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REPRODUCTIVE SUCCESS AND SURVIVAL OF THE  
COMMON GRACKLE IN CENTRAL ILLINOIS

BY

NOAH PRESCOTT HORSLEY

THESIS

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Adviser:

Associate Professor Michael P. Ward

## ABSTRACT

The Common Grackle (*Quiscalus quiscula*) has historically been one of the most abundant bird species in North America. However, based on North American Breeding Bird Survey data, the global population has exhibited a steady decline of -1.75% per year over the past 50 years and has suffered a cumulative loss of 58%. Understanding why the Common Grackle - a habitat and dietary generalist - is declining is vitally important for assessing the risk to other farmland birds and the health of the environment. I collected demographic data from Common Grackle colonies at two rural study sites in Champaign County, Illinois in 2018 and 2019. I monitored 188 nests and tracked the survival of 53 fledglings for the 20-day post-fledging period. I found no evidence that demographic rates during the breeding season were driving the observed decline in Common Grackle populations in Illinois. Average clutch size was 4.26 (SE = 0.07), slightly below the average of 4.35 (N = 14, p = 0.09) for published studies. My estimate of nest success was 62.2% (SE = 3.7%), far above the average of 26.7% (N = 6, p = 0.01) for other studies. Post-fledging survival for Common Grackles had not been estimated before, but the estimate of 61.7% (SE = 7.5%) was comparable to post-fledging survival in other songbirds (range 23-87%). Collectively, these results imply that population decline may be due to low juvenile or adult survival during the non-breeding season. Using population models, I was able to estimate adult survival for a stable population, as well as investigate the relative influence of fecundity and adult survival on population growth. I found that annual adult survival must be at least 65% for a stable population, and that changes to adult survival impact population growth ~2 times more than changes to fecundity. Future research on the decline of this common species should be directed towards quantifying adult survival in the non-breeding season, particularly on the wintering grounds, and investigating potential sources of mortality.

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## CHAPTER 1: THE STATUS AND VALUE OF COMMON BIRDS

Anthropogenic change is accelerating on a global scale and has proven to be a major challenge for avian conservation in North America. Many bird species have suffered dramatic population declines over the past half-century (Sauer et al. 2017, Rosenberg et al. 2019); grassland and farmland guilds have been hit particularly hard (Peterjohn and Sauer 1999). Even invasive agricultural pests and native species that have benefited from anthropogenic change have experienced substantial population decline throughout their range (Sauer et al. 2017). Habitat loss, habitat fragmentation, climate change, free-roaming cats, agricultural intensification, and building collisions are at the forefront of this issue (Andren 1994, Bender et al. 1998, Donald et al. 2001, Crick 2004, Loss et al. 2013, 2014). Unfortunately, because public funding is limited, wildlife managers are forced to make hard decisions about where to focus their efforts. Traditionally, conservation values have prioritized the preservation of biodiversity (Caughley and Gunn 1995, Baillie et al. 2004). The extinction of a species is a permanent loss and threatens ecosystem function and resilience (Elmqvist et al. 2003, Solan et al. 2004). However, as a consequence of prioritizing biodiversity, some of the most abundant species have been neglected. This is evidenced by the plight of common birds in North America, where two-thirds of all individual birds lost since 1970 have belonged to just 15 common species (North American Bird Conservation Initiative 2019). In some cases, the loss of common species, which compromise the majority of biomass in an ecosystem, has been shown to negatively impact ecosystem structure, productivity, and function, far more than the loss of rare species (Jackson et al. 2001, Ellison et al. 2005, Gaston 2008). In the 21<sup>st</sup> century, it is imperative that avian ecology and conservation confront the reality of global environmental change and balance the preservation of biodiversity and biomass in accordance to their merit.

Over the past half-century, the direct monitoring of bird populations has become increasingly rigorous and widespread. Relative to other animal taxa, birds are diverse and easy to monitor. Simple, standardized surveys can be conducted along roads or trails by professionals or volunteers and logged into vast online databases. Over many years and replications, these data provide valuable information about the status and trajectory of bird populations. In North America, the population dynamics of breeding birds are primarily tracked by the North American Breeding Bird Survey (BBS; Pardieck et al. 2019), an extensive, long-term monitoring network founded in 1965. The BBS surveys over 4,100 routes annually and has produced population trend estimates for over 420 species. Other large-scale monitoring efforts in North America include point counts conducted by the Integrated Monitoring in Bird Conservation Regions (IMBCR; White et al. 2012, Pavlacky Jr et al. 2017) program, bird banding stations run by the Monitoring Avian Productivity and Survivorship (MAPS; DeSante 1992) program, and seasonal migration data collected by Next Generation Weather Radar (NEXRAD; Dokter et al. 2018). The benefits of increased monitoring are two-fold: 1) the extent and quality of available information greatly enhances our ability to quantify avian population declines and assess risk, and 2) by tracking population trends across ecosystems and guilds, ecologists can focus conservation resources and make informed management decisions (Donald et al. 2007).

Using count data collected by the BBS, an analysis by Rosenberg and colleagues (2019) revealed a net decline of 29% (roughly 3 billion birds) among North America's avifauna between 1970 and 2015. Over 90% of losses were concentrated among just 12 of 67 surveyed families. Grassland specialists fared particularly poorly, suffering an estimated net loss of 717.5 million birds (53.3%) over the survey period. Such severe losses are consistent with the conclusions of over four decades of research on the topic (Knopf 1994, Peterjohn and Sauer 1999, Vickery et al.

1999). Historically, this trend was driven by the loss of native grazers, the conversion of native prairie to agriculture, and the draining of wetlands (Roe 1951, Mlot 1990, Knopf 1994, Gibbs 2000). In Midwestern states like Illinois, for example, 0.01% of native grasslands and less than 10% of native wetlands remain (Iverson 1988). In recent years, land use has begun to stabilize but grassland birds have continued to decline (Grigg 1993). Europe has documented equally steep declines among its farmland birds (Fuller et al. 1995, Krebs et al. 1999, Gregory et al. 2004).

There is a strong correlation between the population trends of birds that inhabit agricultural landscapes and agricultural intensification (Chamberlain et al. 2000, Donald et al. 2001, Stanton et al. 2018). Agricultural intensification is a multi-faceted driver characterized by reductions in farmland diversity and increases in chemical inputs (e.g. fertilizers and pesticides), irrigation, and mechanization (Fuller 2000). While crop yields have increased in accordance to these changes, it is also clear that long-term agricultural intensification has negative consequences on both a local and global scale (Matson et al. 1997). Agricultural intensification is hypothesized to be reducing the amount of high-quality habitat and food resources for birds, altering factors such as predation risk, exposure to weather, and nutritional condition (Chamberlain et al. 2000, Wilson et al. 2005). Unfortunately, the specific mechanism of agricultural intensification driving declines appears to vary by species and region (Aebischer 2000). Studies directly testing the impact of modern farming practices on rapidly declining grassland and farmland birds are a pressing research need, essential to the development of effective management practices.

Further analysis of BBS trend data also revealed a surprising pattern of decline among North America's most widespread and abundant birds (Rosenberg et al. 2019). Many of these

species have varied life histories, suggesting that the source(s) of decline are likely pervasive throughout North America and not habitat specific. Human-driven avian decline can come from anthropogenic sources of direct and indirect mortality. Factors such as habitat loss, habitat fragmentation, and climate cause avian mortality indirectly by influencing intermediary mechanisms, such as a predation, starvation, and exposure. The degree of their impact on a population varies by species' life history. Generalist species are thought to be less vulnerable than ecologically specialized species (Andren 1994, Owens and Bennett 2000), though the sum effects of indirect drivers can be difficult to quantify. Other factors, such as free-ranging domestic cats, vehicles, collisions with buildings and other man-made structures, pest management, and poisoning from pesticides and chemical pollutants, cause avian mortality directly (Loss et al. 2015). Quantifying the impact of these sources of mortality is less complicated than for indirect sources of mortality, and many have been estimated. For example, every year cats kill between 1.4 and 4.3 billion birds (Blancher 2013, Loss et al. 2013) and buildings, power lines, wind turbines, and communication towers kill between 0.5 and 1.5 billion birds in the United States and Canada (Loss et al. 2015).

Among the 15 bird species driving avian population decline in North America are two non-native species, the European Starling (*Sturnus vulgaris*) and the House Sparrow (*Passer domesticus*). Invasive species are often characterized by high rates of fecundity and tremendous tolerance of environmental change (Sakai et al. 2001). While the eradication of invasive species is a prominent goal in conservation (Clavero and García-Berthou 2005), the decline of European Starlings and House Sparrows, as well as other common native species, is troubling. Abundant bird species contribute heavily to ecosystem function (e.g. seed dispersal, pollination, nutrient cycling) and ecosystem services (e.g. pest insect management, hunting and bird watching,

scavenging; Whelan et al. 2015). Birds are also reliable environmental indicators; such substantial declines among common species may be a sign of decaying environmental health on a continental scale (Morrison 1986, Furness and Greenwood 2013). Even so, the primary focus of modern conservation efforts has been preserving biodiversity. In stark contrast to the decline of common birds, only two breeding bird species (out of over 700) in the contiguous U.S. and Canada have gone extinct since the signing of the Endangered Species Act of 1973: the Dusky Seaside Sparrow (*Ammodramus maritimus nigrescens*) and the Bachman's Warbler (*Vermivora bachmanii*; Sykes Jr 1980, Hamel 2018). Both were likely functionally extinct when the act was signed. The relative stability of biodiversity seems to have masked the presence of a mounting crisis. Considering recent trends among Europe's farmland birds, North America's bird communities may be headed towards large-scale declines (Reif 2013, Inger et al. 2015). There is a pressing need for research on common birds, specifically aimed at identifying the most damaging mechanisms of decline and developing proactive management strategies.

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## CHAPTER 2: THE DEMOGRAPHY OF A DECLINING BLACKBIRD

### Introduction

An increasing number of animal species are experiencing population declines, regional extirpation, and extinction as a consequence of mounting anthropogenic pressures. Conservation efforts frequently focus on preserving biodiversity, and therefore disproportionately target species with a high perceived risk of extinction (Caughley and Gunn 1995, Baillie et al. 2004). Often, these are species that have a small global population, fill a narrow ecological niche, and inhabit a limited geographic range. In North America, this strategy has led to the recovery of species like the Green Sea Turtle (*Chelonia mydas*), Island Fox (*Urocyon littoralis*), and Peregrine Falcon (*Falco peregrinus*; Tordoff and Redig 1997, Coonan et al. 2010, Mazaris et al. 2017). While there is clear merit in protecting rare and threatened species, ecosystem health depends far more on the collective services of common species (Gaston 2008, 2010). Given the breadth and pace of environmental change in modern times, many widespread, abundant species are at great risk (Vitousek et al. 1996, Turner et al. 2007, Quintero and Wiens 2013). This is evidenced by the plight of North American avifauna, which declined by 29% - roughly 3 billion birds - between 1965 and 2015 (Rosenberg et al. 2019). Notably, more than two-thirds of this loss came from just 15 common species (North American Bird Conservation Initiative 2019). Similarly, 33 historically abundant species have lost half or more of their global population in the last 40 years (North American Bird Conservation Initiative 2014). Only five species are included in both of these statistics: Blackpoll Warbler (*Setophaga striata*), Horned Lark (*Eremophila alpestris*), House Sparrow (*Passer domesticus*; non-native), Pine Siskin (*Spinus pinus*), and Common Grackle (*Quiscalus quiscula*).

