

SEASONAL AND ANTHROPOGENIC FACTORS PREDICT BREEDING SUCCESS IN BARN SWALLOWS (*Hirundo rustica*) IN SHARED GREENSPACE

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Abstract—Barn Swallows (*Hirundo rustica*) benefit from a complex relationship with humans and their settlements, through these birds' ability to construct mud nests on artificial structures and feed in the open fields created for diverse human activities. However, nesting in close proximity to humans comes with inherent risks, and even passive recreational activities can have negative consequences for wildlife. This study aimed to understand the impact of different intrinsic and extrinsic factors on a population of the North American Barn Swallow (*H. r. erythrogaster*) and its reproductive success in shared greenspace with humans to help inform suitable management strategies. We analyzed three metrics known to be or potentially related to breeding productivity in an urban public parkland over two years, including clutch initiation dates and anthropogenic disturbance levels. Results from the first, but not the second year, demonstrated that earlier nesting dates were positively related to seasonal reproductive success. Nest site use, through the distance of nests inside structures was a positive predictor of chick survival rate in the first but not in the second year. Also, some metrics of human disturbance levels were found to negatively correlate with the total number of eggs laid per season and the proportion of eggs that produced fledglings in one of the two years but were not significantly related to various other metrics of seasonal breeding success. Monitoring of additional seasons of Barn Swallow nesting success in this site and other shared greenspaces is recommended to better understand the relationships between intrinsic and extrinsic factors towards formulating management recommendations.

Keywords: aerial insectivore, anthropogenic disturbance, clutch initiation date, mud-nesting, passerine, recreational ecology, seasonal onset

The Barn Swallow (*Hirundo rustica*) has become the most widespread of all swallow species and breeds on five continents. These birds are now a common sight over grassy fields and a well-researched study organism in avian research,

particularly regarding behavioral and physiological adaptations and ongoing evolutionary processes (Scordato and Safran 2014).

Ornithologists credit the Barn Swallow's expansive breeding range to its nearly obligatory relationship with human settlements. These birds' ability to construct mud nests on artificial structures, such as buildings, bridges, and barns, has enabled them to capitalize on millennia of human expansion (Scordato and Safran 2014). These aerial insectivores also readily take advantage of the abundant food supply in the farmlands and open greenspaces that accompany civilization (Osawa 2015). Despite these benefits, living amidst humankind poses an inherent risk to wildlife, and emerging evidence in recreational ecology suggests that even passive human activities can significantly disrupt social and breeding behaviors within otherwise healthy ecosystems (Marzano and Dandy 2012).

In contrast to the productive literature on the breeding biology of the Barn Swallow, few studies have reported on how increasing levels of human disturbance might impact the productivity of human-commensal populations of this species. Our work sets out to examine the interaction between the known fitness benefits of earlier nesting in Barn Swallows (Safran 2004; Safran 2006), and the potential detrimental impacts of raising offspring in the presence of humans. The applications of this research may, in turn, inform management decisions in shared greenspace with humans of this federally protected species' populations.

Clutch Initiation Dates

In the now-landmark studies, R.J. Safran investigated the causes and consequences of seasonal productivity in Barn Swallows (Safran 2004; Safran 2006). She reported both a correlative and a causal positive relationship between clutch initiation date and annual reproductive success. Specifically, reusing surviving nests from previous years enables (newly settling) Barn Swallow pairs to breed earlier than those that (need to) construct new nests at the start of a season (Safran 2004). Constructing a swallow mud nest is estimated to take approximately 1000-2000 journeys between the muddy soil and the nesting sites (Ramstack et al. 1998), and the resources of time and energy expended building the nest are thus not without cost. Accordingly, pairs that were allowed to reuse old nests have first clutch initiation dates an average of 12 days earlier than pairs that were experimentally forced to build new nests (Safran 2006).

In turn, earlier first breeding can be critical because it increases the probability of having a second clutch the same season (Safran 2004) and is a predictor of increased overall seasonal reproductive success (Safran 2006). Specifically, Barn Swallows that reused old nests exhibited nearly a 25% increase in their productivity compared to new-nest builders regardless of individual age and whether or not the breeding pair was new to the site (Safran 2004).

Recent observational research also suggests that another advantage to nesting earlier in Barn Swallows may be that it provides them with the availability of

feathers used for nest-lining with fewer detrimental microbes (Rubaiee et al., 2018). Overall, nesting earlier in the season is of such fitness advantage to Barn Swallows that first-time breeders take advantage of the earlier-nesting opportunities through settling at breeding sites where they can reuse already existing old nest(s) (Safran 2006).

