Applying hierarchical resource selection concepts to solving crop damage caused by birds

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Abstract
Recovery of Greater Sandhill Cranes (Grus canadensis tabida) is a conservation success but will increase the potential for crop damage if problems caused by high crane density remain unresolved. In spring, cranes consume planted corn kernels (Zea mays), causing significant damage. From 1999 to 2001 and 2007 to 2009 we experimented with resolving crane damage. Seeds treated with either insecticides or anthraquinone (AQ) were not consumed in planted fields while untreated seeds were, causing a 19.6% reduction in seedling density where cranes foraged. Insecticides tested were inappropriate for future use while performance of AQ mimicked that of insecticides but was environmentally acceptable and economical to use. Though cranes selected germinating corn fields, regardless of treatment, they used fields containing treated corn without causing damage. Cranes were generalists when selecting food items within a field but were specialists when selecting field types within a home range. Deterrence at geographic scales where species are generalists may reduce the chance for habituation. Subsequent deployment of AQ has been replicated with other bird species and crops at landscape scales. Successful solutions enable landowners to value wildlife and promote biological diversity found on those lands.

KEYWORDS
anthraquinone, chemical deterrence, corn, landscape deterrence, lindane, rice, sandhill crane

1 | INTRODUCTION

Agricultural lands, important for human sustenance, also provide habitats for native species (Amano, 2009; Best, Freemark, Dinsmore, & Camp, 1995; Stafford, Kaminski, & Reinecke, 2010; van Velden, Smith, & Ryan, 2016) and other environmental services such as carbon sequestration, ground water recharge and water filtration (Duff, Zedler, Barzen, & Knuteson, 2017). In addition, 60% of U.S. land is privately owned (U.S. Bureau of Census, 1991, p. 201) and 52%, regardless of ownership, is used to produce food, fuel, fiber or medicine (Nickerson, Ebel, Borchers, & Carriazo, 2011). These land-use trends apply worldwide (Lambin & Meyfroidt, 2011). If conservationists wish to engage agricultural landowners to increase biological diversity, they must avoid costly conflicts that pit the needs of
landowners against the needs of native species that use private lands (Barzen, 2018; Conover, 2002; Treves, Wallace, & White, 2009; White & Ward, 2010) by recognizing inherent trade-offs among stakeholders that arise from managed solutions as opposed to unstable scenarios (Redpath et al., 2013).

For native biota, effective and sustainable crop damage prevention projects have been challenging to find (Austin & Sundar, 2019; Conover, 2002), though protocols for achieving effective solutions to damage have been proposed (reviewed in Treves, Wallace, Naughton-Treves, & Morales, 2006). Inherent in successful protocols are three primary criteria: (a) cost effective design, (b) wildlife specificity and selectivity, and (c) sociopolitical acceptability (Treves et al., 2009). In this paper, we experimentally apply damage abatement efforts on a landscape scale and relate ecological criterion, such as hierarchical habitat selection (Johnson, 1980), to cost effectiveness, and sociopolitical acceptability.

While habitat selection theory applies well to scenarios where multiple resources are involved (Fuller, 2012a; Rhodes, McAlpine, Lunney, & Possingham, 2005; Rosenzweig, 1981), hierarchical selection is complicated by occurring at multiple geographic scales among (a) regions within a biome or landscape, (b) home ranges within a region, (c) fields within a home range, and (d) food items within a field (Johnson, 1980). Focus upon inappropriate geographic scales can lead to incorrect conclusions about the extent of resource selection (Fuller, 2012b; Garshelis, 2000). Avian crop damage can arise from intensive selection of a specific resource, such as a field of planted corn seed (Barzen, Gossens, & Lacy, 2018) or a row of swathed, ripened grain (Knittle & Porter, 1988). Applying the concept of hierarchical selection to crop damage abatement might identify an ecological context within which crop damage occurs and thereby improve the efficacy (Barzen et al., 2018; Conover, 2002; Treves et al., 2009).

Though not often attributed as such, crop damage studies that modify habitat selection typically focus upon habitat selection between fields within a home range. Seamans and Gosser (2016), for example, refer to “bird dispersal techniques” such as propane cannons designed to scare birds away from sensitive fields (Bomford & O’Brien, 1990). Lure crops or supplemental feeding programs work in the opposite manner by attracting birds to one field that is isolated from fields sensitive to damage (Amano, Ushiyama, Fujita, & Higuchi, 2004; Shanni, Labinger, & Alon, 2019). Focus upon preventing damage at regional scales, or between food items within a field, has been studied much less (Barzen & Ballinger, 2018). Crop damage prevention by excluding birds from vulnerable fields usually becomes less effective over time because of habituation (Bomford & O’Brien, 1990; Conover, 2002; Seamans & Gosser, 2016). In contrast, lure crops or artificial feeding often fail by causing bird numbers to increase faster than available food, ultimately exacerbating damage (Shanni et al., 2019).