The Common Grackle is a large, conspicuous blackbird native to eastern North America. Often associated with open farmland and rural townships, the species is a staple of Midwestern agricultural landscapes (Erskine 1971). It is a significant pest of grains, sunflowers, and peanuts, and has many ecological traits that make it well equipped to exploit anthropogenic landscapes including foraging in flocks, a generalist diet, a widespread geographic distribution, and the ability to breed in habitat expanded by human development (Ridgway 1889, Musselman 1921, McAtee 1946, Marzluff and Balda 1992). For this reason, the Common Grackle has endured - and arguably thrived - amidst considerable changes in land cover and land use throughout its native range, even demonstrating westward expansion up until the early 1990s (Marzluff et al. 1994). For most of the 20<sup>th</sup> century, it was one of the most numerous birds on the continent (Peterjohn et al. 1994). Today, however, the global population of the Common Grackle is a fraction of what it once was. The species has suffered a net decline of 58% over the last 50 years, and in the core of its breeding range (seven states with highest breeding season relative abundance) is declining by -3.42% per year (Pardieck et al. 2019). The cause of its steep decline is not clear. Contemporary research on the Common Grackle is surprisingly scarce for a prevalent and accessible blackbird (Linz et al. 2017). Fortunately, the Common Grackle shares much of its nesting and foraging habitat with better studied icterids (blackbirds) and grassland birds, many of which are experiencing similar declines. This broader body of work has identified agricultural intensification as a potential driver of avian decline in agricultural landscapes (Donald et al. 2001, Stanton et al. 2018).

Agricultural intensification - the homogenization and mechanization of farms - is a process that began in North America in the 1960s. Small, mixed-farming systems with pasture, livestock, and a variety of cash crops, have gradually transitioned to large, monoculture farms

that rely heavily on agrochemical inputs and reduce ecological heterogeneity (Benton et al. 2003, Butler et al. 2007). Indices of agricultural intensity (e.g. crop yield, livestock density, and pesticide use) are associated with declines in grassland bird communities in Europe and North America (Chamberlain et al. 2000, Donald et al. 2006, Mineau and Whiteside 2013). While the Common Grackle is not a grassland specialist, it shares the agricultural matrix with many grassland species. In agricultural landscapes, structure and biodiversity are maintained by habitat patches such as fallow fields, hedgerows, and field margins (Devictor and Jiguet 2007). When present, such habitats can benefit birds by decreasing predation risk, increasing nesting success, and increasing foraging efficiency (Dennis et al. 1998, Whittingham and Evans 2004, Doxa et al. 2010, Lindsay et al. 2013). Common intensive farming practices, such as mowing along roads and ditches, removing tree lines, and putting pasture into crop production, degrade or remove these essential habitats, potentially reducing the reproductive success and survival of farmland birds.

The suitability of agricultural landscapes can also be altered without changes in land cover. Pesticides have historically been extremely damaging to agricultural ecosystems; chemicals meant to target pest insects, weeds, and fungi are often highly toxic to non-target organisms, such as insects and birds (Wiemeyer et al. 1984, Carson 2002, Blacquiere et al. 2012). In the 21<sup>st</sup> century, the most widely used pesticide in North America is a class of insecticides called neonicotinoids (Sparks 2013, Simon-Delso et al. 2015). They are applied, predominantly as seed treatments, to 79-100% of corn and 34-44% of soybeans in the United States (Douglas and Tooker 2015). Field studies suggest migrating and breeding birds are routinely exposed to neonicotinoids each spring (Lopez-Antia et al. 2015, Humann-Guillemot et al. 2019). Several direct and indirect effects of neonicotinoid exposure have been identified in

birds, including acute toxicity, impaired migration, reduced fat storage, lethargy, and reduced invertebrate prey availability (Hallmann et al. 2014, Gibbons et al. 2015, Eng et al. 2019). Common Grackles migrate and breed earlier than other birds in the Midwest (Erskine 1971),. Because neonicotinoids are seed treatments it is likely at planting these pesticides may be more readily available to unintended organisms. The early breeding season of Common Grackles may result in greater exposure of adults, nestlings, and fledglings to neonicotinoids as compared with species that breed later in the year. The subsequently high risk of neonicotinoid exposure during this period may decrease nest success and/or increase the rate of post-fledging mortality; due to death from exposure or starvation from lack of insects. .

As an agricultural pest, direct human persecution has put significant pressure on Common Grackle populations over the past century (Heisterberg et al. 1987). Most pest control measures occur during the non-breeding season. The Common Grackle is a short-distance migrant that overwinters in the southern United States. Individuals form large, mixed-species flocks with other blackbirds and roost in dense colonies, sometimes containing up to 10 million birds (Meanley 1971, Caccamise et al. 1983). Such dense congregations can be a nuisance, a public health hazard, and a threat to agriculture (Dolbeer et al. 1978). They also make Common Grackles and other roosting blackbirds particularly vulnerable to pest management. Various strategies, such as roost destruction, harassment, and lethal chemical sprays, are used to control blackbird populations at large roosts (Heisterberg et al. 1987, Barnes and Constantin 1993). Lethal pest control was widely and effectively used in the 1970s and 1980s, killing an estimated 18 million Common Grackles in Kentucky and Tennessee from 1974-1992 (Dolbeer et al. 1995). While lethal management action is reportedly uncommon among Common Grackles today (USDA 2018), undocumented and illegal killing of nuisance birds undoubtedly occurs (Stone et

al. 1984, White et al. 1989, Carson 2002). Common Grackle overwinter survival may also be influenced by non-lethal management action (e.g. roost destruction and harassment) or changes in agricultural practices that decrease the availability of winter food resources (Peach et al. 1999, Siriwardena et al. 2007).

In this study, we took initial steps toward investigating the mechanisms responsible for the decline of Common Grackles. Testing each proposed driver of the species population decline was beyond the scope of this study. Therefore, we estimated reproductive success and post-fledging survival and used published trend estimates and a simple population model to predict juvenile and adult survival, allowing us to investigate the demographic rates that may be driving the population decline. Specifically, our objectives were to 1) estimate reproductive success (clutch size, nest success, and nest productivity), 2) estimate 20-day post-fledging survival, 3) compare our estimates from objectives 1 and 2 to estimates from the literature, 4) use a partial life-cycle model to predict rates of juvenile and adult survival in a stable population, and 5) conduct a sensitivity analysis to identify which life stage has the greatest influence on population growth. By doing so, we aimed to improve our understanding of the factors contributing to Common Grackle decline and inform future research exploring the mechanism(s) for the decline of common birds.

## **Methods**

### *Study Species*

The Common Grackle is a large, socially monogamous songbird of the family Icteridae. Its breeding range extends west to the Rocky Mountains, east to the Atlantic Ocean, north into the Interior Plains of Canada, and south to the Gulf of Mexico (Figure 1; McDonough 2013).

Grackles frequent fields, pastures, feedlots, farmsteads, drainage ditches, and other open agricultural areas (Erskine 1971). Common Grackles are not territorial (Ficken 1963, Wiens 1965) and prefer to nest semi-colonially in conifers; farmsteads, shelterbelts, and commercial tree plots are common breeding sites (Maxwell 1970). They also nest on bridges and in open woodlands near agriculture or water (Erskine 1971). Accounts of their historical nesting habitat vary; in Arkansas, Common Grackles often bred in riparian areas and willow thickets (Howell 1911), while in Illinois, “In their choice of location for a nest they are by no means particular...” (Ridgway 1889). In Illinois today, Common Grackles have been documented nesting in large numbers on Christmas tree farms and nursery plots (Peer and Bollinger 1997, Maddox and Weatherhead 2009).

Measures of Common Grackle nesting phenology and activity have been summarized by Peer and Bollinger (1997). A breeding pair typically produces a single clutch of 4-5 eggs (range: 1-9). Re-nesting in response to predation and nest parasitism is uncommon but has been observed. Incubation lasts 12-14 days (range: 11-15) and, in larger clutches, eggs hatch asynchronously (Maddox and Weatherhead 2008). Nestlings are brooded and fed primarily by the female and fledge the nest after 12-15 days (range: 10-17; Peer et al. 1997). Adults continue care during the post-fledging period for two to three weeks (Howe 1976).

The Common Grackle is omnivorous, feeding on a combination of invertebrates, grains, wild seeds, fruits, and other edible matter. Among adults, vegetable matter constitutes 70-80% and animal matter 20-30% of the annual diet (Beal 1900, Meanley 1971). The composition of the diet changes substantially and predictably throughout the year (Linz et al. 2017). During the breeding season, adults and young feed primarily on invertebrates (60-65% of stomach contents in adults, 70-75% in young; Beal 1900). The rest of the year, the diet shifts to grains and seeds,

with fruits, vertebrates, and other edible matter incorporated opportunistically. Crops like corn, rice, oats, sunflowers, and peanuts, make up a large part of the Common Grackle diet in the regions in which the growing season overlaps with Common Grackle presence. In rice growing regions in Arkansas, for example, the winter diet can be up to 60% rice (Meanley 1971).

### *Study Sites*

We sampled our primary study site, named “Maddox” after the property owner, in 2018 and 2019. Maddox was a rectangular 1-hectare plot southwest of Bondville, IL (40°05’35” N, 88°23’16” W) that was planted with 1,000 Scotch Pines (*Pinus sylvestris*) between 2007 and 2008. At the time of our study, the trees were 2.5-4 m in height, growing in a tall (0.75-1.25 m) mix of grasses and forbs. The surrounding landscape was a matrix of conventional (non-organic) corn and soybean agriculture, with a small housing development to the north and a drainage ditch running north-south to the west (Figure 2).

We sampled our second study site, named “Byrd” after the property owner, in 2019 only. Byrd was a rectangular 5-hectare farmstead southeast of Philo, IL (39°58’04” N, 88°06’33” W) that was planted with an Eastern White Pine (*Pinus strobus*) and Blue Spruce (*Picea pungens*) windbreak. At the time of our study, the pine trees were 1.5-5 m in height and the spruce trees were 2-3 m in height, growing in a mowed lawn. Byrd also featured a 0.75-acre pond on the western half of the property and 3.25 acres of row-crop agriculture on the eastern half of the property. The surrounding landscape was a matrix of conventional (non-organic) corn, wheat, and soybean agriculture, with a rural housing development, a small wooded plot, and a modest free-range cattle pasture to the west and a patch of shrubland habitat to the southeast (Figure 3).