Anthropogenic Disturbance

There has been a considerable amount of research into the effects of humankind's disturbance on other species of wildlife, including songbirds in particular. A review of studies (1999-2010) focusing on the effects of human presence on wildlife found that people have both direct and indirect negative impacts on commensalist animals, even when people are unaware of the wild animal companions (Marzano and Dandy 2012).

Specifically, loud anthropogenic noise has been linked to nest abandonment in some bird species, and various forms of common recreational activities, including feeding attempts, photography, dog walking, and bicycle riding, have been found to disturb various species of songbirds (Lowry et al. 2011; Marzano and Dandy 2012). Passive recreation in shared greenspace, such as hiking, has also been found to alter avian habitat use and impact the choice of their breeding sites (Lowry et al. 2011). The presence of humans on a regular basis can have unforeseen effects on nesting passerines as animals can respond to people as potential predators in their natural setting (Marzano and Dandy 2012). These effects may be either limited in duration (Lowry et al. 2011) or become exacerbated over time (Sirot 2010).

One of the most immediate effects of human disturbance is the birds' startle response that results in fleeing, often from the nest or other safe location (Lowry et al. 2011). This directly costs birds both time and energy and also risks exposure to actual predatory threats (Marzano and Dandy 2012). It can also leave any unattended eggs or chicks more vulnerable to nest predators (Lowry et al. 2011).

Lasting impacts of human presence in avian habitats often include moderate to drastic behavioral changes, particularly regarding avian antipredator responses (Marzano and Dandy 2012). Accordingly, studies have found that individual birds in urban environments were bolder and more adapted to loud noises, demonstrating delayed flight responses and allowing humans to approach more closely before initiating a flight response (Sirot 2010), compared to individuals of the same species living in rural or unmodified environments (Lowry et al. 2011).

Assuming that Barn Swallows are susceptible to similar anthropogenic pressures as other passerines and that their proximity to urbanization is not without cost, there must be considerable valuable resources for swallows to settle and concentrate at and around human settlements. However, whereas swallows are quick to take advantage of concrete structures to be used as nesting substrates, yet fully urban environments fail to provide adequate food supplies, and accordingly, Barn Swallow nest density is negatively correlated with the urbanization within their occupied landscape (Osawa 2015). Instead, these aerial

insectivores (Ramstack et al. 1998) benefit from feeding grounds near their nesting sites, with ample amounts of flying insects; accordingly, Barn Swallows' nest density is positively correlated with the presence of rivers, farmlands, and other greenspaces adjacent to human dwellings (Osawa 2015).

Here we set out to gauge the effects of human visitors on the overall productivity of a Barn Swallow population in an urban parkland. Measuring the number of offspring animals produced during the course of a breeding season has become a well-established method for evaluating the impact of human presence in nesting wildlife (Hodson et al. 2010; Kight and Swaddle 2007). By comparing the annual reproductive success of Barn Swallows across subareas of varying degrees of anthropogenic disturbance within the same general nesting grounds provides an ideal opportunity to study the effects of human influence while controlling for confounding variables such as food supply levels and other environmental fluctuations. Specifically, our *predictions* were:

1. *Earlier nesting dates will be positively correlated with Barn Swallow reproductive success;*
2. *Increased levels of anthropogenic disturbance will have a negative impact on Barn Swallow reproductive success; and*
3. *Increased distance of Barn Swallow nests from the entrance of concrete structures (and, thus, further from human activity) will be positively correlated with reproductive success.*

METHODS

Location

The study site was 136-acre peninsula in Bayside, New York, USA, within the New York City borough of Queens. The area had been used as farmland prior to its acquisition by the United States government in 1857 for the purposes of constructing a fortification. The base itself became known as Fort Totten until its official closing in 1995 (New York City Landmarks Preservation Commission [NYCLPC] 1999) and the property has since come under the control of various city agencies with 60.39 acres devoted to public greenspace known as Fort Totten Park in 2005.

The site includes roads, wooded areas, and several large sections of grass-covered open space, which may provide essential feeding grounds for the aerial insectivores (Osawa 2015). Historic structures from the land's time as a military installation remain throughout the park (NYCLPC 1999), and the Barn Swallow population nests exclusively inside the decommissioned fortifications toward the northern section of the peninsula.

The majority of nests monitored during the study, ($n = 10$ in 2016; $n = 8$ in 2017) were located within repurposed munition tunnels known as Torpedo Magazines (see Fig. 1). These concrete chambers were built in 1876 to store floating harbor mines, known then as torpedoes (Beyer Blinder Belle Architects

& Planner LLP [BBBAP] 2000), and are covered by an artificial berm such that they are functionally underground. Entranceways to the structures face southward, and are the sole means of accessing the magazines.



Figure 1. Illustration of the study's nesting site entrances including the Visitors' Center (left) and torpedo magazines (right). Illustration by Melissa Zavala.

