernels that were colored pink, red, or green. Yellow kernels, left from harvest in fall 2008, were also available in spring 2009. Some growers treated planted corn with a taste deterrent, Avipel®, whose active ingredient was the biopesticide 9,10-anthraquinone (Lacy et al. 2013). Both powder and liquid formulations were used. AQ did not change kernel color sufficiently to detect from a distance. If observed at ingestion, we used color of corn kernel to identify whether or not the corn kernel was newly planted or older waste corn in the field. We examined sandhill crane foraging behavior in both AQ-treated and non-treated cornfields.

Statistical Analysis

We used 2-way analysis of variance from the program R (R Core Team 2015) to compare foraging rates by main effects of treatment (treated and untreated) and stage (CP and CG) with interactions between main effects. A similar model, using jab/probe ratios by main effects of treatment and stage, and with interactions, was also used. We used Welch's *t*-test (R Core Team 2015) to compare individual means and regression to examine change in the jab/probe ratios over time. Means were reported with \pm SE.

RESULTS

Habitat Use Surveys

We completed 6 habitat use surveys during the 3 weeks of study. The first survey was completed when most fields that were intended for corn production in 2009 had been planted but seed had not yet germinated (Table 1). Surveys continued while planted seed germinated and grew to a point where no endosperm remained in the planted seeds. By the last survey, most

Table 1. Status of cornfields, and sandhill cranes seen in them, during surveys of fields throughout the Briggsville, Wisconsin, study area 10-30 May 2009.

	10-12 May	13-16 May	17-19 May	20-23 May	24-26 May	27-30 May	Mean \pm SE
Cranes in all fields							
Cranes/survey ^a	480	424	426	373	406	382	415 \pm 13.2
Cranes/route ^b	80	71	71	62	68	64	69 \pm 2.6
Cranes in cornfields							
Cranes/survey ^a	176	156	121	145	144	153	149 \pm 7.3
Cranes/route ^b	29	26	20	24	24	26	25 \pm 1.2
% Cranes in corn ^c	37	37	28	39	35	40	36 \pm 1.7
Total no. of cornfields	98	100	104	105	105	105	
% Fields – CP ^d	70	30	19	7	5	1	
% Fields – CG1-10 ^e	30	70	75	65	28	20	
% Fields – CG11-17 ^f	0	0	6	28	61	52	
% Fields – CG>17 ^g	0	0	0	0	6	27	

^a Cranes/survey = all cranes seen in each of 6 routes for each survey and for all 3 surveys combined (18 total routes).

^b Cranes/route = total number of cranes divided by 6 routes run for each survey.

^c % Cranes in corn = total number of cranes in corn/total number of cranes \times 100.

^d No. of fields planted with corn but not yet germinated/no. of all cornfields in study area \times 100.

^e No. of fields planted with corn where seeds have germinated for 1-10 days/no. of all cornfields in study area \times 100. This is the period when planted corn seed is vulnerable to damage by sandhill cranes.

^f No. of fields planted with corn where seeds have germinated for 11-17 days/no. of all cornfields in study area \times 100. During this period the presence of endosperm in the kernel depends upon temperature at the time of germination. Corn is possibly vulnerable during this period.

^g No. of fields planted with corn where seeds have germinated for >17 days/no. of all cornfields in study area \times 100. Under any conditions, endosperm is gone by this time.

cornfields in our study area were no longer vulnerable to damage by cranes (Table 1).

The average number of cranes seen per survey was 415 ± 13.2 ; the number of cranes found in planted and germinated cornfields averaged 149 ± 7.3 per survey (36%) and varied from 28% to 40% of the total number of cranes seen (Table 1). The average number of cranes seen per route was 69 ± 2.6 while the average number of cranes seen in corn per route was 25 ± 1.2 (Table 1). When not in corn, surveyed sandhill cranes were recorded in wetland, pasture, ungrazed grass, or other agricultural fields.