### *Nest Monitoring*

We conducted nest searches at each site weekly, during which every tree was visually inspected for Common Grackle nests. An active nest was defined as a nest with  $\geq 1$  Common Grackle egg. We recorded nest height and location when a nest became active. We checked active nests, at minimum, once every three days until success or failure. When nests approached the predicted fledge date, we increased the frequency of nest checks to once per day. We recorded the number of eggs and nestlings at each visit, as well as any notes about parental behavior or signs of abandonment, starvation, predation, or fledging. When nestlings were developed enough to fledge the nest (~12 days post-hatching), we banded them with a size 3 USGS metal band and a unique combination of three 5.5-mm plastic coil color bands. We also collected morphometric measurements including weight, taken with a portable electronic scale (g), wing and tail length, taken with a wing rule (mm), and culmen and tarsus length, taken with digital calipers (mm) for each nestling. Handling time was <5 minutes per bird. We returned all nestlings to the nest after being banded and processed. The nest was monitored daily henceforth until all nestlings had fledged or the nest failed. We assumed nests that were found empty around the expected fledging date had fledged unless there were clear signs of fledgling mortality. A nest was considered successful if  $\geq 1$  nestling fledged the nest. All capturing and handling of Common Grackles was approved under University of Illinois IACUC protocol #18011.

### *Nest Survival*

We created logistic exposure models in Program R to estimate daily nest survival from our nest monitoring data (Shaffer 2004, R Core Team 2018). The method uses a generalized linear model with a binomial probability distribution. It also uses a customized logistic link

function to account for the uncertainty around predicting the date of nest termination (Zhao and Sun 2018).

### *Radio Telemetry*

We randomly selected one nestling to attach a radio transmitter to at fledging. Transmitters (Lotek, Newmarket, Ontario) weighed 1.2 g and were attached using the backpack harness method (Raim 1978). Transmitter weight was <3% of bird body mass, per Bird Banding Lab protocol (Protocol #23959). We monitored radio-tagged fledglings using a hand-held Yagi antenna connected to a telemetry receiver (Model R-1000, Communications Specialists Inc., Orange, California). We attempted to locate tagged birds on days 1, 2, 3, 5, and 7 post-fledging, and once every three to five days after that in 2018, and on days 1-5 post-fledging, and every other day after that in 2019. If detected, we attempted visual confirmation to verify the fledgling's status. Fledglings were tracked until they were confirmed dead or until the transmitter's battery died, typically around 25 days post-fledging.

We complemented hand-held radio-telemetry with an automated radio-telemetry system (ARTS; Ward et al. 2013, 2014) operating on-site. Towers were 10 m tall and had six three-element Yagi antennas mounted on top, each connected to an autonomous radio-telemetry receiving unit (JDJC Corp., Fisher, IL; ARU) mounted in a metal housing near the base. We used marine deep-cycle batteries to power the ARUs. Each tower collected signal strength (in dB), pulse width (milliseconds), and noise (in dB) every 30-60 seconds for each active transmitter (Celis-Murillo et al. 2017). This yielded ~115,000 data points per active transmitter per day. At Maddox, we erected one tower in the northeast corner of the plot and another in the southwest corner of the plot. At Byrd, we erected a single tower at a high point along the northern perimeter of the property. Telemetry towers could detect transmitters at a range of up

to ~1.5 km, allowing us to more thoroughly document movement and activity during the post-fledging period.

### *Post-fledging Survival*

We created known fate models in Program MARK to estimate daily post-fledging survival (White and Burnham 1999). The method requires an encounter history for each fledgling, which contains the status (alive or dead) of the individual at each tracking occasion. The probability of encounter is assumed to be 1.0 if the individual is alive. To create 20-day (daily intervals) post-fledging encounter histories, we used handheld telemetry data when available and ARU tower data in all other cases. We used 20 days post-fledging because fledglings are relatively independent and highly mobile after 2-3 weeks out of the nest and because our guaranteed transmitter battery life was only 21 days.

The final fate of each fledgling was either success (confirmed success or presumed success), failure (presumed failure, depredated, or dead by exposure), or unknown. A fledgling was considered alive while it could be tracked using handheld telemetry or while its signal was strong and active in the ARU tower data. If a fledgling was confirmed alive the full 20-day period, its fate was considered “confirmed success.” If a transmitter was recovered and the dead fledgling, or part of the fledgling, was still in, or around, the transmitter, it was considered “depredated” or “dead by exposure,” depending on its condition. If the fledgling showed clear signs of predation (dismemberment or significant injury) it was considered “depredated.” If the fledgling appeared uninjured, it was considered “dead by exposure.” We did not specify a cause of death in cases of exposure.

If a fledgling was not recovered dead or confirmed alive for the full 20-day period, its fate was assumed based on how many days it was confirmed alive and its final ARU tower data.

After two weeks, fledglings can fly well and will begin moving around the landscape with adult flocks. Therefore, if a fledgling was confirmed alive for 15 days post-fledging and showed no signs of being depredated in its final ARU tower data (Nawrocki et al. 2019), it was assumed to have moved outside of tower range and its fate was considered “presumed success.” Signs of depredation included transmitter failure (strong signal followed by no signal at all) or rapid departure from tower range, especially if these events occurred at a time of day that did not make ecological sense (e.g. at night). If a fledgling was not confirmed alive for 15+ days or showed signs of being depredated in its final ARTS data, it was considered “presumed failure.” If a fledgling’s fate was unclear, its fate was considered “unknown.” We excluded three fledglings with unknown fates from the final analysis (transmitter battery failure).

### *Model Selection*

For all candidate model sets, models were ranked using Akaike Information Criterion (AICc; Akaike 1998). The top model had the lowest AICc value and models with  $\Delta\text{AICc} \leq 2$  were considered competitive. The relative strength of the top model was evaluated by considering its AIC ranking relative to the null model, the Akaike weight ( $w_i$ ) of the top and competitive models, and the confidence intervals of any included covariates.

We created a set of candidate models to investigate factors that influence nest success. Our covariates of interest were clutch size (eggs per active nest), seasonality (ordinal date of nest initiation), and nest age (days since initiation at success/failure). Clutch size may be indicative of parental fitness (Hegner and Wingfield 1987). Nest age (age-specific mortality) and seasonality have been shown to influence nest success in other species (Young 1963, Holcomb 1972, Martin 1987, Sperry et al. 2008). A seasonality trend in nest success may implicate drivers of nest failure, such as neonicotinoids. Neonicotinoid exposure is expected to vary predictably

during the breeding season; exposure risk is greatest around planting (mid-late April). Year and site were included in all models as nuisance variables to control for year- or site-specific variation. Because these variables were categorical with only two levels, we did not model them as random effects but instead included them as additive fixed effects. The nest initiation date for nests that were found after eggs had been laid or nestlings had hatched was back calculated based on the stage of the nest, egg laying rates, incubation length, and brooding length. We excluded 13 nests from the final analysis because their initiation date was uncertain. The full candidate model set consisted of single variable models, additive models (three to five variables), and a null model; no interaction models were considered to avoid overly complex models, given our sample size.

Constructing models to investigate factors that influence post-fledging survival was a two-step process (Jones et al. 2017). The first step was to determine the best age structure for our data. Fledgling age, the number of days post-fledging, is an established predictor of post-fledging survival and must be accounted for prior to modeling other covariates. We began by running a fully parameterized age model that estimated daily survival rate (DSR) for each fledgling age. Using these estimates, we created and ranked 6 age structures and included the top-ranked age structure in all future models. We applied a linear trend to all age structures based on the assumption that fledgling growth and development was linear across the post-fledging period. A linear fit also normalized the parameter count across age structures. The second step was to model and rank our other covariates: body condition (condition index), nest productivity (number of nestlings fledged), and seasonality (ordinal date at fledging). Body condition can influence post-fledging survival in other songbirds (Naef-Daenzer et al. 2001). In our models, we created a condition index for body mass using the residuals of a linear regression

between mass and tarsus. Again, year and site were included in all models to control for year- or site-specific variation. The candidate model set included single variable models, additive models, and a null model. No interaction models were considered to avoid overly complex models, given our sample size. We used the 85% confidence intervals of the  $\beta$  coefficients to provide support for highly ranked covariates.

### *Literature Comparison*

We used all available studies with records of Common Grackle reproductive success to compile literature estimates for clutch size, brood size, nest productivity, fledge rate, and nest success. We used a weighted one-sample *t*-test to compare these values with estimates from our study. Trautman (1940), Eyer (1954), and Hamel (1974) combined eggs and nestlings, did not publish the sample size, and had incomplete records, and thus could not be used in the analysis. Fledge rate estimates were not calculated by Howe (1977) and Snelling (1968) because of unclear nest success and human influence on nest success, respectively, and were also excluded from the analysis.

### *Simulation Models*

We created a partial life-cycle model (Oli and Zinner 2001) in Program R (R Core Team 2018) to predict juvenile and adult survival in Common Grackles based on the current population size, demographic rates (clutch size, fledge rate, and post-fledging survival) from our study, and population trend estimates for North America, Illinois, and a stable population. The Breeding Bird Survey (BBS) is a long-term monitoring program that is widely used to assess the status and trajectory of North American bird populations (Pardieck et al. 2019). Population trend estimates were taken from an analysis of BBS surveys done between 2005 and 2015 (Sauer et al. 2017). Reported as annual percent change, the trends were -1.87 for North America and -7.03 for

Illinois. The stable population was assigned a trend estimate of 0.00. The overall goal of this model was to determine the rate of juvenile and adult survival needed to maintain a stable population, given the other estimated parameters, and then to estimate their relative influence on population growth using a sensitivity analysis.

We simulated population growth over a 50-year period using the number of breeding pairs, clutch size, fledge rate, post-fledging survival, juvenile survival, and adult survival to estimate population size from one year to the next. Normally distributed variation was built into each demographic rate to simulate stochasticity. The standard deviation for stochasticity was set at a level that produced no more than 2.5% variation per year, which we determined to be realistic based on annual fluctuations in BBS data. This 50-year growth projection was iterated 1,000 times and averaged across iterations to produce a population growth curve and a trend estimate. The estimates produced by this model make several assumptions, including 1) no re-nesting or double brooding, 2) all birds reach sexual maturity at the start of their second year (i.e. one year old), 3) all sexually mature birds reproduce, 4) a sex ratio of 1:1, and 5) estimates of reproductive success in Illinois are representative of the rates for the global population.

Juvenile survival was assumed to be the same as adult survival in our initial models. Once a survival rate had been estimated for each population trend estimate (BBS and stable), we began projecting population growth under various scenarios of reduced juvenile survival. We defined juvenile survival as the period from post-fledging independence to the start of the breeding season the following year (~10 months in the Common Grackle). In birds, juvenile survival of migratory species is poorly studied, but is generally thought to be lower than adult survival (Noon and Sauer 1992, Donovan et al. 1995). Keeping our adult survival estimates constant, we modeled population growth while reducing juvenile survival by 0-40%. This

produced new population growth curves and trend estimates. Finally, we increased juvenile and adult survival proportionately, retaining an 8:10 ratio between juvenile and adult survival, until the projection produced a stable population.