Both study years also had two active nests inside the concrete passageway that is buried beneath the same artificial berm as the adjacent magazines, known as the Transport Tunnel, located directly to the west of the first torpedo magazine. The remaining active nests ($n = 1$ in 2016; $n = 3$ in 2017) were located inside nearby Endicott Period batteries completed in 1900, named Battery Baker and Battery Mahan (NYCLPC 1999). Each Endicott battery is a two-tiered structure composed of reinforced concrete that formerly held disappearing guns on the second level and storage magazines on the first level (BBBAP 2000). All Barn Swallow nests were built on the lower levels of these batteries.

Although no official records of the Barn Swallows were maintained prior to the ownership of the fortifications having been transferred to New York City, there are photographs of nests dating back to 2000 at some of the same locations as above (BBBAP 2000). It appears, therefore, that this is a breeding site-faithful species (Safran 2004), and had established a breeding population at least 16 years prior to this study.

Protocol

The study was conducted from 1 May through 31 August for two breeding seasons (2016 and 2017). Nests were monitored every third day using an automotive telescopic-inspection mirror to gain visibility to high nests. An iPhone was used to take photos and document nest content. Nests were generally checked between 18:00 and 20:00 each day, but no earlier than 15:00 and never later than nightfall.

First Clutch Initiation Dates

During monitoring sessions, each nest was checked for freshly layered mud, the addition of grasses, and/or the addition of down feathers, the last of which indicating that a mated pair was prepping to lay eggs. The presence and number of eggs and/or chicks were counted and recorded, documenting the dates each item first appeared. We considered newly discovered eggs to have been laid on the day found because most passerines lay at dawn or in the early morning hours (Wiebe et al. 2007). As in previous research studying the effects of egg laying dates in Barn Swallows (Safran 2004; Safran 2006), the appearance date of a pair's first egg of the season is termed here as that pair's first clutch initiation date (hereafter FCID). The appearance of a new egg in the nest after the first breeding attempt had ended (either via fledging or predation) is considered as the pair's second clutch initiation date. We enumerated FCID as the number of days since 1 January of each year (Jan 1 = Day 1).

Human Disturbance Levels

To gauge whether human presence and recreational activities are impacting the reproductive success of the Barn Swallows, each nest site was *a priori* categorized into one of three levels based on the amount of actual and potential human disturbance level (HDL) in its location. The distribution of the nests within Fort Totten Park provides a valuable opportunity to examine the reproductive success of the birds because nests are all within the same general area, but within sections of varying degrees of human interference. All the Barn Swallows in the park likely share the same foraging space, food availability, weather events, and other conditions, which helps control for confounding variables.

The level HDL1 consisted of sections of the Fort with a minimal amount of human interference. These sections are gated from the public so that only the data collector (JC) and a handful of park employees had access. These magazines are locked, preventing anyone from approaching the nests and give the birds a much higher degree of privacy than nests located in other areas.

HDL2 areas were those of moderate human disturbance and consisted primarily of sections that were usually vacant but where employees, but not the public, could be present for extended periods. These areas included magazines used by maintenance staff for storage with varying periods of commotion, ranging from a few minutes to a couple hours; however, the area could also be vacant for several days at a time.

HDL3 areas were those with ongoing human disturbance. These areas were open to park patrons two to five days per week, and almost always had people present during daylight visiting hours. Members of the public are encouraged to enter these areas to educate and immerse themselves in the history of the park and are required to sign in at the Visitors' Center in order to do so. From May through August the Visitors' Center's log showed 1585 park patrons being granted admittance into these sections of the fort in 2016, and 3073 patrons in 2017.

Finally, it is important to note that the inception of the Barn Swallow population and its establishment as a nesting site occurred prior to our categorization of the HDLs. Though not a manipulative experiment, through altering the usage of these areas after the sites were originally chosen by the swallows, the humans working in the park inadvertently created the varying anthropogenic disturbance levels prior to the onset of the study.

Tunnel Entrance to Nest Distances

We also measured and explored whether the distance from the entrance of a tunnel to a nest (hereafter: TEND, Tunnel Entrance to Nest Distance), and thus further away from potential disturbances, had a positive influence on reproductive success.

Statistical Analyses

All correlation tests were performed using Microsoft Excel or via VassarStats (<http://vassarstats.net/kw3.html>). We used Student's t-tests for analyses of reproductive success and/or effects of TENDs. Non-parametric analyses were used to compare HDLs, due to the small sample size, and were performed using Kruskal-Wallis tests. No individuals were captured or marked between seasons and all analyses were conducted separately for 2016 and 2017 so as to avoid inflated sample sizes due to potentially resampling the same breeding philopatric individuals.