Worldwide, avian damage to agricultural fields occurs in many crops but most economic loss arises from damage to corn (Zea mays), small grains, rice (Oryza sativa), and sunflower (Helianthus annuus; Conover, 2002). Damage is caused primarily by birds consuming mature seed, sprouting/growing vegetation, or planted seed (Conover, 2002). Though crops and bird species that cause damage vary greatly worldwide, ecological explanations related to habitat selection are similar.

We applied hierarchical habitat selection concepts to Greater Sandhill Cranes (Grus canadensis tabida) in Wisconsin because the species is abundant (Lacy, Barzen, Moore, & Norris, 2015; Su, Harris, & Barzen, 2004) and crane-related damage to seeded corn fields is widespread in the Midwest (Barzen & Ballinger, 2018). In addition, crane damage has lacked effective solutions (Barzen & Ballinger, 2017). Further, we had an ongoing long-term field project in an area where damage was occurring which allowed ecological contexts of habitat, social and population dynamics to be understood (e.g., Hayes, 2015; Su, 2003; Wheeler, Barzen, & Crimmins, 2019). To our knowledge, this study represents a rare approach for solving avian damage to crops at a landscape level (Treves et al., 2006).

Specifically, we tested a solution for damage of planted corn seed that was caused by foraging cranes through applying resource selection concepts at two geographic scales: between fields within home ranges and between food items within a field. Our objectives were to: (a) compare the efficacy of two seed deterrents: Lindane (an organochlorine) plus Diazinon (an organophosphate) and 9,10-anthraquinone (AQ), (b) test selection between food items within fields by examining seedling density in areas that cranes used and did not use within the same field, and (c) test habitat selection between fields of germinating corn located within home ranges of local non-territorial and territorial cranes.

2 | METHODS

2.1 | Study area

Our study was conducted April through July, 1999–2001 and 2007–2009, and was located at the junction of Marquette, Columbia and Adams counties of Wisconsin, USA. The center of the 6,251 ha study area (Figure 1) was 43°39’04”N, 89°35’10”W. Wetland vegetation
consisted of sedge-dominated areas (*Carex* spp.) (18.4%), many of which were bisected by streams and contained open water (Figure 1, Barzen, Su, Lacy, Gossens, & Moore, 2016). Forests (25.4%) were located primarily on recessional moraines (Dott & Attig, 2004) while row crop fields of corn, grains or soybean (35.2%) were located primarily in valleys as were grassland and alfalfa fields (16.9%). Other land use types composed the remaining category (4.1%) (McKinney, Barzen, Riddle, & Ginnett, 2016; Su, 2003). Broad vegetative composition of the study area has changed little in 30 years of observation.

### 2.2 Crane use

We measured crane use of agricultural and non-agricultural areas along three routes within the study area in all six study years and followed the protocol of previous studies (Barzen et al., 2018; McKinney et al., 2016; Wheeler et al., 2019). Each route surrounded a large wetland in the Neenah and Widow Green Creek basins (Barzen et al., 2016) and was surveyed six times a day. We monitored all three routes within a 3.5-day period, sampling the entire study area two times per week, with randomized starting point and order for each survey conducted. For each of the six crane-use surveys within a route, we mapped crane numbers and habitat. Crane use was defined as the total number of cranes seen in each habitat, summed for each of the six surveys in 1 day, and for each of the 3 routes in 1 sample period (henceforth, interval). Within a day, surveys were stratified from 30 min after sunrise to 30 min before sunset. These measures were not independent because cranes moved between fields and could be counted multiple times within a day. However, this system measured a greater extent of habitat use than could be determined from one measure alone (Barzen et al., 2018; Hayes & Barzen, 2016). As such, our metric indexed crane use rather than providing an actual count of cranes. Crane

**FIGURE 1** A 6,251 ha study area in Wisconsin with primary land uses identified. Three survey area routes were run in all study years (1999–2001, 2007–2009). Any field that was planted with corn in at least one of the six study years is mapped along with wetland and forest areas which did not change during the study. Corn fields were further designated as treated (at least one of 6 years was treated and sampled), untreated (at least one of 6 years was untreated and sampled), treated/nontreated (at least one of 6 years as treated and at least one of 6 years as untreated fields with sampling in each year), and other corn field (no sampling was conducted).
use of corn fields was used in two ways: (a) to compare crane use to the amount of damage among food items within a field and (b) to examine habitat selection between fields within a home range. For each interval we divided crane use for an individual field by that field’s area and called the subsequent variable crane use index (CUI). CUI was then compared to damage of seed densities within a field. Where we measured selection, a measure of crane use versus habitat availability, crane use was incorporated into a selection index (see Section 2.4).