We conducted a sensitivity analysis by adjusting fecundity and annual adult survival in our simulation model and comparing the changes in trend estimate (Oli and Zinner 2001). We defined fecundity as the net productivity of the previous breeding season i.e. the number of birds transitioning from their hatch year to their second year. For juvenile and adult survival, we used estimates from the model that produced a stable population with an 8:10 ratio between juvenile and adult survival. We used fecundity and adult survival because, due to the simplicity of our model, only demographics of equal temporal duration could be compared (rates that represent a year of growth can only be compared with other rates that represent a year of growth). Fecundity is an annual rate, which could be directly compared to adult survival, also an annual rate. Trend estimates were simulated for adjustments of +/-10%. The population trend estimates were then compared to an unadjusted estimate to determine change. The demographic rate that produced the greatest variance was determined to have the strongest influence on population growth.

## **Results**

### *Nest Monitoring*

We monitored 188 nests across two sites in the spring of 2018 and 2019 (Table 1). The average clutch size (eggs per active nest) was 4.26 (range 1-6, SE = 0.07). The average brood size (nestlings per nest that hatched  $\geq 1$  nestling) was 3.80 (range 1-6, SE = 0.09). The average nest productivity (fledglings per successful nest) was 3.43 (range 1-5, SE = 0.10). Our results show that successful nests, on average, lost ~1 egg/nestling (0.83) during the incubation/nestling

period. Roughly 40% of nests failed and the number of fledglings produced per active nest was only 2.05 (SE = 0.14). Known sources of egg and nestling mortality include predation, starvation, extreme weather, and exposure, but these were not quantified. Anecdotally, predation was the primary source of nestling mortality. We found no evidence of abnormally high rates of brood abandonment (4% of nests showed signs of abandonment) or nestling starvation (0.36 nestlings disappeared per successful nest).

### *Nest Success*

The top ranked model included our nuisance variables (site and year) and seasonality ( $w_i = 0.60$ ; Table 2). Using this model, we estimated a nest daily survival rate (DSR) of 0.982 (SE = 0.002, 95% CI: 0.977-0.986) and a nest success rate of 0.622 (SE = 0.037) for the 26-day nesting period (Figure 4). The second ranked model ( $\Delta AIC_c = 1.69$ ,  $w_i = 0.26$ ) included nest age, seasonality, and our nuisance variables. Despite its high AIC ranking, it was not considered competitive due to collinearity between nest age and seasonality ( $r = 0.70$ ,  $VIF < 2$ ). Seasonality was the only significant predictor of nest success in our study. As the season progressed, nest success declined non-linearly.

### *Radio Telemetry*

We tagged and tracked 53 fledgling Common Grackles; 19 at Maddox in 2018, 12 at Maddox in 2019, and 22 at Byrd in 2019. With hand-held telemetry, average tracking duration was 9.57 (SE = 1.07) days post-fledging. The addition of ARU tower data increased this average to 15.06 days (SE = 1.09). In total, 22 fledglings (41.5%) survived the entire 20-day tracking period. Another eight fledglings (15.1%) were presumed alive but could not be located after 15 days post-fledging. Of the remaining 23 fledglings, 11 (20.1%) were assumed dead but never

found and 12 (22.6%) were confirmed dead. The cause of death in the 12 cases of confirmed mortality was split evenly between predation (6) and exposure (6).

### *Post-fledging Survival*

We began by constructing and ranking five age structures using estimates from a fully parameterized age model. The best model grouped fledgling ages 0-5, 6-11, and 12-20 days ( $w_i = 0.48$ ; Table 3). A daily age structure was also competitively ranked ( $\Delta AICc = 0.41$ ,  $w_i = 0.39$ ), but we chose to use the less complex, higher ranked model.

The second step of modeling yielded a top model that included all the covariates we tested (age, seasonality, condition index, and nest productivity;  $AICc = 142.12$ ,  $w_i = 0.58$ ; Table 4). Using this model, we found a DSR of 0.969 (SE = 0.007, 95% CI: 0.953-0.980) and a cumulative 20-day post-fledgling survival rate of 0.617 (SE = 0.075; Figure 5). Age ( $\beta = 15.83$ , 85% CI from 7.67 to 24.00) was the primary predictor of post-fledging survival. Survival increased with fledgling age (Figure 5); most mortality occurred from ages 0-5. The covariates seasonality ( $\beta = -0.09$ , 85% CI from -0.14 to -0.04), condition index ( $\beta = -0.52$ , 85% CI from -0.91 to -0.14), and nest productivity ( $\beta = -0.09$ , 85% CI from -0.16 to -0.02) were negatively associated with post-fledging survival but had a much small influence than age.

### *Literature Comparison*

We reviewed 17 accounts of Common Grackle reproductive success (Table 5). From this, we derived 14 estimates of clutch size (eggs per nest), four estimates of nestlings per total nests, seven estimates of nest productivity (fledglings per successful nest), seven estimates of fledge rate (fledglings per total eggs), and six estimates (raw or Mayfield's) of nest success (percentage of nests that fledged  $\geq 1$  nestling). Our results were significant or marginally significant for three demographic rates. Clutch size ( $t = 1.44$ ,  $df = 13$ ,  $p = 0.09$ ) was marginally

lower in our study (4.26) than in the literature (4.35). Fledge rate ( $t = -4.38$ ,  $df = 6$ ,  $p < 0.01$ ) and nest success ( $t = -3.33$ ,  $df = 5$ ,  $p = 0.01$ ) were both significantly higher in our study (0.48, 0.62) than in the literature (0.28, 0.27). For the other two demographic rates, nestlings per total nest ( $t = 0.16$ ,  $df = 3$ ,  $p = 0.44$ ) and nest productivity ( $t = -0.45$ ,  $df = 6$ ,  $p = 0.67$ ), our results (2.99, 3.43) were not significantly different from the literature (3.04, 3.37).

### *Simulation Models*

Obtaining a stable population with average rates of reproductive success and post-fledging survival required a juvenile survival rate (JSR) and annual adult survival rate (AASR) of 61.30% (Figure 6). To match the trend estimate globally (-1.85%), the necessary JSR and AASR drops to 60.16%. For the population breeding in Illinois, which is experiencing steep decline (-7.03%), the estimated JSR and AASR is 57.00%. In a breeding population of 69 million (the current estimated population), this 4.3% reduction in JSR and AASR (from 61.30% to 57.00%) would reduce the current population to just 2 million birds in 50 years, a 97% loss.

We demonstrated the importance of accurately estimating JSR by reducing JSR in a stable population by 0-40% (Figure 7). A 10% reduction in JSR produced an annual trend estimate of -3.87%, a steep but sustainable decline over short periods. Reducing JSR by 20% produced an annual trend estimate of -7.70%. A 40% reduction in JSR produced an annual trend estimate of -15.50%. In the case of the Common Grackle, assuming JSR incorrectly by as little as 5% would have a significant impact on the reliability of the model predictions. Using our median reduction in JSR (20%), we found that AASR would have to be 66.45% (making JSR 53.16%) to maintain a stable population. Further investigation using our population growth simulation model suggests that AASR in the Common Grackle is likely between 65-80%, depending on the reduction in JSR. We were also able to provide a minimum estimate of JSR

using our post-fledging survival data. Assuming daily survival is not lower than 0.995 (post-fledging DSR for ages 6-20) during the juvenile life stage, minimum JSR in Common Grackles is roughly 22%.

We found that population growth in the Common Grackle was most sensitive to AASR (Figure 8). In our model, a 10% increase in AASR yielded an annual trend estimate of 6.66%, while a 10% increase in fecundity yielded an annual trend estimate of 3.37%. Therefore, changes in AASR have a 1.98 times greater effect on population growth than changes in fecundity.

## **Discussion**

We did not find any evidence of low reproductive success or post-fledging survival in our study. In fact, some metrics of reproductive success were greater than mean values from the 15 previous studies of Common Grackles (Table 5). Nonetheless, the Common Grackle is experiencing steep population declines, both in Illinois and throughout its breeding range (Sauer et al. 2017). If our estimates of reproductive success and post-fledging survival are indicative of the Illinois population as a whole, the observed decline likely stems from low juvenile or adult survival. Simulations using data from this study suggest that 1) adult survival must be >60% to support a stable population (Figure 6) and 2) population growth is particularly sensitive to the survival of breeding adults (Figure 8). We conclude that Common Grackle decline is not being driven by rates of reproductive success or post-fledging survival, but rather by survival during the non-breeding season. Adult survival, in particular, appears to be a critically important and understudied demographic.

The demographic rates of reproductive success that we quantified, including nest success, clutch size, nestlings per total nests, nest productivity, and fledge rate, suggest that net productivity among our colonies was remarkably high. For example, our estimate of nest success (62.2%) was the highest ever recorded, more than double the literature average (27%). Clutch size, the only metric of reproductive success that was below average in our study, is highly variable in the Common Grackle literature (3.98-4.90, mean = 4.35) and can vary latitudinally in songbirds (Lack 1947). Our clutch size estimate of 4.26 is unlikely to represent a meaningful reduction in reproductive potential. Once our birds fledged the nest, survival was comparable to post-fledging survival in other songbirds. Common Grackle post-fledging survival has not been studied before, so our estimate (61.7%) is difficult to evaluate. Post-fledging survival is generally an understudied life stage. However, in other songbirds, post-fledging survival can range from 23% to 87% during the first three weeks (Cox et al. 2014). In the Eastern Meadowlark (*Sturnella magna*), a slightly smaller icterid, cumulative post-fledging survival has been estimated at 66% and 75% (Kershner et al. 2004, Suedkamp Wells et al. 2007). Additional research is warranted into this little-studied life stage.

Our estimates of nest success and post-fledging survival were influenced by seasonality and fledging age, respectively. Seasonality can have a strong temporal effect on songbirds (Sherry and Holmes 1995, Calvert et al. 2009, Gullett et al. 2014). Seasonality during the breeding season is known to influence predation risk, rates of brood parasitism, clutch size, food availability, thermoregulatory costs, and re-nesting potential in altricial songbirds (Martin 1987, Crick et al. 1993, Pease and Grzybowski 1995, Sperry et al. 2008). Our results showed that seasonality affected Common Grackle nest success; nests initiated early in the season were more successful than nests initiated late in the season (Figure 4). This relationship has been

demonstrated in other songbird species (Perrins 1970, Price et al. 1988). For the Common Grackle, predation risk is the most probable mechanism of seasonal variation in nest success. Predation is the most common source of nest failure in passerines (Ricklefs 1969) and, in fragmented agricultural landscapes, where Common Grackles often nest, nest predation risk is especially high (Andren et al. 1985, Andren 1992, Vander Haegen et al. 2002). We anecdotally observed predation as a major source of nest mortality late in the breeding season. However, the influence of seasonality on predation risk is mixed in the literature (Perrins 1979, Roos 2002, Grant et al. 2005) and the fact that Common Grackles breed earlier than other songbirds in Illinois further complicates this relationship (Erskine 1971).