To determine if earlier nesting has a positive relationship to the likelihood of laying a second clutch, correlation analyses between known FCID and the number clutches each pair laid in each season were performed. To examine if earlier nesting might increase a pair's reproductive fitness, correlation analyses were performed between FCID and total number of eggs laid (hereafter: Tot Eggs), the total number of offspring surviving to fledge (hereafter: ARO, Annual Reproductive Output), and the percentage of eggs in a season surviving to fledge in each season (hereafter: SR, Survival Rate).

To determine if the HDL of nesting sites influenced reproductive success in each year, nest productivity in each of the three HDLs was compared using Kruskal-Wallis tests to FCID, Tot Eggs, ARO, and SR.

To determine if TEND is positively correlated with reproductive success, seasonal correlation analyses were performed between the TEND and FCID, Tot Eggs, ARO, and SR.

RESULTS

Prediction 1: Earlier FCID is positively associated with seasonal reproductive success.

Correlation analyses did not reveal statistically significant relationships between FCID and the number of clutches in either 2016 ($r(11) = -0.343, p = 0.252$) or 2017 ($r(10) = -0.442, p = 0.150$; Fig. 2). Barn Swallow pairs had statistically similar FCIDs in 2016 ($M = \text{Day } 143.46, SD = 11.67$) as in 2017 ($M = 149, SD = 11.38; t(23) = -1.2, p = 0.242$).

FCID showed no significant relationship with Tot Eggs in either the 2016 ($r(11) = -0.458, p = 0.115$) or in the 2017 season ($r(10) = -0.539, p = 0.071$; Fig. 3). In both years, those pairs that laid second clutches ($M = 9.13, SD = 1.642$) produced more eggs than pairs that laid only a single clutch ($M = 4.56, SD = 0.705; t(24) = 10.08, p < 0.001$).

Pairs with earlier FCIDs were significantly more likely to produce an increased ARO in 2016 ($r(11) = -0.653, p = 0.016$; Fig. 4), whereas this relationship was again positive but not significant in 2017 ($r(10) = -0.554, p = 0.062$; Fig. 4).

FCID showed a significantly negative correlation with offspring SR ($r(11) = -0.656, p = 0.015$; Fig. 5) in 2016, illustrating that earlier nests fledged a greater proportion of their eggs hatched, and a non-significant relationship with pairs' SR in 2017 ($r(10) = -0.396, p = 0.201$; Fig 5).

Prediction 2: HDL has negative relationship with seasonal reproductive success.

There was no statistical relationship between HDL and FCID in either 2016 ($H(2) = 0.17, p = 0.919$) or in 2017 ($H(2) = 4.52, p = 0.104$; Fig. 6). There was also no significant relationship between HDL and Tot Eggs in 2016 ($H(2) = 3.2, p = 0.19$; Fig. 7). The 2017 season, however, demonstrated a significantly negative relationship between HDL and Tot Eggs ($H(2) = 8.4, p = 0.015$; Fig. 7): increased human interference was inversely related to the total number of eggs a Barn Swallow pair produced per season.

The relationship between nests' HDL and ARO was not significant in either 2016 ($H(2) = 2.7, p = 0.25$; Fig. 8), or in 2017 ($H(2) = 4.7, p = 0.095$; Fig. 8).

HDL and SR did not have a significant relationship in either 2016 ($H(2) = 1.3, p = 0.50$) or in 2017 ($H(2) = 4.04, p = 0.133$; Fig. 9).

Prediction 3: TEND will have a positive correlation with seasonal reproductive success.

The relationship between TEND and FCID was not significant in both 2016 ($r(11) = -0.387, p = 0.192$) and in 2017 ($r(10) = 0.382, p = 0.219$). The correlation between TEND and Tot Eggs was not significant in either 2016 ($r(11) = -0.037, p = 0.907$) or in 2017 ($r(11) = -0.027, p = 0.930$).

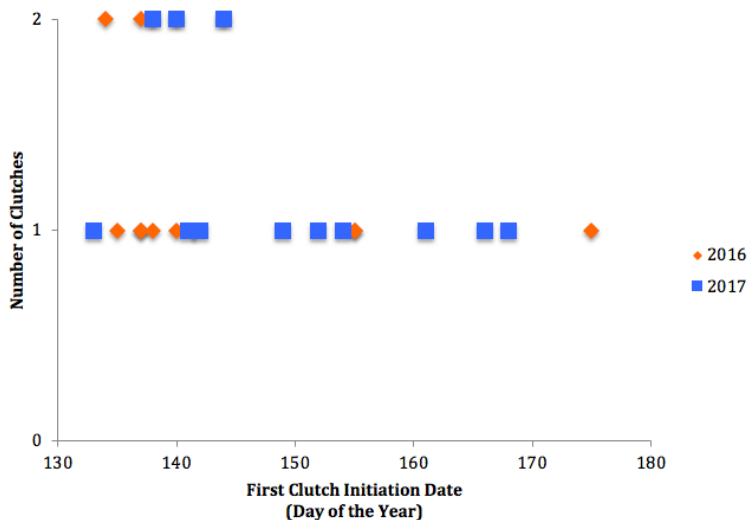


Figure 2. Scatterplot showing the relationship between FCID (First Clutch Initiation Date) and Number of Clutches in 2016 and 2017.