2.3 Habitat availability

Land cover information was described hierarchically and monitored daily. Classification levels were (a) habitat type (e.g., corn), (b) stage of agricultural fields (e.g., germinated), and (c) length of development (e.g., germinated for 5 days). Some land cover types, therefore, had complicated classifications (e.g., corn/germinated + 2 days) whereas other habitat types had simple classifications that persisted for the entire year (e.g., wetland). Treated (fields planted with deterrent-treated seed) and nontreated cornfields were considered different habitat types.

We analyzed data from cornfields during the first 17 days of germination to understand crane use when planted seeds were vulnerable to crane damage and compared the vulnerable period to an equal period (Days 18–35) after germination (labeled as vulnerable and nonvulnerable periods). Though environmental variables (e.g., soil temperature) influenced the time necessary for corn endosperm to be metabolized, kernels essentially retained no endosperm at our latitude after 17 days post germination and were thus not vulnerable to crane consumption (Lacy, Barzen, & Gossens, 2018).

2.4 Crane habitat selection

We measured crane habitat selection of germinating corn fields (CG) during the vulnerable period with Jacobs’ Index (Jacobs, 1974):

\[ SI = \frac{r - p}{(r + p) - 2rp} \]

where \( r \) = proportion of availability (area of vulnerable corn/total area of the study area). \( SI \) was calculated for each interval and ranged from −1.0 to 1.0 where \( SI > 0.0 \) indicated selection for and \( SI < 0.0 \) indicated selection against (Jacobs, 1974). Following Lele, Merrill, Keim, and Boyce (2013), \( SI \) was our resource selection probability function, using a probability of occupancy during the period of corn vulnerability. This metric focused upon habitat selection at a scale of between fields within a home range but focused narrowly upon corn during the vulnerable period only.

2.5 Corn treatment and crane damage estimates

During the first phase of our study (1999–2001), growers used products containing both Lindane (gamma-hexachlorocyclohexane) and Diazinon (\( O,O-O-diethyl \ O-[4-methyl-6-[propan-2-yl]pyrimidin-2-yl] \) phosphorothioate), hereafter labeled “insecticide” to prevent insect damage to planted corn kernels. In doing so, they noticed that fields treated as such received no crane damage. We worked with growers to leave some fields untreated to observe if the corn seed insecticide provided real crane deterrence and, if deterrence was found, how it worked. Both Lindane and Diazinon occurred in the seed treatments used by growers and both were known as avian repellents (Werner & Avery, 2017). Either insecticide, however, was inappropriate for promotion because they were an organochlorine (Lindane) or an organophosphate (Diazinon) that persisted in the environment (Cheah, Kirkwood, & Lum, 1998), were resistant to photolysis and hydrolysis (except at high pH) and degraded slowly by microbial actions (Walker, Vallero, & Lewis, 1999). These insecticides did, however, test a process for deterrence, efficacy and, if proven effective, suggested that new deterrents should be sought. In our study, growers used three rates of powered insecticide on planted corn: 28.5, 12.5, and 10.6 g active ingredient/kg seed. Of all insecticide-treated fields, 88% were treated at the highest rate. Corn was mixed with powdered insecticide while seed corn was in the hopper box of the planter.

During the second phase of our study (2007–2009) we obtained experimental use permits and section 18 exemptions from the U.S. Environmental Protection Agency and the Wisconsin Department of Agriculture, Trade and Consumer Protection to treat corn with a new deterrent, AQ, which showed promise as a replacement to insecticides (Barzen et al., 2018; Blackwell, Helon, & Dolbeer, 2001; Lacy et al., 2018). Here we report on corn seed treated with liquid AQ to a concentration of 0.5% AQ by seed weight which is within the known effective concentration for crane deterrence (2,500 ppm AQ/kg of seed; DeLiberto & Werner, 2016). Corn seed was treated with AQ before being placed in planters. The only difference in experimental design between 1999–2001 and
2007–2009 was that we worked with growers to leave some fields untreated and to treat some fields with AQ.

Prior to crane arrival in spring, we worked with growers to establish what fields would be left untreated by either deterrent. Locations of untreated fields were stratified throughout the study area (Figure 1) and, from previous observations (Su, 2003), stratified through areas that typically received high crane use. Treatment tests focused upon food items within a field (planted corn vs. other foods) and not characteristics that would exist between fields such as distance from corn field to night roost. Our goal was to provide treated and untreated fields that would be sampled by cranes. Final determination of which treated fields would be analyzed was determined by crane use. Only fields where cranes were observed foraging were investigated further (Figure 1) and, throughout the study area, not all corn fields were used by cranes in any 1 year (Table 1).