Similar to seasonality in nest success, fledgling age is a strong predictor of post-fledging survival in many songbird species (Maness and Anderson 2013, Cox et al. 2014). For the first few days out of the nest, young birds have poor feather development and limited mobility (Jones et al. 2017). Rates of mortality due to predation and exposure are particularly high during this period (Ausprey and Rodewald 2011, Naef-Daenzer and Gruebler 2016). We found that post-fledging survival in the Common Grackle mirrors this trend (Figure 5). The DSR for fledglings from days 0-5 post-fledging was 0.93, then increased to 0.99 from days 6-11 and to 1.00 after day 12. Several other covariates were also predictors of post-fledging survival in our top model, including seasonality, body condition (condition index), and nest productivity. All three had a slight negative relationship with post-fledging survival and were much poorer predictors than fledgling age. It is unclear why body condition would worsen fledgling survival. Body condition has been shown to improve post-fledging survival in some species (Naef-Daenzer et al. 2001) and to have no effect in others (Hedgren 1981, Harris et al. 1992, 1994), though it is important to note these studies are not all on passerines and significant methodological

differences exist. We hypothesize nest productivity may decrease post-fledging survival because parental care (e.g. feeding, protection from predators) is divided among more fledglings. It has been suggested that nest productivity is optimized in birds to maximize post-fledging survival i.e. the modal brood size is the most productive (Ormerod and Tyler 1993). We found a negative influence of seasonality on post-fledging survival. There is much support in the literature for this relationship (Naef-Daenzer and Gruebler 2016); in some cases, the impact of seasonality on post-fledging survival is quite strong (Naef-Daenzer et al. 2001). Additionally, we can use these results to infer the influence of neonicotinoids on post-fledging survival. The risk of neonicotinoid exposure varies predictably during the breeding season based on the timing of corn and soybean planting. Neonicotinoids were proposed to disproportionately impact Common Grackles because in late April when, in Illinois, most planting occurs, they are one of the few songbirds that has fledglings. If neonicotinoids were a major driver of post-fledging survival, we would expect early season fledglings to have worse survival than late season fledglings. We found the opposite trend, suggests that neonicotinoid exposure is likely not directly influencing the survival of Common Grackle fledglings. However, other aspects of agricultural intensification may influence age-dependent post-fledging survival.

Two mechanisms of agricultural intensification - structural changes in the landscape and widespread pesticide application - could be affecting post-fledging survival. Structural changes are hypothesized to reduce shelter availability and decrease food availability, increasing the risk of predation and starvation (Dennis et al. 1998, Whittingham and Evans 2004). Pesticide application is hypothesized to increase exposure to toxic chemicals and decrease food availability, again increasing the risk of predation and starvation, as well as introducing a risk of mortality from acute toxicity (Hallmann et al. 2014, Gibbons et al. 2015, Eng et al. 2019). In our

study, predation was the primary source of post-fledging mortality. Of the 12 fledglings that were confirmed dead, six (50%) showed clear evidence of depredation. For the majority of birds that were presumed dead, we attributed their disappearance to predation. For a bird killed by other sources of mortality, such as starvation or hypothermia, we would be able track and recover the transmitter. If the battery had failed, we would see evidence of this in the ARU data. Predation as the primary source of post-fledging mortality is consistent with other studies on post-fledging survival (Anders et al. 1997, Naef-Daenzer et al. 2001, Kershner et al. 2004, Berkeley et al. 2007, Suedkamp Wells et al. 2007). The other six fledglings that were confirmed dead appeared to have died from exposure. Identifying the cause of death in these cases was challenging, but by hand-tracking each fledgling at regular intervals, we were able to monitor their condition across time. No birds, alive or dead, showed clear signs of lethargy, malnourishment, or poisoning. Anecdotally, most birds that died of exposure were found dead after heavy rainstorms or unusually cold nights. Though it could be argued that structural diversity and habitat fragmentation are influencing predation rates, our results suggest that agricultural intensification is not a major source of Common Grackle population decline during the breeding season.

Similar to post-fledging survival, juvenile survival is a poorly understood life stage in birds. It has not been quantified for the Common Grackle and, in other species, is often estimated indirectly. Juvenile survival is particularly difficult to study in migratory birds because, in many species, juveniles exhibit low site fidelity and disperse great distances. Therefore, traditional mark-recapture studies underestimate juvenile survival due to the prevalence of permanent emigration. This is true for the Common Grackle, where hatch year (HY) birds disperse 46% further from their nest location than after hatch year (AHY) birds

(Dolbeer 1982). Nonetheless, reliable estimates of juvenile survival are essential for accurately modeling population dynamics. Juvenile survival has been shown to be as low as 45% of adult survival and as high as nearly 100% of adult survival (Marra and Holmes 2001, Sillett and Holmes 2002, Gardali et al. 2003). If not properly accounted for, population growth projections could be highly misleading. We demonstrated the importance of accurately quantifying this life stage using our Common Grackle population model (Figure 7). Estimates of AASR are also critical for assessing the health of a population, but are more common (Sæther 1989, Karr et al. 1990, DeSante and Rosenberg 1998). For the Common Grackle, minimum estimates of survival have been calculated from band recovery data: 49.9% for males and 53.5% for females (Fankhauser 1971). Our simulations of population growth suggest adult survival is, at minimum, 65% and potentially as high as 80%. We justify this range as follows: 1) Our estimates of reproductive success and post-fledging survival, which are used to simulate this range, are defensible representations of net productivity among Common Grackles breeding in Illinois, 2) Assuming JSR and AASR are equal - AASR must be at least 60% (Figure 6), 3) JSR is, conservatively, 80% of AASR, which would require an AASR of 66.45% to maintain a stable population, and 5) A more liberal estimate of JSR, such as 60% of AASR, is also realistic and would require an AASR of >80% to produce a stable population. However, it is important to consider our assumptions, particularly our assumptions that breeding pairs are not re-nesting or double brooding and that our estimates of reproductive success in Illinois are representative of rates in the global population. Increased productivity from second broods would slightly decrease our estimate of adult survival. Regional variation in Common Grackle reproductive success is likely, though without contemporary data it is difficult to predict how our estimates would compare with global estimates. Even so, AASR has clearly been critically underestimated

in the literature and reduced the perceived importance of adult survival in population stability, consequently discounting the potential harm of lethal pest control (Dolbeer et al. 1995). Our sensitivity analysis supports this conclusion, showing that AASR was almost twice as influential on population growth as any other life stage (Figure 8). Our findings that 1) reproductive success and post-fledging survival is healthy for Common Grackles breeding in Illinois, 2) annual adult survival must be 10-20% higher than the minimum estimates from the literature, and 3) annual adult survival is the most sensitive life stage, suggest that the demographic source of Common Grackle population decline is likely annual adult survival.

In migratory songbirds, rates of adult mortality are thought to be highest during migration and on the wintering grounds (Lack 1954, 1968; Newton 2004). Migration is energetically stressful and increases the risk of both natural (e.g. predation, disease, extreme weather, starvation) and anthropogenic (e.g. buildings, wind turbines, vehicles) sources of mortality (Erickson et al. 2005, Newton 2008). As much as 85% of annual adult mortality can occur during spring and fall migration (Sillett and Holmes 2002), though this varies by species (Klaassen et al. 2014). In the Common Grackle, survival during migration is likely quite high. Grackles are short distance migrants, travel in flocks, and are habitat and dietary generalists (Dolbeer 1982, Clark and Mangel 1984). There is little evidence that starvation or other migratory risks, such as predation, building collisions, or extreme weather, are significant sources of annual mortality in blackbirds (Lindström 1989, Erickson et al. 2005, Loss et al. 2014). Overwintering is less energetically stressful than spring or fall migration but lasts far longer (November to April) and has at least one well-documented source of mortality among blackbirds: direct persecution.

Common Grackles overwinter in large, mixed-species flocks with Red-winged Blackbirds (*Agelaius phoeniceus*), European Starlings (*Sturnus vulgaris*), Rusty Blackbirds (*Euphagus carolinus*), and Brown-headed Cowbirds (*Molothrus ater*). Because the winter ecology and management of blackbird flocks is well documented and often not sub-divided by species, we will be addressing Common Grackle overwinter survival through the broader topic of blackbird overwinter survival. Blackbirds roosts have been studied extensively because they can cause significant agricultural damage (Linz et al. 2017). Though the financial cost of blackbirds as agricultural pests has been debated (Robertson et al. 1978), management action is widespread (White et al. 1985, Dolbeer et al. 1995, Linz et al. 2017). Direct persecution can take the form of chemical repellants, lethal sprays, lethal bait, roost destruction, and physical harassment. The most aggressive Common Grackle management occurred in Kentucky and Tennessee from 1974-1992, where PA-14 (alpha-alkyl[C11-15]-omega-hydroxypoly[oxyethylene]), an avian stressing agent, was used to treat 83 roosts, killing an estimated 38.2 million overwintering blackbirds (2.1 million birds per year; 48% Common Grackles). In the winter of 1978 alone, an estimated 4.2 million grackles were killed. Contemporary management action utilizes DRC-1339 (3-chloro-p-toluidine hydrochloride), also known as Starlicide, an acutely toxic chemical that can be added to bait. Despite the implications of its name, it is highly toxic to many bird species, not just European Starlings. In 2009, the USDA reported killing or euthanizing over 4 million blackbirds, roughly double the annual average between 1974-1992 (USDA 2009). Blackbirds may also be killed by private landowners with permission from the US Fish and Wildlife Service or by private landowners acting illegally. Such action is not uncommon but is rarely documented or reported (Stone et al. 1984:19; White et al. 1989, Carson 2002). Non-lethal forms of direct persecution may locally displace Common Grackles and marginally increase their energetic

expenditure. Even so, they are not likely a significant source of winter mortality. Common Grackles are not faithful to winter roosts and appear to base their movements more on the location of consistent food sources than on the location of any particular roosting site (Dolbeer 1982). Other potential sources of overwinter mortality include starvation, exposure, and predation (Johnson et al. 1980, Peach et al. 1999). In Europe, starvation is a major driver of overwinter survival in farmland birds. Many species rely on field types that support invertebrates, weed seed, and vegetation year-round, such as pasture and cereal stubble (Tucker 1992, Peach et al. 1999). Agricultural intensification impacts the availability of these food resources through changes in land use and pesticide application, consequently increasing the likelihood of overwinter starvation for granivorous and insectivorous birds (Shrubb 1997, Donald 1998, Siriwardena et al. 2007). Common Grackles and other blackbirds rely on agricultural landscapes for food over the winter and could be similarly impacted.