Foraging Observations

We observed 33 marked sandhill cranes during 10-30 May, of which 13 birds were territorial and 20 were non-territorial. Some individuals were observed multiple times. Of 121 observation bouts collected from cranes in cornfields, 28 were collected from territorial and 93

were collected from non-territorial individuals. Seven observation bouts (162 min of observation) included provisioning flightless chicks, most of whom received earthworms procured by adults that were probing. Only 1 kernel was observed being consumed by a chick. We found no difference between male (6.42 items/min) and female (5.84 items/min) ingestion rates ($t = -0.38$, $P = 0.71$). Of 20 cornfields where observation bouts were recorded, 7 were planted with seeds containing a deterrent and 13 were not treated (Fig. 1, Table 2).

From 42.7 hours of observation bouts we estimated that cranes actively foraged $54.2 \pm 5.7\%$ of the time (Table 2). The average observation bout was 21.2 ± 1.3 minutes (range 2-97 min) within which cranes spent an average of 10.2 ± 0.8 minutes actively foraging (range 0-37.5 min). The number of food items swallowed was closely associated with the number of observation bouts collected and peaked 20-22 May, so ingestion rates, relative to the number of observation bouts, were similar throughout the study (Fig. 2). Cranes swallowed

Table 2. Summary of focal foraging observations for 33 color-marked sandhill cranes in fields treated (TR) and non-treated (NT) with taste deterrents near Briggsville, Wisconsin, 11-29 May 2009.

Field	Treatment status	Total no. of cranes in fields during surveys	No. of observation bouts	Total time observed (min)	Active forage time (min)	% observation time actively foraging
A	NT	10	7	141	74.6	52.9
B	TR	22	1	2	1.8	88.3
C	NT	19	1	2	2.3	100.1
D	NT	n/a ^a	2	32	14.7	45.9
E	NT	8	3	71	37.0	52.2
F	TR	101	11	300	166.1	55.4
G	NT	212	52	1,009	530.6	52.6
H	NT	0	2	10	6.7	67.3
I	TR	22	8	79	48.0	60.7
J	NT	71	2	60	5.6	9.3
K	TR	16	3	86	9.7	11.3
L	NT	32	3	90	32.1	35.7
M	NT	7	2	28	15.2	54.3
N	NT	67	7	247	119.4	48.4
O	TR	17	1	16	13.4	84.0
P	TR	4	1	4	4.0	100.0
Q	NT	19	3	68	33.3	48.9
R	NT	n/a ^a	5	121	77.6	64.1
S	TR	5	3	29	9.1	31.4
T	NT	3	4	167	37.0	22.2
Sum		635	121	2,562	1,238.1	54.2 ^b
Mean NT (\pm SE)		40.7 ± 18.6	7.2 ± 3.8	157.4 ± 73.5	75.9 ± 39.1	50.3 ± 6.0
Mean TR (\pm SE)		26.7 ± 12.7	4.0 ± 1.5	73.7 ± 39.9	36.0 ± 22.5	61.6 ± 12.1

^a n/a = field adjacent to, but not in, survey area.

^b Mean ($n = 20$) percent time spent actively foraging per field.

an average of 6.08 ± 0.7 food items per active minute of foraging ($n = 121$ observation bouts, range 0-69.73). The highest ingestion rate observed was 214 food items consumed in 19 minutes of active foraging (11.3 items/min) over a 28-minute observation bout.

Only 10.4% of the 6,445 food items swallowed were identified. Known foods included earthworms, insect larvae, and corn kernels but most items swallowed (93% of all identified items) were kernels. We observed 624 swallowed kernels in 56 of 121 (46%) observation bouts, of which in 13 observation bouts the color of the seed was noted. Based on kernel color, the origin of consumed kernels was both from the previous fall and from seeds planted in spring 2009. No coleoptile or true leaves of corn seedlings were consumed by cranes, though many plants were uprooted. Probing cranes often inserted their bill directly next to the corn seedling (2-4 leaf stage) and obtained the seed with, or without, pulling up the plant (Fig. 3).