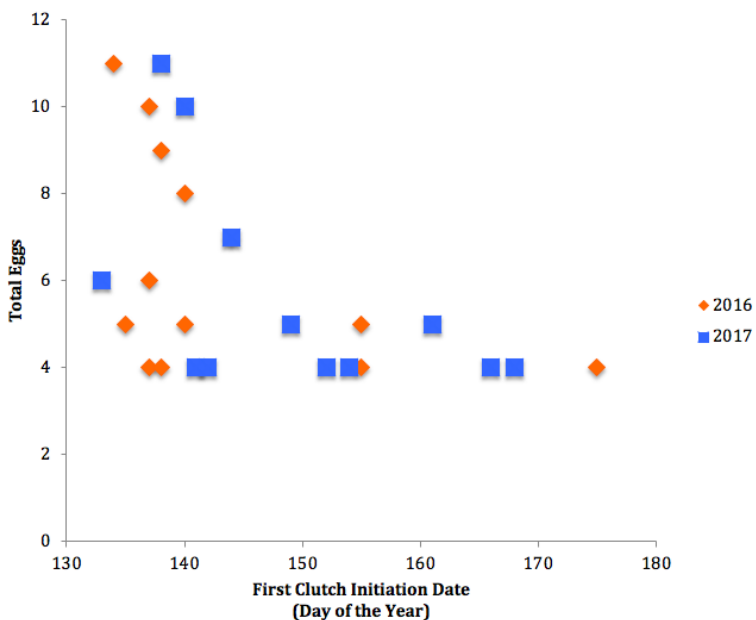


Figure 3. Scatterplot showing the relationship between FCID (First Clutch Initiation Date) and Tot Eggs (total eggs laid) in 2016 and 2017.

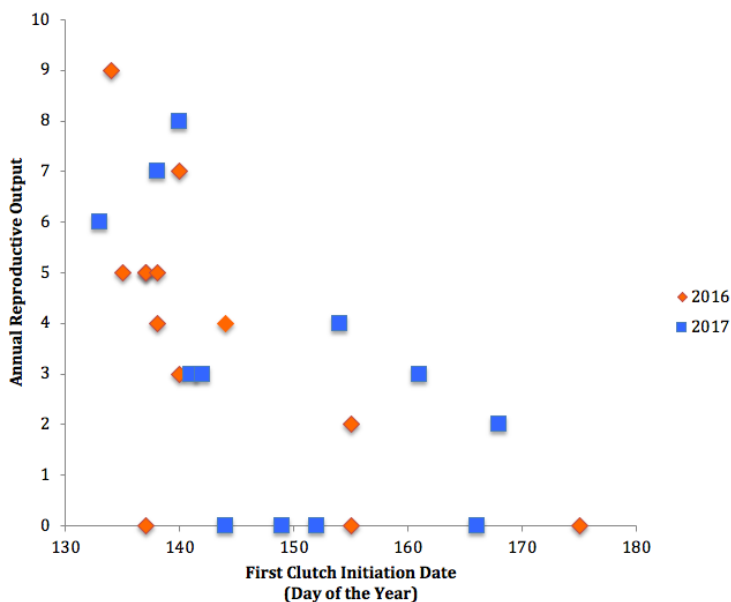


Figure 4. Scatterplot showing the relationship between FCID (First Clutch Initiation Date) and ARO (Annual Reproductive Output) in 2016 and 2017.