The five species that overwinter in North American blackbird roosts are all in various states of population decline. The Red-winged Blackbird, European Starling, and Common Grackle are three of ten songbird species that have collectively lost over 1.5 billion individuals since 1970 (Sauer et al. 2017). The Rusty Blackbird has declined by 85-95% globally over the same period, representing one of the largest population declines documented by the BBS (Greenberg et al. 2011). Even the Brown-headed Cowbird, which has benefited from widespread forest fragmentation (Brittingham and Temple 1983, Cox et al. 2012), declined by 28.2% between 1965 and 2015 (Sauer et al. 2017). Drivers of decline in certain blackbird species may not be applicable to Common Grackles. For example, the Rusty Blackbird has more restrictive breeding habitat requirements, is far less abundant, and may be negatively impacted by mercury exposure or climate change (Edmonds et al. 2010, Greenberg et al. 2011). Regardless, the

overwhelming trend of decline among blackbirds is concerning. Blackbird winter ecology as it relates to agricultural damage has been thoroughly addressed in the literature, but little is known about survival during this period. Assessing survival during the non-breeding season and sources of winter mortality is critical for addressing the decline of blackbirds, specifically native species like the Common Grackle.

This study has demonstrated the importance of demographic data in investigating population decline and projecting population growth. It has also shown that current agricultural practices in Illinois do not appear to be impacting the reproductive success or post-fledging survival of Common Grackles. Because this study was limited by the duration and extent of our sampling effort (we collected data for two years, worked at rural sites with large breeding colonies, and sampled exclusively in Champaign County, Illinois), these inferences should be extrapolated with care. More work is required to solidify the demographic rates of Common Grackles globally and confidently identify a mechanism of decline. We encourage the replication of this study in other regions, as well as research aimed at directly quantifying juvenile and adult survival.

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## TABLES AND FIGURES

**Table 1.** Summary of the monitoring effort for Common Grackle nests in Champaign County, Illinois from 2018-2019.

Common Grackle Nest Monitoring in Illinois, 2018-2019

<i>Year</i>	<i>Site</i>	<i>Nests</i> <sup>a, b</sup>			<i>Eggs</i> <sup>a, b</sup>		
		<i>No.</i> <sup>c</sup>	<i>Hatched Eggs</i>	<i>Fledged Young</i>	<i>Laid</i>	<i>Hatched</i>	<i>Fledged</i>
2018	Maddox	46	42 (91.3)	32 (69.6)	181	150 (82.9)	97 (53.6)
2019	Maddox	43	30 (69.8)	24 (55.8)	189	110 (58.2)	79 (41.8)
2019	Byrd	99	76 (76.8)	56 (56.6)	430	302 (70.2)	209 (48.6)
<i>Total</i>		188	148 (78.7)	112 (59.6)	800	562 (70.3)	385 (48.1)

<sup>a</sup> Percentages of *No.* given in parentheses

<sup>b</sup> Includes all potential sources of failure

<sup>c</sup> Nests with  $\geq 1$  eggs

**Table 2.** Candidate model set ranked using AICc for factors influencing Common Grackle nest success in Champaign County, Illinois during 2018-2019.

Model Selection for Common Grackle Nest Success

Model <sup>a</sup>	No. Par	loglik	$\Delta$ AICc	ModelLik	$w_i$	Cum. weight
Seasonality <sup>b</sup>	4	-215.33	0.00	1.00	0.60	0.60
Seasonality + Nest Age	5	-215.17	1.69	0.43	0.26	0.85
Seasonality + Nest Age + Clutch Size	6	-214.74	2.84	0.24	0.14	1.00
Nest Age <sup>c</sup>	4	-223.30	15.94	0.00	0.00	1.00
Intercept Only (null)	1	-233.43	30.19	0.00	0.00	1.00
Clutch Size <sup>d</sup>	4	-232.86	35.05	0.00	0.00	1.00

<sup>a</sup> All models include year and site as control variables

<sup>b</sup> Ordinal date of nest initiation

<sup>c</sup> Number of days between nest initiation and nest success/failure

<sup>d</sup> Number of eggs per active nest

**Table 3.** Model set ranked using AICc for age structure of Common Grackle post-fledging survival in Champaign County, Illinois during 2018-2019.

Model Selection for Age Structure of Post-fledging Survival

Age Structure <sup>a</sup>	No. Par	loglik	$\Delta$ AICc	Model Likelihood	$w_i$	Cum. Weight
0-5,6-11,12-20	2	157.20	0.00	1.00	0.48	0.48
0,1,2,3...20 (daily)	2	157.61	0.41	0.82	0.39	0.86
0-5,6-20	2	160.08	2.87	0.24	0.11	0.98
0,1,2,3,4,5,6-20	2	163.61	6.41	0.04	0.02	1.00
0,1,2,3-9,10-20	2	166.83	9.62	0.01	0.00	1.00
Intercept (null)	1	187.47	28.25	0.00	0.00	1.00

<sup>a</sup> All models were built with a linear fit

**Table 4.** Candidate model set ranked using AICc for factors influencing Common Grackle post-fledging survival in Champaign County, Illinois during 2018-2019.

Model Selection for Common Grackle Post-fledging Survival

Model <sup>a</sup>	No. Par	loglik	$\Delta$ AICc	ModelLik	$w_i$	Cum. Weight
Age <sup>b</sup> + Seasonality <sup>c</sup> + Cond. Index <sup>d</sup> + Nest Prod. <sup>e</sup>	7	142.12	0.00	1.00	0.58	0.58
Age + Seasonality + Cond. Index	6	146.39	2.23	0.33	0.19	0.77
Age + Seasonality	5	149.36	3.17	0.21	0.12	0.89
Age + Condition Index	5	151.45	5.26	0.07	0.04	0.94
Age	4	153.94	5.71	0.06	0.03	0.97
Age + Nest Productivity	5	152.08	5.89	0.05	0.03	1.00
Intercept (null)	1	187.47	33.19	0.00	0.00	1.00

<sup>a</sup> All models include year and site as control variables

<sup>b</sup> The highest ranked structure, ages 0-5, 6-11, 12-20

<sup>c</sup> Ordinal date at fledging

<sup>d</sup> Residual for linear regression of weight and tarsus

<sup>e</sup> No. of nestlings that fledge a nest

**Table 5.** Summary of accounts of Common Grackle reproductive success since 1950.

Literature Review of Common Grackle Reproductive Success and Survival, 1950-2020

<i>Author(s)</i>	<i>Year</i>	<i>Location</i>	<i>No.</i> <sup>a</sup>	<i>Clutch Size</i>	<i>Nestlings</i> <sup>b</sup>	<i>Nest Prod.</i> <sup>c</sup>	<i>Fledge Rate</i>	<i>Nest Success</i>	<i>PF Survival</i>	<i>Adult ASR</i>
Peterson, A. & Young, H.	1950	Wisconsin	62	4.87	3.37	4.00 (34)	0.45	0.55		
Wiens, J.A.	1965	Wisconsin	33	4.42	3.55	3.85 (20)	0.53	0.61		
Long, C.A. & Long, C.F.	1968	Michigan	23	4.21						
Snelling, J.C.	1968	Wisconsin	47	3.98	2.64	2.87 (15)	0.23	0.32		
Jones, H.P.	1969	Kentucky	64	4.70						
Maxwell II, G.R.	1970	Ohio	18	4.30						
Erskine, A.J.	1971	North America	677	4.35						
Fankhauser, D.P.	1971	United States	734							0.52
Willson, M.F., et al.	1971	Illinois	66	4.90				0.04		
Maxwell II, G.R. & Putnam, L.S.	1972	Ohio	19	4.21	2.05	2.60 (10)	0.33	0.53		
Howe, H.F.	1977	Michigan	140	4.60		3.07 (44)	0.21			
Howe, H.F.	1978	Michigan	275	4.55		3.30 (129)	0.34			
Peck, G.K. & James, R.D.	1987	Ontario	517	4.11						
Twedt, D.J.	2011	Louisiana & Mississippi	169	4.05		3.58 (24)	0.13	0.14		
Archived Museum Samples	Varied	United States	93	4.65						
<i>Literature</i> <sup>d</sup>	1973	Varied	157	4.36	3.04	3.37	0.28	0.27		0.52 <sup>e</sup>
<i>Our Results</i>	2019	Illinois	188	4.26	2.99	3.43	0.48	0.62	0.61	

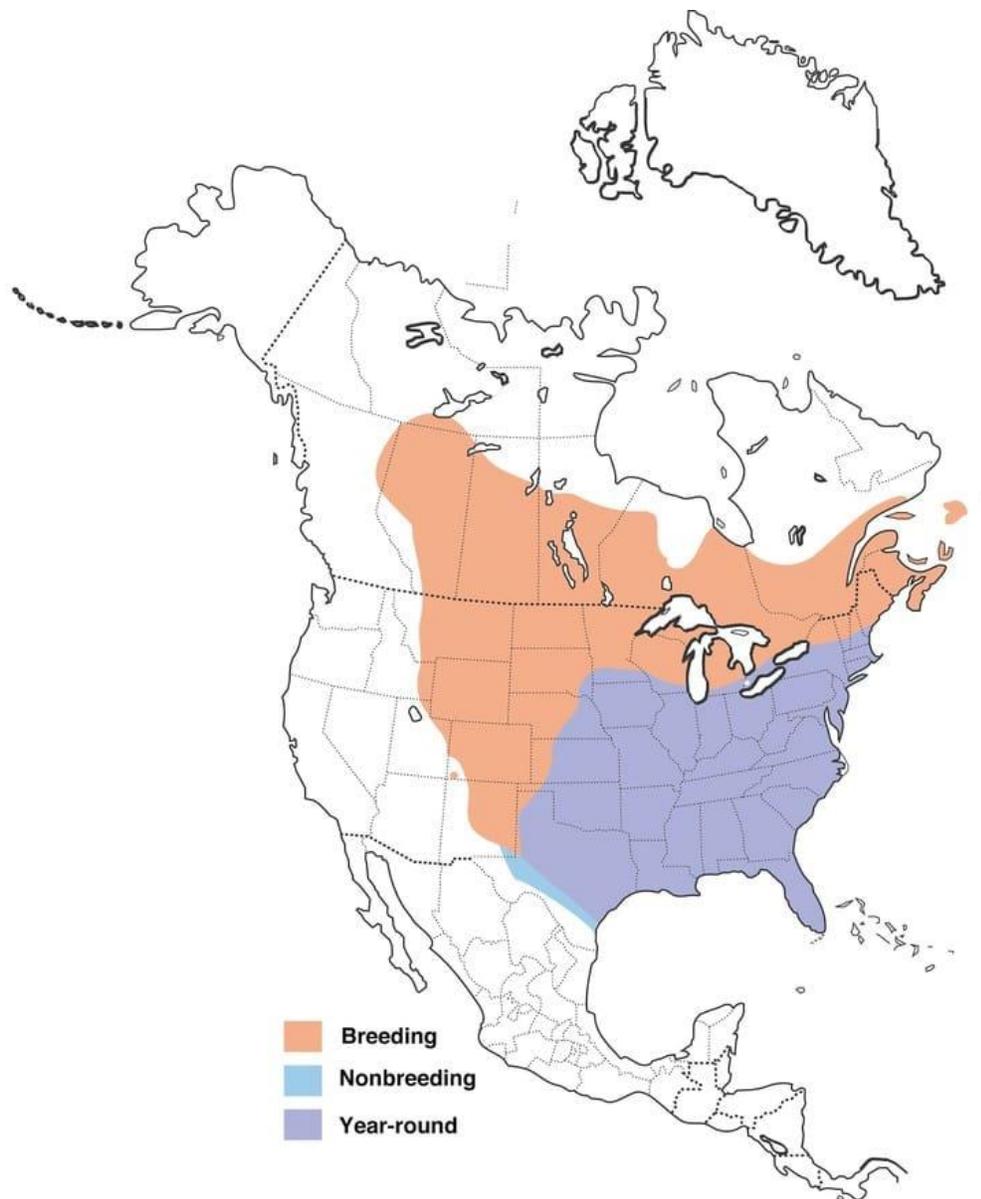
<sup>a</sup> Nests with  $\geq 1$  Common Grackle eggs

<sup>b</sup> Number of nestlings divided by *No.*

<sup>c</sup> Number of successful nests in parentheses

<sup>d</sup> Weighted means

<sup>e</sup> Estimated from recaptures



**Figure 1.** Range map, produced by the Cornell Lab of Ornithology, showing the global breeding, non-breeding, and year-round distribution of the Common Grackle (McDonough 2013).