Foraging observations in most fields began before corn germinated (Table 1). The number of kernels swallowed that were associated with corn seedlings (i.e., not waste corn) was noticeably high 17-24 May, peaking 20 May (Fig. 4), and lagged behind peak germination of corn on 13-16 May (Table 1). Correspondingly, the ratio of jabs to probes increased rapidly throughout May (Fig. 4, $F = 12.0$, $P = 0.001$, $R^2 = 0.75$) and was <1 until 25 May when the number of vulnerable cornfields began to decline rapidly (Table 1). Jabs exceeded probes thereafter. The field with the heaviest crane use (Table 2, Field G) germinated by 13 May and was at CG+16 by 30 May. Corn seedlings were past the 4-leaf stage at this date.

Seed Treatment

We observed 986.0 minutes of active foraging in non-treated fields and 252.1 minutes of active foraging in treated fields. Though the average ingestion rate of all food items was similar between treated (6.44 items/min) and non-treated fields (6.21 items/min; $t = -0.15$, $P = 0.88$), corn kernels, where foods were identified, were ingested at more than 3 times the rate from non-treated fields than from treated fields (Table 3; $F = 3.84$, $P = 0.05$). Ingestion rates were similar between CP and CG fields ($F = 0.34$, $P = 0.34$), and there was no interaction between field stage and treatment ($F = 0.24$, $P = 0.63$). Comparing treated and non-treated fields, the total number of cranes in fields, observation bout

Table 3. Mean active foraging rates (kernels/min) for corn kernels by treatment status of the field, crop stage, and the ratio of jab frequency over probe frequency for sandhill cranes near Briggsville, Wisconsin, May 2009. NT = non-treated and TR = treated.

Treatment	Crop stage ^a	Foraging rate		Jab/probe ratio	
		<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE
NT	CG	75	0.82 \pm 0.19	70	1.0 \pm 0.5
NT	CP	16	0.45 \pm 0.17	16 (15) ^b	16.3 \pm 16.2 (0.1 + 0.03) ^b
TR	CG	23	0.23 \pm 0.10	21	1.7 \pm 0.7
TR	CP	5	0.21 \pm 0.21	4	1.2 \pm 0.9

^a CG = A field with planted corn seed that has visible cotyledons; CP = A field that has corn planted without visible cotyledons.

^b Jab/probe ratio with observation bout from field R removed (259 jabs/1 probe).

length, number of observation bouts, active foraging time, and % observation time spent foraging did not differ ($P > 0.33$, Table 2).

Within treated fields, we observed 3 instances of cranes acquiring planted corn seeds and subsequently rejecting the seeds by shaking their heads and spitting the kernels out. Rejection of acquired kernels was not seen in untreated fields. Conversely, within non-treated fields, we saw cranes forage on seeds or seeds attached to coleoptiles 18 times but only saw this foraging behavior 4 times in treated fields. In only 1 of those foraging behaviors from treated fields did cranes appear to swallow more than 1 or 2 kernels.

Jab/probe ratios were higher in CP versus CG fields (Table 3; $F = 4.00$, $P = 0.05$) but did not differ between treated and untreated fields ($F = 0.12$, $P = 0.72$), and there was no interaction between field stage and treatment status ($F = 1.10$, $P = 0.30$). One crane made 259 jabs to 1 probe in an observation bout observed at field R; if omitted and our data re-analyzed (Table 3), there was no difference in jab/probe ratios between CP and CG stages ($F = 0.85$, $P = 0.36$).

Radio-tracking Data

We tracked 11 individual cranes for a total of 12 days and 174.5 hours of observation. Tracking days were evenly distributed throughout the study. Eight of 12 (67%) tracking days measured cranes in CP or CG fields while 15 of 88 (17%) locations occurred in this habitat (Table 4). We tracked cranes from sunrise