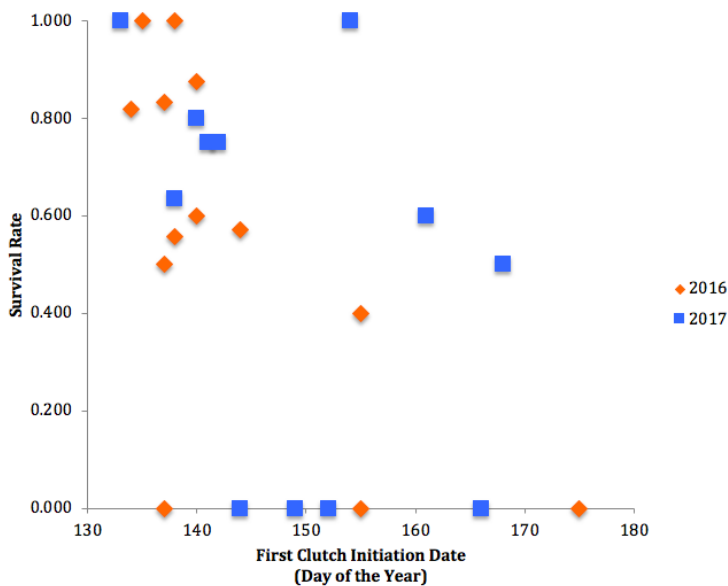
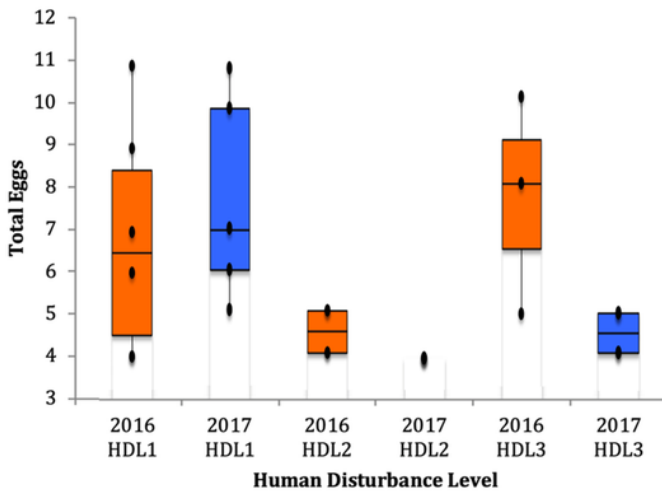
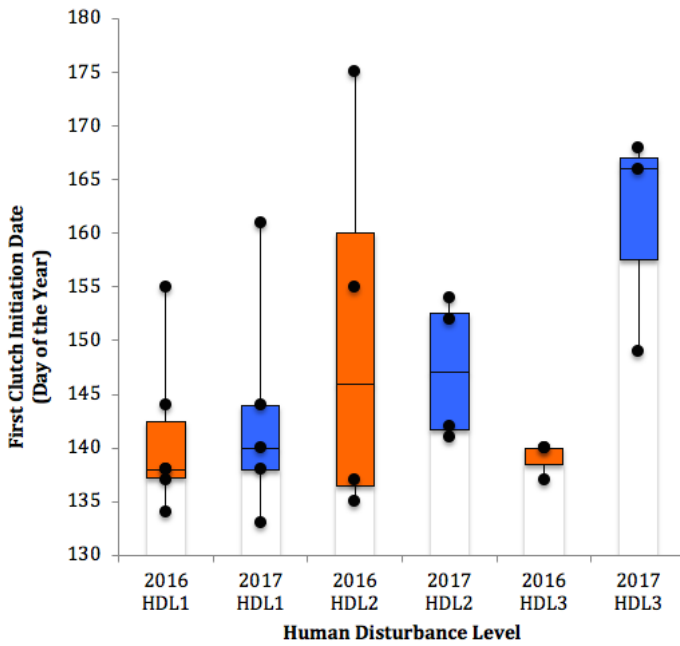
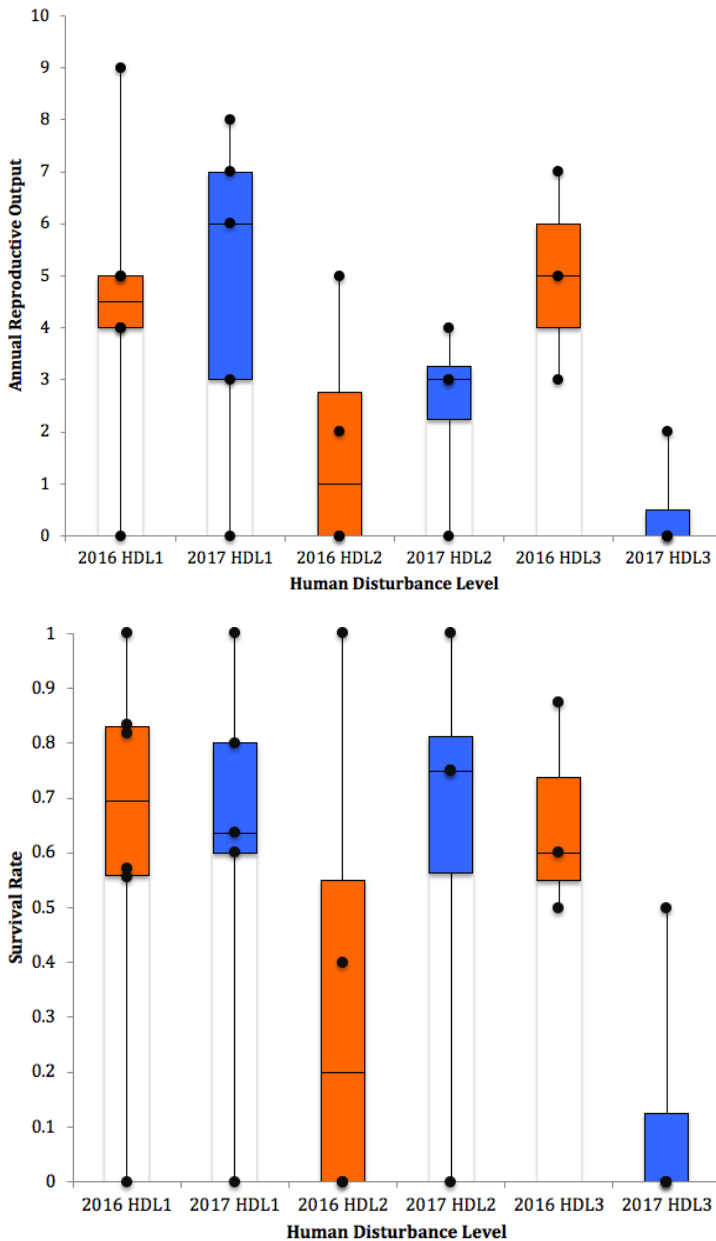