[https://www.allaboutbirds.org/guide/Common\\_Grackle/maps-range](https://www.allaboutbirds.org/guide/Common_Grackle/maps-range)



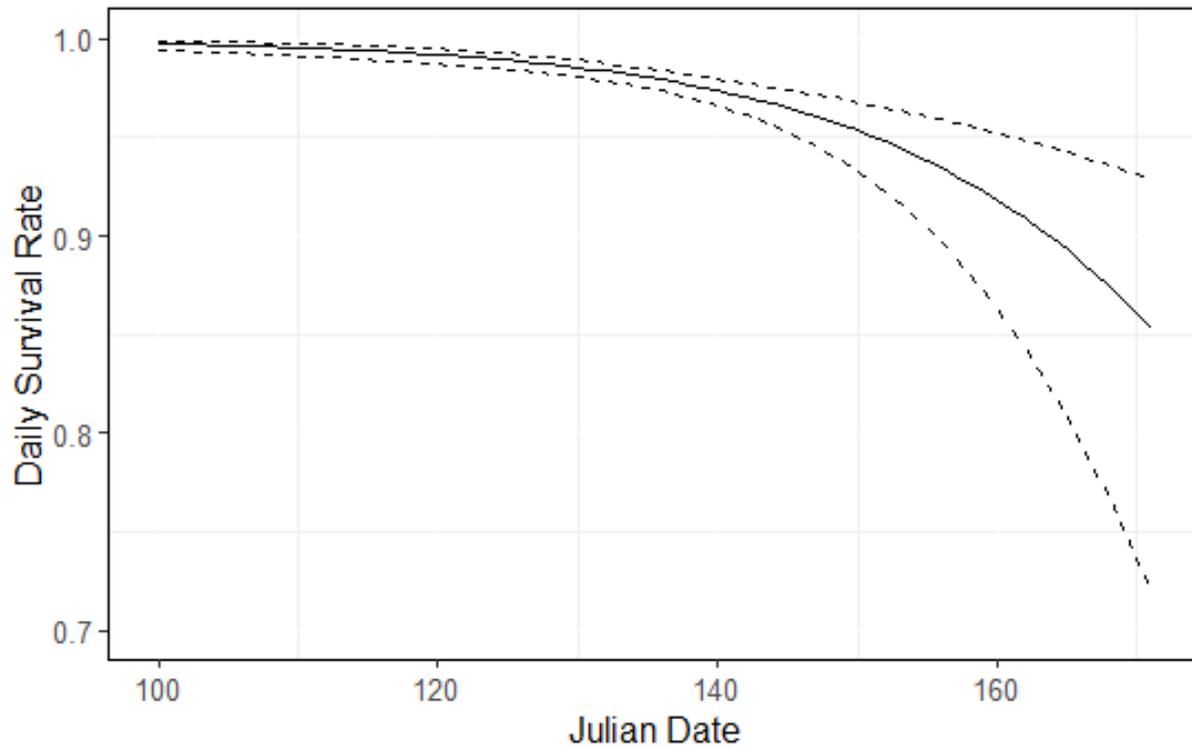
**Figure 2.** Aerial view of the landscape surround Maddox, showing the site location (striped box) and a zoomed view of the site itself (top right).



**Figure 3.** Aerial view of the landscape surrounding Byrd, showing the site location (striped box) and a zoomed view of the site itself (top right).

## Influence of Seasonality on Nest Success

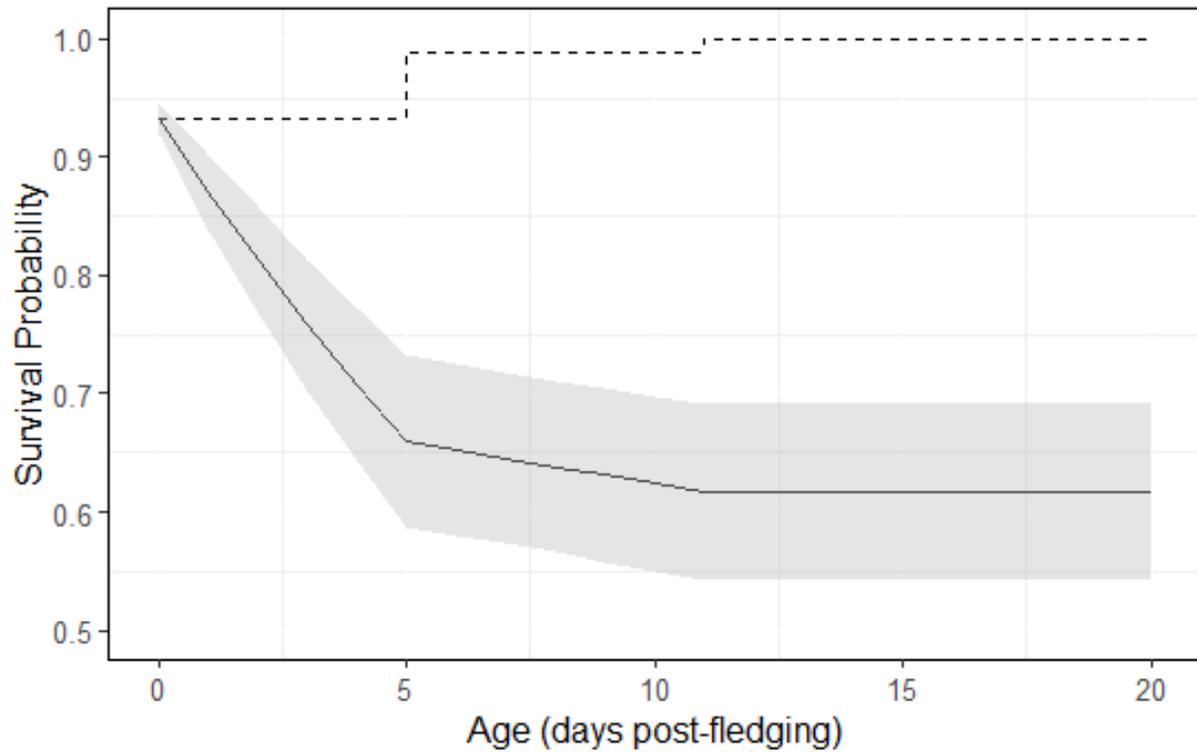
Logistic Exposure |  $p < 0.001$  |  $n = 188$



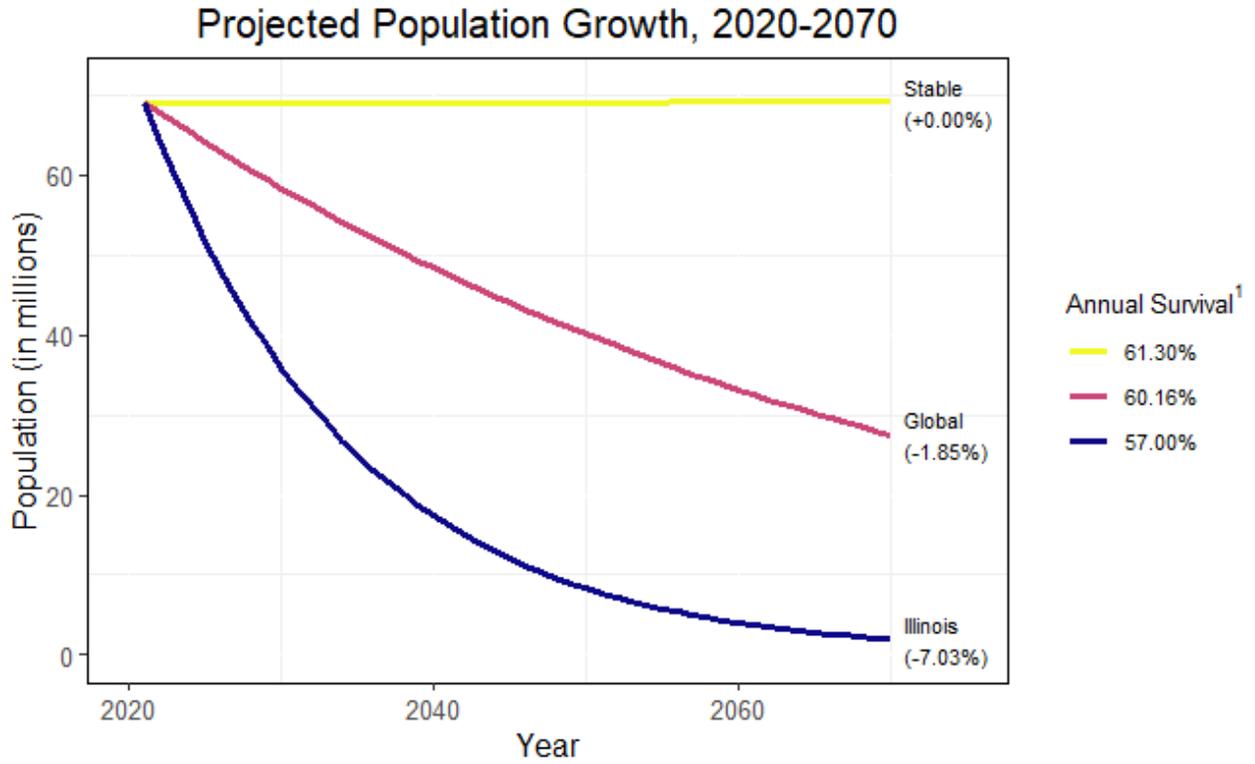
**Figure 4.** The negative effect of seasonality on Common Grackle nest survival in central Illinois during spring 2018-2019. Dashed lines represent the upper and lower bounds of the 95% confidence interval.