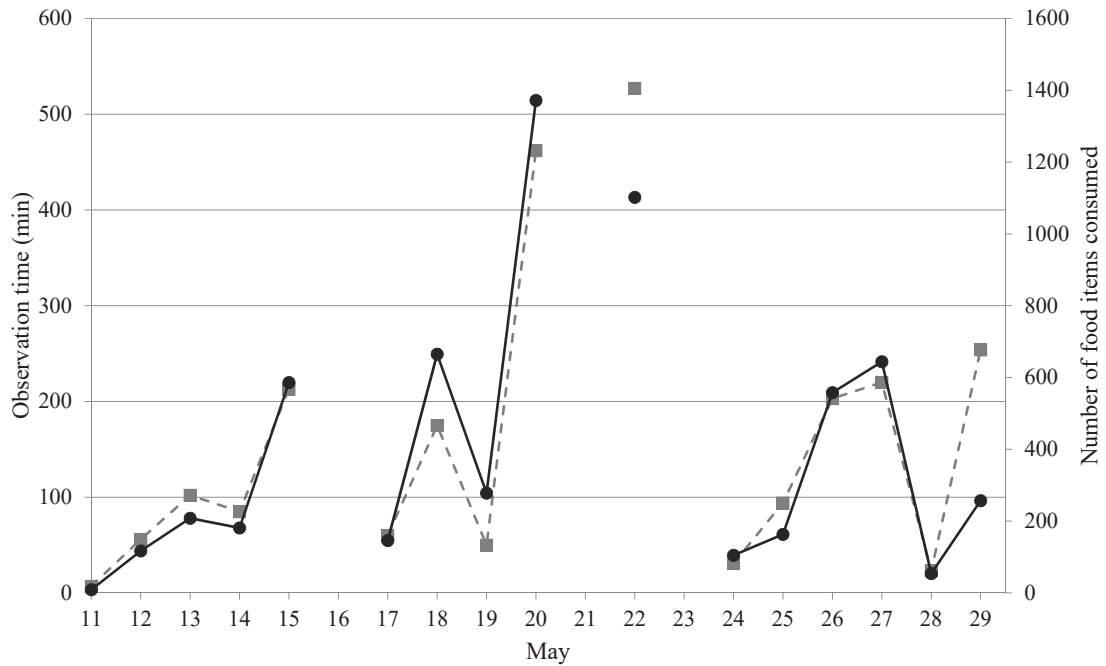


Figure 2. Total observation time in minutes (gray squares, dashed line, left axis), and total number of all food items swallowed by day (solid circles, solid line, right axis) by sandhill cranes during 10-30 May 2009. Data collected from behavioral observations of marked individuals foraging in cornfields near Briggsville, Wisconsin.



Figure 3. Crane damage in field C, 22 May 2009, Briggsville, Wisconsin. Holes at base of the seedling are from crane bill probing for seed at base of plant. Seedlings were either lying on ground or barely rooted in ground. Photo by Anne Lacy.