Estimation of crane damage to cornfields where cranes were observed involved counting corn seedling density within 1 week after the vulnerable period concluded. We sampled fields during mid-afternoon to minimize our influence on crane use of fields (Su, 2003). Growers often planted fields at variable seed densities within the same field (Bullock et al., 1998) so we collected two samples of seedling density from each field: an area of field that had been used by cranes and an area of the field where crane use had not been observed (Figure S1). Crane use locations were identified by surveys and by physical sign of crane presence (tracks, probe holes, feces, or feathers). Areas marked as not used by cranes had no mapped or physical sign. Crane use and nonuse sampling plots were also selected from areas of the field with similar soils to reduce variation from other environmental factors. Seedling density of young plants was our focus because damage to a germinating field can be large enough to force the replanting of that field, a significant cost to any grower. Predicting yield at harvest, based on damage at germination, was not done.

Seedling density was determined in plots of 40 m × 15 cornrows. One plot per used and unused portion of a field characterized seedling density for each field and plots were located in the center of the crane used or unused area as identified on aerial photos prior to sampling the field. To make seedling densities comparable (Table 2), we next subtracted average seedling densities of used and unused areas that were located within the same field (unused–used = difference).

Concurrent with the first phase of our study, experiments were conducted to assess efficacy of other chemical treatments to deter corn damage by cranes (Lacy et al., 2018). The experimental area totaled 10.2 ha in 2000 and 20.4 ha in 2001 and was planted during and after the normal planting time of other fields in the area. These data were not included in the seedling density analyses but were included in analyses for measuring selection of germinating corn during the vulnerable period.

### Statistical analysis

To test if planted corn was being consumed by cranes within each field we used three-way ANOVA to examine the relationship between main effects of treatment

| Metric                                    | Insecticide treatment period | AQ treatment period |
|-------------------------------------------|-----------------------------|---------------------|
|                                           | 1999 | 2000 | 2001 | Average | 2007 | 2008 | 2009     |
| Range in area for all corn fields (ha)    | 0.4–38.4 | 0.6–32.6 | 0.8–72.9 | 7.1    | 12.4 | 1.6–66.8 | 0.5–72.0 | 0.7–57.7 |
| Range in area for corn fields used by cranes (ha) | 1.2–38.4 | 1.6–32.6 | 0.8–72.9 | 7.6    | 14.3 | 2.0–66.8 | 1.8–72.0 | 0.7–57.7 |
| Total area of all corn fields (ha)        | 1,210.5 | 1,014.2 | 1,074.9 | 1,099.9 | 1,020.4 | 1,020.5 | 1,129.9 | 910.9    |
| Total area of corn fields used by cranes (ha) | 775.5 | 756.7 | 782.1 | 771.4 | 879.2 | 895.7 | 926.3 | 815.6    |
| % area of corn fields used by cranes       | 64.1 | 74.6 | 72.8 | 70.5    | 86.4 | 87.8 | 82.0 | 89.5    |
| # of corn fields                          | 203 | 168 | 94 | 155    | 82 | 77 | 86 | 84    |
| # of corn fields used by cranes           | 98 | 99 | 54 | 84    | 62 | 60 | 61 | 66    |
| % of corn fields used by cranes           | 48 | 59 | 57 | 55    | 76 | 78 | 71 | 79    |
Table 2. A comparison of corn seedling densities and crane numbers in agricultural fields 1999–2001 and 2007–2009, located near Briggsville, Wisconsin, where seeds were treated with an insecticide deterrent (Lindane and Diazinon) or 9,10-anthraquinone (AQ) prior to planting.