Figure 5. Scatterplot showing the relationship between FCID (First Clutch Initiation Date) and SR (Survival Rate) in 2016 and 2017.



Figures 6 and 7. Ranges of FCIDs (First Clutch Initiation Dates; top) and ranges of Tot Eggs (total eggs laid; bottom) for each HDL (Human Disturbance Level) in 2016 and 2017.



Figures 8 and 9. Ranges of ARO (Annual Reproductive Output; top) and ranges of SR (Survival Rate; bottom) for each HDL (Human Disturbance Level) in 2016 and 2017.

There was no significant correlation between TEND and ARO in either 2016 ($r(11) = 0.323, p = 0.283$) or in 2017 ($r(11) = 0.402, p = 0.172$). However, TEND had a significantly positive correlation with SR in 2016 ($r(11) = 0.599, p = 0.031$) but not in 2017 ($r(11) = 0.500, p = 0.081$; Fig. 10).

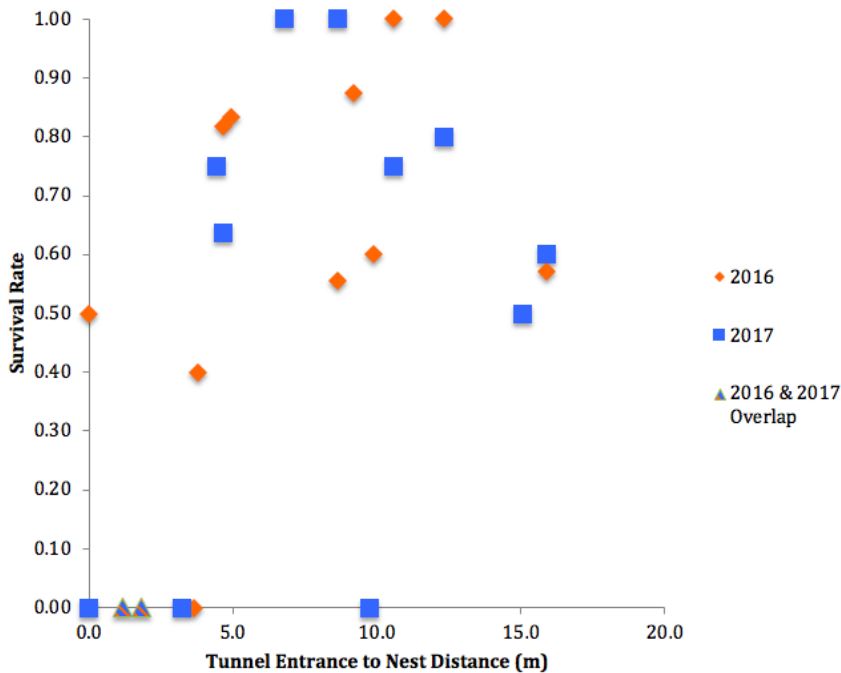


Figure 10. Scatterplot showing the relationship between TEND (Tunnel Entrance to Nest Distance) and SR (Survival Rate) in 2016 and 2017.

DISCUSSION

First Clutch Initiation Date

In our sample, FCIDs were not found to be a predictor of the number of clutches a pair laid in a breeding season; nevertheless, FCID patterns positively covaried with other metrics of seasonal breeding productivity. The timing of the earliest FCID of any pair at our study site was also consistent for both years within one day of each other (Days 134 and 133, respectively), and both years saw no pair with a FCID after Day 144 produce a second clutch (Fig. 2). This is suggestive of consistent onset of the laying season across our two study years, and supports that laying too late in the season prevents a pair from producing a second clutch (Safran 2006). In turn, pairs that laid second clutches produced consistently more eggs than those pairs that laid a single clutch in both years (Safran 2004).