## Common Grackle Post-fledging Survival in Central Illinois

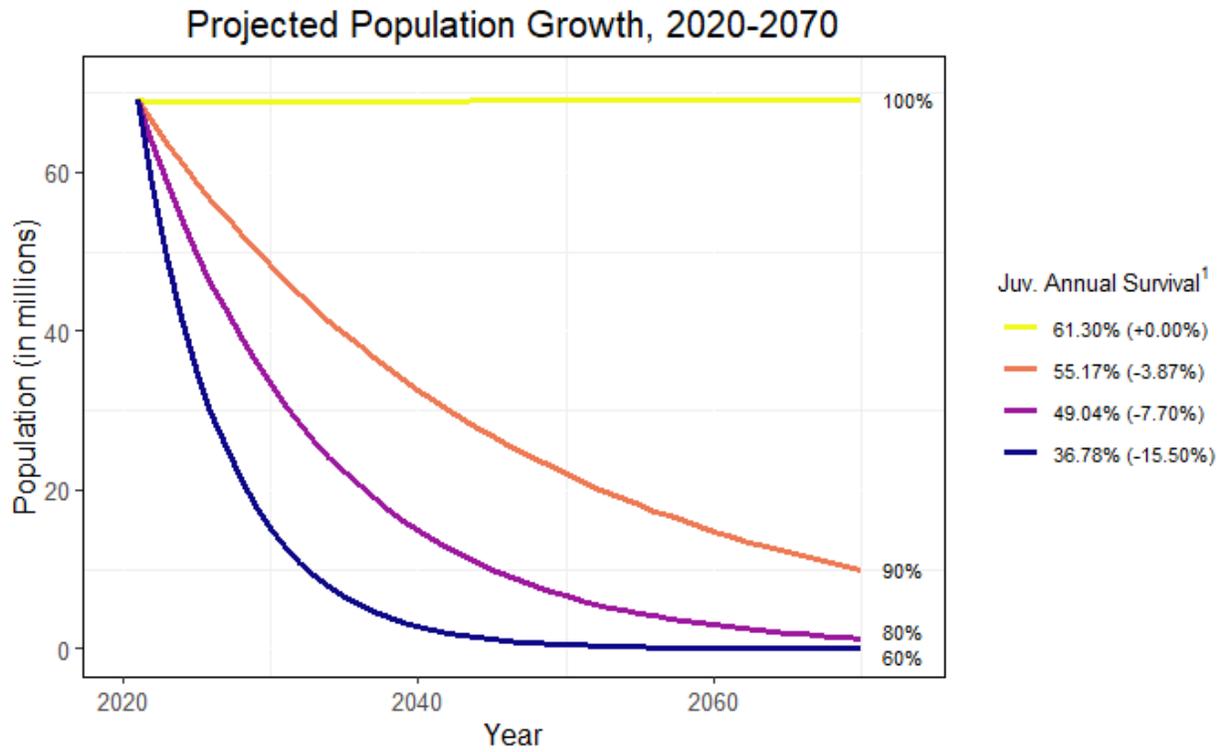
Known Fate | n = 53



**Figure 5.** The cumulative survival rate (solid line) and DSR (dashed line) over the first 20 days post-fledging for Common Grackle fledglings in Champaign County, Illinois during 2018-2019. Standard error is shown as gray shading for cumulative survival.

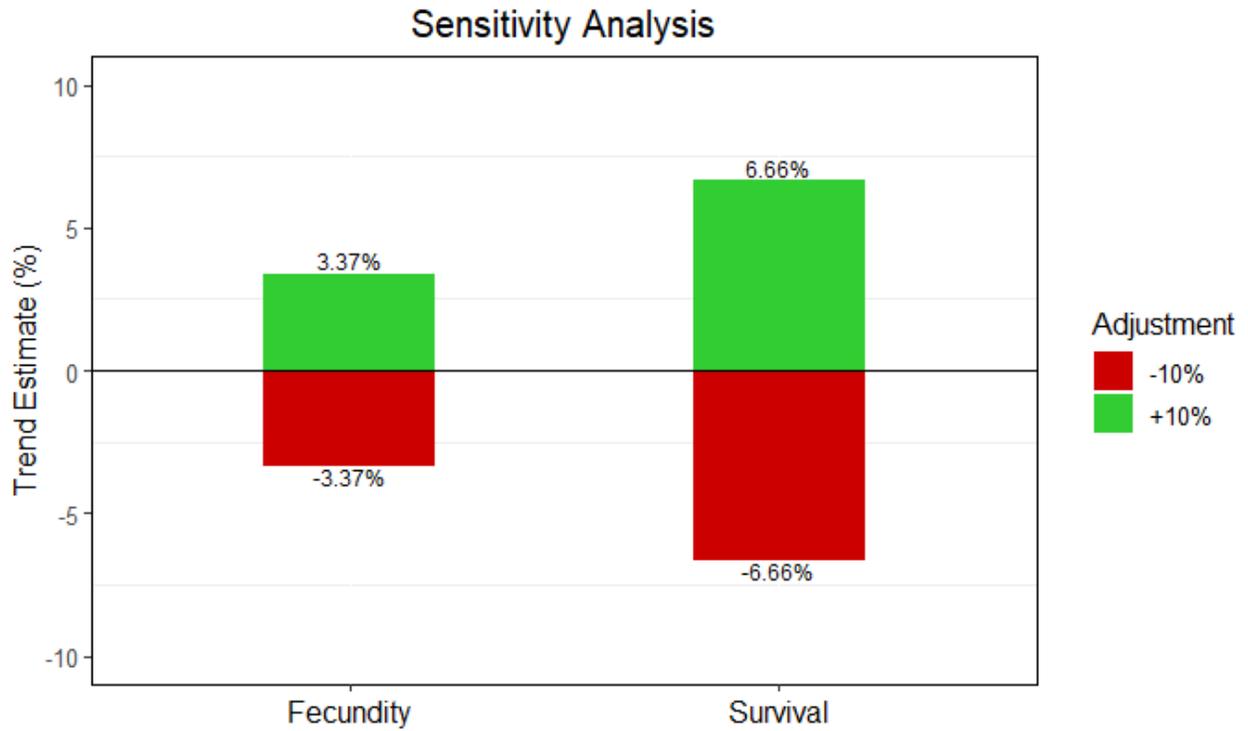


**Figure 6.** Trend lines showing Common Grackle projected population growth for a stable population, the global population, and the breeding population in Illinois, over the next 50 years.  
<sup>1</sup> Estimated juvenile and adult annual survival rates using demographic estimates from our study



**Figure 7.** Trend lines showing Common Grackle projected population growth for four estimates of juvenile survival (labeled as % of adult survival) over the next 50 years.

<sup>1</sup> Trend estimates in parentheses



**Figure 8.** A simple sensitivity analysis showing the relative influence of 10% adjustments in Common Grackle fecundity (clutch size, fledge rate, post-fledging survival, juvenile survival) and survival (adult survival) on population growth.

## APPENDIX A: PARTIAL LIFE-CYCLE MODEL R CODE

The following R code was used to predict Common Grackle juvenile and adult survival from demographic data collected by our study and trend estimates collected by the Breeding Bird Survey. It is a formulaic adaptation of a matrix-style partial life-cycle model and produces simulated data for 50 years of population growth. To use, copy the code into R and begin by providing the model with inputs for each variable (# of simulations, # of years, clutch size, fledge rate, post-fledging survival, juvenile survival, and adult survival; lines 10 to 17) under SETUP. Save your inputs by running line 8. Next, under SIMULATION, you can *optionally* adjust the number of hatch year (HY) and after hatch year (AHY) birds you want in your initial population (lines 43 and 44) and adjust environmental stochasticity (lines 47 to 51). Start a simulation run by running line 41. You can explore the simulated results on your own or run line 85 under RESULTS to view the average annual trend estimate (% change), average demographic distribution, and average population count, by year.

```
# SETUP

if(T){
  # inputs
  simulations <- 1000
  years <- 50
  c <- 1 # counter
  iClutch <- 4.255 # clutch size
  iFledge <- 0.481 # fledge rate
  iPostfledge <- 0.617 # post-fledging survival
  iJuvenile <- 0.570 # juvenile survival
  iAdult <- 0.570 # adult survival
  # trackers
  tEggs <- vector()
  tFledglings <- vector()
  tJuveniles <- vector()
  tHY <- vector()
  tAHY <- vector()
  tBreeders <- vector()
  # outputs
  oChange.p <- vector()
  oHY.p <- vector()
}
```

```

# sim means
mChange.p <- vector()
mHY.p <- vector()
# data frames
dfSims <- as.data.frame(matrix(nrow = simulations, ncol = 7))
colnames(dfSims) <- c("Year", "Breeder", "Eggs", "Fledglings", "Juveniles", "HY
Breeder", "AHY Breeder")
rm(dfTrend) # won't be found the first run
}

# SIMULATION

for(sim in 1:simulations){
  # presets
  HY <- 21000000 # initial number of HY birds
  AHY <- 48000000 # initial number of AHY birds
  tBreeder[1] <- HY + AHY
  # stochasticity
  rClutch <- rnorm(years, iClutch, 0.0025)
  rFledge <- rnorm(years, iFledge, 0.005)
  rPostfledge <- rnorm(years, iPostfledge, 0.005)
  rJuvenile <- rnorm(years, iJuvenile, 0.005)
  rAdult <- rnorm(years, iAdult, 0.005)

  for(yr in 1:years){
    # annual growth
    c <- tBreeder[yr]
    tEggs[yr] <- c <- (c/2) * rClutch[yr]
    tFledglings[yr] <- c <- c * rFledge[yr]
    tJuveniles[yr] <- c <- c * rPostfledge[yr]
    tHY[yr] <- HY <- c * rJuvenile[yr]
    tAHY[yr] <- AHY <- tBreeder[yr] * rAdult[yr]
    # trackers
    tBreeder[yr+1] <- tHY[yr] + tAHY[yr]
    oHY.p[yr] <- tHY[yr]/(tHY[yr] + tAHY[yr])
    oChange.p[yr] <- (tBreeder[yr+1] - tBreeder[yr])/tBreeder[yr]
  }

  # sim means
  mChange.p[sim] <- mean(oChange.p)
  mHY.p[sim] <- mean(oHY.p)
  # data frames
  tBreeder <- tBreeder[-51]
  dfPopulation <- cbind(1:50, tBreeder, tEggs, tFledglings, tJuveniles, tHY, tAHY)
  if(!exists("dfTrend")){
    dfTrend <- tBreeder
  } else{
    dfTrend <- cbind(dfTrend, tBreeder)
  }
  dfSims[sim,] <- colMeans(dfPopulation, na.rm = TRUE)
}

```

```
# RESULTS

if(T){
  print(mean(mChange.p)) # trend (annual % change)
  print(colMeans(dfSims, na.rm = TRUE)) # average demographic distribution
  print(rowMeans(dfTrend, na.rm = TRUE)) # average population count (yearly)
}
```