| Year and Treatment | # fields | Average seedling density (s/m) — Unused | Average seedling density (s/m) — used | Average seedling density (s/m) — difference | Standard error — difference | Average # cranes | Average area (ha) | Crane use index (# cranes/area) |
|--------------------|----------|----------------------------------------|--------------------------------------|---------------------------------------------|---------------------------|----------------|----------------|-------------------------------|
| 1999 Insecticide   | 8        | 4.4                                    | 4.3                                  | 0.1                                         | 0.11                      | 14.4           | 26.3           | 0.9                           |
| 1999 NT            | 8        | 5.3                                    | 3.5                                  | 1.8                                         | 0.21                      | 25.0           | 11.8           | 2.6                           |
| 2000 Insecticide   | 9        | 4.8                                    | 4.5                                  | 0.3                                         | 0.13                      | 27.1           | 15.4           | 1.3                           |
| 2000 NT            | 7        | 4.6                                    | 4.3                                  | 0.3                                         | 0.21                      | 44.1           | 13.0           | 2.4                           |
| 2001 Insecticide   | 7        | 4.9                                    | 4.7                                  | 0.3                                         | 0.15                      | 30.6           | 26.5           | 1.1                           |
| 2001 NT            | 7        | 4.5                                    | 3.1                                  | 1.4                                         | 0.40                      | 149.7          | 18.7           | 4.3                           |
| 2007 AQ            | 5        | 5.1                                    | 5.1                                  | 0.0                                         | 0.38                      | 4.4            | 6.3            | 0.7                           |
| 2007 NT            | 6        | 5.0                                    | 3.9                                  | 1.1                                         | 0.40                      | 51.5           | 25.3           | 1.3                           |
| 2008 AQ            | 7        | 5.5                                    | 5.5                                  | 0.0                                         | 0.23                      | 30.4           | 11.4           | 1.9                           |
| 2008 NT            | 7        | 4.3                                    | 4.0                                  | 0.3                                         | 0.20                      | 23.6           | 16.7           | 1.7                           |
| 2009 AQ            | 7        | 4.9                                    | 4.9                                  | 0.0                                         | 0.19                      | 20.4           | 8.6            | 2.4                           |
| 2009 NT            | 4        | 5.0                                    | 4.0                                  | 1.0                                         | 0.46                      | 48.0           | 5.2            | 6.4                           |

Note: Seedling densities of field areas used by cranes were subtracted from seedling densities in areas not used by cranes to create a difference in seedling density for each field. Positive differences in seedling density suggest damage by cranes.

aq, Plant seed not treated with chemical deterrent.
bs/m, seedlings per meter.
cAverage number of cranes, average area, and crane use index had seven field samples.

Finally, linear regression compared the number of cranes using vulnerable corn with the area of vulnerable corn available.

3 | RESULTS

The area of planted corn, number of fields, amount of crane use and area of corn where cranes were observed all varied among the 6 years of this experiment (Table 1). Averaged between the two treatment periods, more area (79.5 ha) and more corn fields (73) were available 1999–2001 than 2007–2009. Cranes used, however, a higher percentage of corn field area (15.9%) and number (11%) more 2007–2009 than 1999–2001 (Table 1). Even though a high percentage of corn fields was used during both treatment periods, 21–52 corn fields (10.5–35.9% of all corn area) were unused by cranes during the study (Figure 1). More corn was available than there were cranes available to utilize this habitat.

3.1 | Insecticide versus AQ treatment

We first examined treated fields generally and asked if seedling differences for fields treated with insecticides...
and fields treated with AQ differed (Table 2). A total of 43 treated fields were studied (24 fields planted with insecticide-treated seeds and 19 fields planted with AQ-treated seeds; Table S1). In comparison, 31 fields were planted with nontreated seeds. Using three-way ANOVA to look only at fields with treated seed, the difference in seedling densities for insecticide-treated seed did not differ from the difference of seedling density treated with AQ (Table 2; \( F = 1.96, p = .17 \)). In addition, neither CUI (\( F = 2.49, p = .12 \)), nor year (\( F = 0.25, p = .91 \)), were significant as main effects, nor was any interaction significant (maximum \( F = 0.57 \), minimum \( p = .46 \)). We combined insecticide-treated data with AQ-treated data as a single treatment for all further tests related to seedling damage.

### 3.2 Treated versus untreated seed

All three main effects (Treatment, Log10(CUI) and Year) for a three-way ANOVA using both treated and untreated seed were significant (\( F = 33.1, p < .001; F = 19.2, p < .001; F = 3.9, p = .004 \); respectively). Seedling density difference averaged 0.101 seedlings/m for treated fields and this amount did not differ from zero (\( t = 1.70, p = .10 \)) while for nontreated fields, seedling density difference was 0.980 seedlings/m (\( t = 8.60, p < .001 \)), representing a loss of 19.6% of the seedling density for nontreated fields in areas where cranes foraged. In 2000 and 2008 (Table 2) differences in seedling density for nontreated fields were not >0 (2000: \( t = 1.73, p = 0.09; 2008: t = 1.82, p = .07 \)), suggesting that little or no damage may have occurred in those years.

Of all possible interactions, only Log10(CUI) * Year (\( F = 2.4, p = .04 \)) and Treatment * Year (\( F = 3.6, p = .006 \)) were significant and likely due to the same influence. Log10(CUI) was directly related to the difference in seedling density for nontreated seed in 2 of 6 years (2001: \( t = 3.54, p < .001; 2009: t = 2.61, p = .01 \)), meaning that as the density of cranes in a field increased, so did damage but only for 1 year where insecticides were the deterrent and 1 year where AQ was the deterrent. Log10(CUI) was never related to seedling difference in treated fields (range: \( t = -0.15 \) to 1.51, \( p = .14 \) to 0.88).