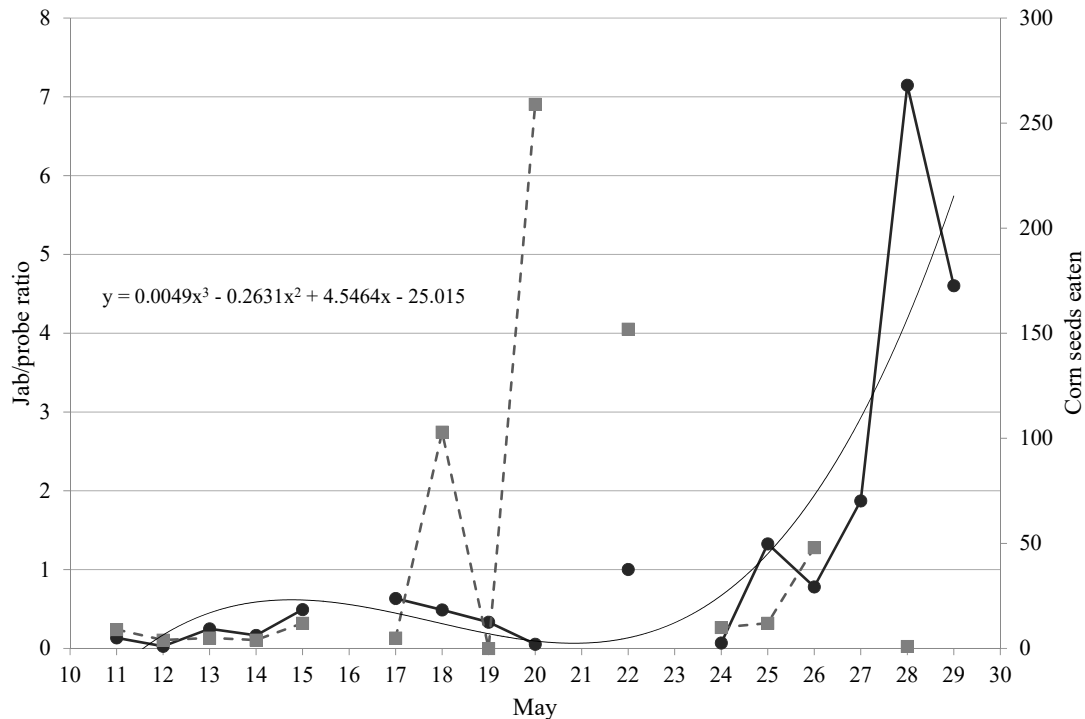


Figure 4. The ratio of jabs to probes (left axis, solid line, solid circle) and corn seeds eaten (right axis, dashed line, gray square) for all birds observed in study area near Briggsville, Wisconsin, May 2009. A ratio less than 1 indicates more probing than jabbing behavior; greater than 1 is more jabbing than probing behavior. Numbers on the x-axis refer to the date in May in which the sample was collected. The light gray line is a curvilinear regression for jab/probe ratios during May.

to sunset (averaging 15 hr in May) so cranes spent an average of 2.6 ± 0.7 hours per day in cornfields. Seven of 12 tracked cranes utilized the study area, at least in part, while the regions used by 5 other tracked cranes included Rush Lake, Portage, Ripon, and Oxford, Wisconsin.

Damage Estimates

Independent estimates of habitat use by cranes in cornfields obtained from surveys (36%) and from radio-tracking (17%) differed, so we used each data set where they were most applicable. The total time sandhill cranes in the study area spent in corn each day was estimated at 387.4 hours (149 cranes in corn per survey [Table 1] \times 2.6 hr foraging/crane in corn [radio-tracking data]). While in corn, 54.2% of observation bouts was spent actively foraging. Cranes in our study area, therefore, spent an estimated 210.0 active foraging hours in corn each day (387.4 hr in corn \times 0.542 active foraging/time in corn) or 12,600 minutes. On average, these cranes consumed 6.08 food items/minute of active foraging, so 12,600 minutes of active foraging would account for

76,608 food items consumed by all the cranes that we observed in cornfields each day (6.08 food items/min \times 12,600 min). This is equivalent to individual cranes consuming an average of 514 food items/day (6.08 items/min \times 60 min/hr \times 0.542 active foraging/observation \times 2.6 hr/day in corn/crane) or 478 kernels/day (514 food items/day \times 0.93 kernels/food item), assuming that the types of foods consumed for identified and unidentified ingested items were similar. Ingestion rates were also assumed to be constant. We estimate, therefore, that 71,245 kernels could be consumed (76,608 \times 0.93 kernels/all food) for the entire Briggsville population during 1 day. During our study, at least 1 cornfield in the entire study area could have been vulnerable to damage by cranes from 5 May to 6 June, a total of 32 days. For the entire vulnerable period of corn, cranes in the Briggsville population could consume a total of 2,279,840 kernels (32 days of vulnerable corn \times 71,245 food items consumed per day in corn) or the equivalent of 30.7 ha of corn planted at 74,147 kernels per ha in Wisconsin (as recommended by Lauer and Cusicanqui [2017] and then converted from acres to ha). If we used the maximum time that corn was possibly vulnerable

Table 4. Number of locations from 12 days of radio-tracking 11 cranes and the habitats where each crane was located near Briggsville, Wisconsin, 9-29 May 2009.

Land cover	Crane ID												Total	% of Total
	473	474	480	485	486	486(2)	488	492	520	524	531	536		
Alfalfa	5	0	1	0	2	0	0	0	1	0	1	1	11	12.5
Corn planted/Germinated	1	3	2	0	0	0	3	0	2	1	2	1	15	17.0
Forest	1	0	0	0	1	0	0	2	1	0	0	0	5	5.7
Wetland	0	3	2	3	0	6	1	5	2	0	1	1	24	27.3
Grass/Pasture	0	3	0	0	0	2	0	0	0	1	2	1	9	10.2
Fallow/Corn stubble	0	0	1	0	1	0	1	0	0	0	0	0	3	3.4
Soybeans	0	0	0	5	1	0	2	0	1	5	1	2	17	19.3
Other row crop	0	0	0	0	1	0	0	2	0	0	0	1	4	4.5
Total	7	9	6	8	6	8	7	9	7	7	7	7	88	99.9

(17 days post-germination), crane damage could occur for 41 days (5 May to 15 June) in the study area, with a total of 2,921,045 kernels consumed (41.0 ha of planted corn). In 2009, 1,075.5 ha of corn were planted, so a loss of 41.0 ha would represent 3.8% of the corn planted in the study area.

Individual variation in sandhill crane foraging behavior, however, was great. The longest time spent by a radio-tracked individual in corn during 1 day was 6.4 hours (3 of 7 locations in a 15-hr day). Within the study area, 1 color-marked crane (no. 489; a paired, 2-year-old, non-territorial male), was observed nearly every day in field G. Survey data noted crane 489 in field G an average of 52% of each day. If Crane 489 was in the field an estimated 7.5 hours each day, then he spent 4.1 hours actively foraging ($7.5 \text{ hr} \times 0.542 \text{ active/total}$). Crane 489, therefore, may have swallowed 1,459 items/day ($6.08 \text{ items/min} \times 60 \text{ min/hr} \times 4.1 \text{ hr} = 1,496 \text{ items}$) and a total of 25,432 items over the 17 days that corn was vulnerable in the field that he used (0.34 ha of planted seed). As such, the daily rate of consumption for crane 489 was over 6× the average daily ingestion rate.

DISCUSSION

We found an average of 69 cranes/route in our study area during May, while mark/recapture analysis estimated the population of the study area to be 52.1 territorial and 27.5 non-territorial cranes (79.6 cranes total) for April through mid-June 2009 (McKinney et al. 2016). Our population surveys did not account for crane movement in and out of the study area, especially

for non-territorial individuals, so our underestimate was not surprising. Depending upon their age, home range estimates for non-territorial cranes ranged from 28.3 km² (for all non-territorial cranes >3 years old) to 197.3 km² (for second-year birds; Hayes and Barzen 2016a). The home range of second-year birds was larger than our 62-km² study area. Su (2003) also found considerable movement by non-territorial cranes in the same primary area. The home range of territorial cranes, in contrast, was 1.3 km² in spring (Miller and Barzen 2016), so our population estimate was not likely influenced by movement of territorial cranes.

Among individuals within the study area, not all cranes used cornfields during May. Well under half of the cranes/survey seen used cornfields each day (28-40%) and 4 of 12 crane tracking days (3 of 11 cranes) did not use cornfields at all. Some cornfields received no crane use (Fig. 1). Other habitats within a crane's home range were important for foraging or other behavior. Individual variation among marked cranes was extensive with some individuals (like crane 489) using cornfields more extensively than others while some individuals avoided use of cornfields altogether. Bennett (1978) found that unmarked cranes used cornfields 1.5 hours/day, which was less than our estimate of 2.6 hours/day for radio-tracked cranes that used cornfields.