### 3.3 Habitat selection

To indirectly examine selection among fields within a home range we examined patterns of sandhill crane use in corn fields within the entire study area. First, we examined the number of cranes observed using corn fields compared to the period of vulnerability for planted corn. Within a field, crane numbers using vulnerable and nonvulnerable fields did not differ (\( F = 1.8, p = .18 \), Figure 2). Treatment, however, was related to the number of cranes using corn fields (\( F = 10.8, p < .001 \)). AQ-treated fields had less crane use than did insecticide-treated fields (\( p = .007 \)) or nontreated fields during either phase of research (1999–2001: \( p < .001; 2007–2009: p < .001 \)). Crane use of insecticide-treated fields did not differ from crane use of nontreated fields (\( p = .64 \)). The interaction between vulnerability and treatment was insignificant (\( F = 1.8, p = .15 \)). In all years crane use of corn fields persisted after more than 25 days post germination.
but dwindled, presumably as corn height and foliage density increased (Figure 2). Timing of diminished use varied between the two phases of study. Crane use of corn fields remained strong (>50 cranes) well after CG + 40 1999–2001 while crane use was <50 cranes post CG + 40 2007–2009 (Figure 2). We concluded that, if selection among fields within home ranges were occurring in relation to corn vulnerability, we should have seen differences in crane numbers using vulnerable and nonvulnerable corn fields. We did not.

To directly examine crane selection of corn fields versus all other field types in aggregation during the period of corn vulnerability (i.e., between field habitat selection) we assessed crane use of vulnerable corn fields relative to all cranes seen on surveys and compared this proportion to the availability of vulnerable corn fields among all habitats of the study area present for each of the 6 years under study (Figure 3). The resulting Jacobs Index did not vary among years ($F = 0.78, p = 0.57$) nor did the average Jacobs Index for insecticide-treated years differ from the Jacobs Index for AQ-treated years ($F = 0.06, p = 0.81$). When germinating corn fields having no crane use were removed from analysis, SI for insecticide-treated years was greater than SI in AQ-treated years ($p < 0.001$). Overall, $SI > 0$ ($t = 3.73, p < 0.001$). Within a year, Jacobs Indices were variable and some years (e.g., 1999) tended to have lower SI even though this difference was not significant (Figure 3). A noticeable increase in Jacobs Index ($SI > 0.80$) occurred late in seedling phenology 1999–2001 when cranes continued using vulnerable corn extensively while the area of vulnerable corn decreased dramatically (Figure 3). This pattern occurred 2007–2009 but was not as distinct ($SI < 0.87$). As an alternative measure of between-field selection, cranes used vulnerable corn fields in direct relation to the area of vulnerable corn field availability in all years, even when availability changed daily (Table 2). Selection for vulnerable corn fields by foraging cranes was, therefore, strong.

4 | DISCUSSION

Treating planted corn kernels with a chemical deterrent proved effective and our two trials, one with insecticides and one with AQ, were equally effective in deterring crane herbivory. AQ, however, is more environmentally acceptable (Barzen & Ballinger, 2018) than either insecticide, both of which have had their use restricted in recent years (U.S. Environmental Protection Agency, 2006, 2007) and are not intended for use as a deterrent. The insecticides did, however, identify a mechanism through which deterrence of crane damage could be achieved.

In areas where cranes foraged, the 19.6% loss in seedling density with untreated seed is important to growers because it can force them to replant entire fields at substantial cost (Barzen et al., 2018). Loss of seedlings in treated fields did not differ from zero but was close to significant. The biological magnitude of any difference in treated seedling density, however, was within 2% of the unaffected seedling density, well within the annual variation in corn crops, and would not force replanting of a field (Barzen et al., 2018). Loss of treated seed could have been due to crane sampling of seeds before deterrence was achieved or simply through sampling error. Among years, damage was not uniform among untreated fields. In 2000 and 2008, 1 year with insecticide treatment and 1 year with AQ treatment, little damage to untreated fields occurred while no treated field was ever damaged. Patterns of crane damage may often be driven by broader habitat, social, and behavioral variables and therefore be difficult to predict for any given area or year (Fuller, 2012b). Likewise, as the CUI for untreated fields increased so did the amount of damage in 2001 and 2009. Conversely, the relationship between crane use and amount of damage in treated fields was never significant. Crane foraging is implicated as the primary cause of damage but CUI did not fully capture the dynamics of crane foraging (Barzen et al., 2018). Though following marked individuals would provide more detailed habitat selection metrics (Rhodes et al., 2005), only 36% of all cranes in our study area, estimated at 425 individuals (Barzen et al., 2018), used vulnerable corn fields, making it difficult to study crop damage with marked birds alone. In addition, nonterritorial cranes of summer populations caused the most damage to planted corn (Barzen et al., 2018) and individuals older than their second year had home ranges of 30–50 km² (Hayes & Barzen, 2016).