Our estimated ingestion rate of 197.7 items/hour in a cornfield ($6.08 \text{ items/active min} \times 0.542 \text{ active min/min observation bout} \times 60 \text{ min/hr}$) was almost double Bennett's (1978) estimate of 102 corn plants/bird/hour. Ingestion rates can vary greatly, as illustrated in the experimental foraging trials conducted by Barzen et al. (2018) where 2-293 kernels of corn were consumed

from bait piles in intense feeding bouts that lasted 2-3 minutes ($\bar{x} = 127.1$ kernels). Differences between Bennett's (1978) and our estimates of ingestion rates could, therefore, be due to density of planted corn, soil type or condition, previous experience, degree of hunger, or sampling variance. Our average ingestion rate (514 items/crane/day) was also equivalent to almost twice the maximum ingestion ability for an individual crane that began a foraging bout with an empty stomach and fed on corn until sated (Barzen et al. 2018). This volume of food would, therefore, be equivalent to 2 complete foraging bouts/day. Though variable, ingestion rates of individual cranes that we measured appeared realistic and were consistent with the few other crane foraging studies that exist.

Similar to Bennett (1978), and reported by Melvin (1978), most identified foods consumed in our study were corn kernels. The coleoptile could serve as guides to locating planted kernels efficiently through probing. Either seedlings were discarded after removing the attached kernel or seedlings were discarded after a bird found no endosperm remained. Importantly, crane response to foraging on planted corn appeared to lag behind corn seedling phenology suggesting that learning was required. Further, food acquisition behaviors (jab to probe ratios) changed markedly as corn vulnerability declined suggesting that cranes changed their choice of food items (Barzen et al. 2018). Though crane diet changed as corn became unavailable, or as deterrents were deployed, cranes often remained feeding in the same cornfields. Since approximately 1/3 of the study population utilized cornfields, many cranes encountered novel situations where behavioral responses were required and experience might increase the probability of learning. All cranes in our study were marked and ≥ 2 years old. Age and experience were important criteria for cranes that adapted to new winter habitats quickly (Mueller et al. 2013, Teitelbaum et al. 2016). On breeding areas, cranes utilized similar home ranges (Hayes and Barzen 2016a) or territories (Miller and Barzen 2016) between years and could likely adapt to new habitat conditions quickly as done on winter areas because they had previous experience with these habitats. Within a year, experienced cranes may also learn to adjust more quickly to novel experiences through direct experience with deterrents in treated fields and with changes in maturation of untreated corn or with indirect learning through observations of other foraging individuals. Regardless, rapid adjustments of

winter distribution parallel rapid adjustments within a habitat or year. Collectively, these behavioral traits would suggest that cranes do not need to consume many AQ-treated seeds before learning to alter their diet.

Rapid learning, accompanied with long-term memory, has also been observed by Barzen (unpublished data). Recapture of cranes with a sedative, even when capture attempts were separated by up to a decade, were more difficult because cranes would quickly detect the sedative during recapture attempts and avoid eating from sedative-treated bait piles that they had previously been conditioned to consume when the sedative was absent.

Bennett (1978), Melvin (1978), and our study all identified non-territorial cranes as the primary consumers of spring corn. Territorial cranes had small home ranges (Miller and Barzen 2016), and family groups in our study consumed mostly earthworms. Only 1 kernel was identified as being fed to a chick during our study, while others were provisioned with 17 earthworms and 159 unknown items. No non-territorial cranes consumed earthworms. Chicks were only 2-3 weeks old at this time and may have been too small to ingest corn kernels, or chicks required high protein meals that highly-digestible invertebrates offer (Wellington et al. 1996).

Kernel ingestion rates of identified foods in AQ-treated fields were 3 times lower than that of untreated fields, even though the ingestion rates for all foods did not differ between treated and untreated fields. The same was true for jab/probe ratios. This is further evidence that the diet of cranes while foraging in cornfields includes more than just planted kernels. Melvin (1978) experimented with methiocarb as a taste deterrent and concluded that it was not effective. This was not the case with AQ as, compared to untreated fields, uprooted seedlings were not found in treated fields. Even with deterrents applied, however, it appeared that some plants were still damaged by cranes as they sampled and discarded seeds, but this behavior was infrequent.