It was necessary to test the exposure of corn to crane damage throughout the 62.5 km² study area (Figure 1) to be sure that cranes did not move outside the study area and resume damage elsewhere.

Even though selection for vulnerable corn fields was high (Figure 3), and crane use appeared driven by availability of vulnerable fields (Table 3), corn was likely more available than cranes could utilize during some intervals within the vulnerable period. The balance between field availability and crane use was dynamic (Figure 3). When peak vulnerable corn availability exceeded 1,000 ha, the phenology of corn maturation appeared to exceed the crane population's ability to respond within our study area and $SI$ was low. $SI$ was higher when peak vulnerable corn availability was ≤800 ha. Higher $SI$ values found during insecticide-treated years was likely due to the lower area of vulnerable corn that was available during insecticide-treated years (Figure 3). Further, the high values of $SI$ late in the period of corn vulnerability suggest that crane numbers can concentrate in relatively few
vulnerable fields such as in 2000 when over 300 cranes were found in 12.6 ha of vulnerable corn. Crane population numbers within the study area were constant for all 6 years (Wheeler et al., 2019) and were at carrying capacity (Barzen et al., 2016). The full potential of crop damage pressure in the population was likely realized.

Crop damage trials in 2000 and 2001 allowed for untreated fields to become vulnerable in July when few other vulnerable corn fields were available and damage to untreated fields was extensive (Lacy et al., 2018). Later trials were not conducted during the AQ phase of our experiment (2007–2009). Even without experimental trials creating vulnerable fields that were out of phase with most corn fields in the area, growers that were forced to replant corn fields would have vulnerable fields that matched the out-of-synch phenology that we experimentally created in 2000 and 2001. Replanted fields would be at higher risk for damage.

Ecologically, consumption of planted corn, when not treated with a deterrent, was high whereas consumption of treated corn was low. Further, as CUI increased, so did damage to untreated corn but not treated corn. Finally, cranes continued to use untreated and treated fields long past their period of vulnerability but continued to forage so, even in untreated fields, cranes must alter their diet each spring (Barzen et al., 2018). Alternative foods included waste corn from previous years and earthworms. Barzen et al. (2018) documented no other food items being consumed in treated, vulnerable corn fields. Cranes acted as generalist feeders when selecting food items within a field (Rosenzweig, 1981). In contrast, the high selection of vulnerable corn fields, regardless of treatment, suggests that cranes are specialists at the between field scale of selection that occur within home ranges (Rosenzweig, 1981). Whooping Cranes (Grus americana) exhibit a mixture of generalist and specialist habitat selection behavior as well but they appear to be...
specialists among home ranges within regions and specialists among regions within biomes (Austin, Hayes, & Barzen, 2019). Reiley and Benson (2019) demonstrated that similar differences between fine and landscape scale selection was related to fitness in Bell’s Vireo (Vireo bellii) and Willow Flycatchers (Empidonax traillii). Presumably, where scale of selection has strong influence on fitness, individuals will be more sensitive to changes in habitat conditions.

A broad array of chemical repellents has been applied to protect plants from bird and mammal herbivory (Werner & Avery, 2017; Werner, DeLiberto, Baldwin, & Witmer, 2016). In addition to this study, AQ has been applied as an effective chemical deterrent to diverse bird groups as protection against damage to corn, sunflowers, wheat (Triticum spp.), rice, and specialty crops (Werner et al., 2011; Werner et al., 2015; Werner, Carlson, Tupper, Santer, & Linz, 2009). Hierarchical habitat selection concepts suggest that damage protection for this array of species and crops can be reduced to two basic strategies: (a) protecting one food item (the crop) while continuing to allow use of the remaining resources within the crop field or (b) protecting the crop field by preventing access to the field by target species and moving them elsewhere.