All sandhill crane individuals in our study area could consume an estimated 71,245 kernels/day (100% of planted kernels from 0.96 ha/day) or 478 kernels/crane/day. Averaged across the entire study area, the estimated damage caused by foraging cranes was small (a maximum of 3.8% of all planted corn), but the use of cornfields by cranes was not uniformly distributed. Crane aggregation in some fields, but not others, could concentrate damage. Non-territorial birds, the primary

social group that foraged on planted corn, had no territory maintenance constraints and had large home ranges that varied greatly from day to day (Su 2003, Hayes and Barzen 2016a). If foraging success was quickly communicated among individuals that shared the same night roosts on summer areas, then widely scattered individuals could learn from each other and quickly coalesce on a few fields as a large flock and damage could occur throughout an entire field. This mechanism is similar to individuals that quickly learned to adjust winter locations (Mueller et al. 2013, Teitelbaum et al. 2016), except that the change occurs within days, rather than years.

Wisconsin cornfields are often replanted when losses exceed 20% of the field. The maximum loss of corn to crane damage, therefore, could have been as high as 205.0 ha if each field received broad damage sufficient to require replanting (41.0 ha total loss/0.20 damage for partial loss) or 19.1% of all corn planted in the study area.

When many cornfields germinated simultaneously, crane foraging response could not as readily concentrate on any 1 field because there were not enough cranes available to utilize every field available. In 2009 we observed an average of 415 cranes/survey over our entire study area, or 415 cranes for every 1,075.5 ha of corn (0.38 cranes/ha of corn). Fields that germinated after peak corn emergence, however, could be particularly vulnerable to damage because flocks could concentrate on these more isolated fields after cranes became accustomed to foraging on planted kernels. Fields planted after the average planting time, therefore, might be particularly vulnerable to damage.

AQ as a deterrent was effective in this study by removing only planted corn seed from the diet of cranes foraging in cornfields, mimicking the natural disappearance of corn from the diet as seedlings develop (Fig. 4) but at an earlier time. Both AQ and natural decline of seed availability operated at the smallest scale of habitat selection (food items within a field; Johnson 1980). Deterrence provided protection of corn from planting through 17 days post-germination. Since alternative foods existed during the period of corn vulnerability, the earlier diet shift imposed by AQ would be more sustainable for foraging cranes than if no alternative foods existed. If true, AQ treatment may prove to be a strategy that is less likely to fail in the future because it does not remove all resources that cranes seek from a desirable habitat (Barzen and Ballinger 2017).

In the 1970s, crane damage to germinating corn became sufficiently noticeable to require a response by WI DNR. Estimates for crane damage to sprouting corn in Wisconsin during 1975-1977 (Table 2 in Melvin 1978) were 47.60, 21.61, and 7.25 ha, respectively, and totaled 19.04 and 25.80 ha in 1978 and 1979 (R. A. Hunt, WI DNR, unpublished data). Though no current crane damage data exist that can be compared to damage levels in the 1970s, the extent of damage has widened as the distribution of breeding sandhill cranes has expanded to virtually all of Wisconsin (Lacy et al. 2015). The area of corn treated with AQ in Wisconsin alone was 60,756, 54,675, 30,685, 50,586, and 58,072 ha during 2013-2017, respectively (K. Ballinger, Arkion Life Sciences LLC, unpublished data) and was concentrated primarily where the greatest overlap of cranes and corn occurs in the state (Lacy et al. 2013). Though the distribution of potential crane damage is now large, no state or federal funds pay for abatement or compensate for damage. Treatment with AQ has occurred through the private sector for more than a decade now. Conversely, payments for crane damage to untreated corn is neither effective nor affordable by any single organization because crane distribution is so extensive. Lacy et al. (2013) estimated that 1.4 million ha of corn were located near enough to crane habitat to receive damage if cranes were present. Currently AQ is an effective taste deterrent. Future effectiveness of AQ may depend upon how foraging behavior of cranes, and availability of alternate foods in cornfields, will co-evolve as agricultural practices adjust to changing climate and human population growth, both of which may influence the abundance of alternate foods.

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