Removing food items becomes challenging when that food item is the only component of a species diet (i.e., a specialist). Feeding experiments demonstrate that cranes and other bird species will eat treated seed but at much lower rates (Blackwell et al., 2001; Dolbeer, Seamans, Blackwell, & Belant, 1998). AQ is considered a post-ingestive deterrent in birds (Avery, Humphrey, Primus, Blackwell, & Belant, 1998) meaning that individuals learn to avoid contact with AQ because it makes them sick if consumed. Individuals can detect and avoid post-ingestive substances in future encounters (Avery, Humphrey, & Decker, 1997). Called conditioned taste aversion (Karasov & del Rio, 2007), the post-ingestive deterrent is thought to be more effective than simple oral irritants (Barzen & Ballinger, 2018; Provenza, 1996; Werner et al., 2012; Werner & Provenza, 2011). Wild, omnivorous Sandhill Cranes are generalist feeders among food items within a field (Barzen et al., 2018), and for most other bird species tested so far, planted seeds are an ephemeral food source and a deterrent would modify only one component of the diet. By remaining in the field, individual cranes switch from causing damage by consuming planted corn to being neutral or beneficial to the grower because they eat other foods that might be harmful to the crop (e.g., weed seeds or deleterious insect larvae). Removing the entire field from availability, a scale of selection where cranes are specialists, requires a translocation of individuals from one field to the next, effectively shifting the problem elsewhere. Removing resources for specialists could cause a reduction in fitness and subsequent population decline. Alternatively, where fields are highly selected (corn in our case), removing the entire field from availability would encourage habituation in damage-causing species to maintain fitness. In our case, it was more effective to provide alternative foods than alternative fields.

AQ is effective in part because it mirrors plant/bird interactions (Barzen & Ballinger, 2018; Izhaki, 2002; Werner & Avery, 2017). Where management scenarios minimize the amount of resource withdrawn, the incentive to habituate is reduced. Further, refinement in the scale at which chemical deterrents are deployed reduces costs (Werner et al., 2012) and improves the chance that deterrents can be deployed through the marketplace (Barzen & Ballinger, 2018). For the last decade, AQ has been deployed on over 50,000 ha of corn per year to protect against crane damage in Michigan, Minnesota and Wisconsin (Barzen & Ballinger, 2018) and near 80,000 ha in 2019 (K. Ballinger, unpublished data). Acreage of applied AQ in the U.S. currently exceeds 480,000 ha annually for bird deterrence (K. Ballinger, personal communication). Across this broad area, AQ has worked from removing a food item (Barzen et al., 2018; Cummings et al., 2002) to removing whole fields (Werner et al., 2011; Werner et al., 2014).

Use of AQ in the European Union is currently restricted (as cited in Fouillaud, Caro, Venkatchalam, Grondin, & Dufossé, 2018). Early tests found AQ to be mutagenic and carcinogenic (National Toxicology Program, 1999). Further examination of materials tested by the National Toxicology Program (NTP), however, concluded that the tested AQ was derived from anthracene (i.e., coal tar) and contained impurities sufficient to cause the carcinogenic response seen in mice (Butterworth, Mathre, & Ballinger, 2001; Butterworth, Mathre, Ballinger, & Adalsteinsson, 2004). Evidence for mutagenicity has been inconclusive in more recent studies (International Agency for Research on Cancer, 2013). Current production of AQ is through the Friedel-Crafts formulation process that produces AQ containing only small amounts of one impurity, 2 methyl AQ (International Agency for the Research of Cancer 2013, Arkion Life Sciences LLC, unpublished data). AQ is also an effective rodent repellent and starvation effects may have confounded the NTP results on mice. Following formal review EPA has continued label registration on corn and rice (U.S. Environmental Protection Agency, 2016, 2017). Given that human exposure to naturally-produced and industrially-produced AQ is frequent (Fouillaud et al., 2018) further studies that directly assess risk levels of AQ in low concentrations are important and are underway (K. Ballinger, personal communication).

Long-term success of varied deterrence strategies in myriad species and numerous crops may depend upon
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CONFLICT OF INTEREST

Several organizations funded portions of this project have business interests that might be influenced by the outcome of this research. None of these organizations (Adventis Seed Corporation, Arkion Life Sciences LLC, Tryon Group, Springborn Smithers Laboratories, Wisconsin Potato and Vegetable Growers Association and Wolf River Valley Seeds), however, contributed more than 5% of the total cost of the project and no funding organization influenced the project outcome in any way.

AUTHOR CONTRIBUTIONS

Jeb Barzen was involved with this study from inception to completion with major roles in project design and implementation as well as manuscript preparation, revision, and guidance. Andrew Gossens provided primary data collection and supervision of field research staff as well as assistance with data analysis and writing of the manuscript. Anne Lacy provided data collection, data management and manuscript creation. Brian Yandell supervised all data analysis and provided most data analysis as well as assistance with manuscript writing and revision.

ETHICS STATEMENT

All applicable ethical guidelines for the use of birds in research have been followed, including those presented in the Ornithological Council’s “Guidelines to the Use of Wild Birds in Research” (Fair, Paul, & Jones, 2010). No portions of this paper have been published elsewhere.

DATA AVAILABILITY STATEMENT

Data for this paper are available at https://data.mendeley.com/datasets/pfy37yc9sx/draft?a=898d7891-e1d2-4206-bbad-386d5e98a84d.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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