In the first year of our study, we detected significant correlations between FCID and the nests' ARO and SR, supporting the hypothesis that earlier nesting (perhaps through reusing the previous year's nests) by Barn Swallows is a positive predictor of seasonal reproductive success. These findings are consistent with those of Safran (2006) and are valuable data to inform management of Barn Swallow populations in parkland breeding sites and other shared natural and artificial greenspace areas, where old nests from the previous year may be prone to intentional or accidental removal by park staff.

Results of the 2017 season suggested that the ARO and SR were not associated with a pair's FCID; however, there is evidence that this discrepancy is the result of varying environmental factors between seasons. Foremost, Barn Swallows tended to nest over a week later in 2017 than in 2016 (Figs. 2-5). In turn, in both years, once a swallow pair's FCID fell after the 144th day of the year, birds did not produce a second clutch. Because a pair's ARO is dependent on their ability to produce multiple clutches (Results), this generally delayed timing of FCIDs in 2017, compared to those in 2016, and could be the reason for the inconsistent statistical relationship of FCID and ARO between the two years of the study.

The interannual fluctuation in FCID's influence on SR, however, was also likely affected by an increase of interaction from other birds in the nesting site. The 2016 season lost three clutches to depredation, perhaps by Common Grackles (*Quiscalus quiscula*), which were regularly observed near the torpedo magazines entrances. In addition to the continued presence of grackles, the 2017 season identified an additional threat to the Barn Swallow eggs. House Wrens (*Troglodytes aedon*) took up residence in the park. That year had five Barn Swallow clutches fail due to interference from wrens where two of those nests were filled with twigs following the destruction of the eggs. House Wrens use these tactics to prevent insectivorous competitors from re-nesting (Finch 1990). The 2017 season also saw three additional clutches (two from the same nest) eliminated by an unseen species, presumed to be again grackles, and one nest destroyed by human vandals.

These varying environmental factors of delayed overall FCID and disparate depredation levels are the primary reasons for the inconsistency between seasons and represent, in part, why we have chosen not to pool the two years' worth of data. Because the components contributing to the reproductive success of the Barn Swallows were distinct in each of the seasons, combining the two seasons would misrepresent the influences of the population's statistics. Should the study be continued, it would be unsurprising for one to find additional season(s) where the FCID was significantly and negatively correlated with the ARO and the SR and other seasons without these statistical effects.

Human Disturbance Level

We did not find any evidence that FCIDs were influenced by HDLs in 2016 or 2017 (Fig. 6), suggesting the birds start laying eggs at approximately the same

time regardless of exposure to humans or noise levels. These findings are consistent with our ad hoc observations during monitoring. When people are within a few meters of an active nest, the parent Barn Swallows were hesitant to approach and instead opted to cause distraction through alarms or flying in circles.

There was also no association between HDL and Tot Eggs for the 2016 season (Fig. 7). Barn Swallows were not observed expending additional energy by distracting potential predators prior to laying their eggs, and it follows that increased human activity would not inflict negative consequences upon the birds before eggs were laid to reduce clutch size. In contrast, however, HDL was significantly and negatively associated with the metric of Tot Eggs during the 2017 breeding season, (Fig. 7). This discrepancy may have stemmed from the contrasting environmental factors between seasons, such as the delayed laying and fewer pairs producing second clutches in 2017. It would be interesting to see whether this variation in egg outputs is more or less likely to occur when there is a later median FCID and shall require further data collection in additional years.

The data also suggested that if HDL were to affect ARO or SR, its influence is minor (Fig. 8-9), or there are other factors that are overshadowing its effects. One such factor outside the control of the study was nest depredation. In 2016, 16.67% of clutches were lost to depredation, whereas in 2017 31.25% of the clutches were lost due to inference from other birds. Studying additional years with fluctuating predation levels would indicate more clearly whether HDL directly affects seasonal reproductive success, or perhaps works through a mediating factor of the varying the levels of interspecific avian predation and competition.

Tunnel Entrance to Nest Distance

The distance to nests from the entrance of the magazines or tunnels that the Swallows built their nests inside was examined as a more direct and objective proxy metric of whether noise and other activities attributable to people outside the structures were a contributing factor to swallow reproductive success. We found no evidence to suggest that TEND statistically affected a pair's FCID, Tot Eggs, or ARO. However, TEND was a positive predictor of SR in 2016, and the correlation was also still positive but not quite significant the following season (Fig. 10). Four clutches in 2016 had an SR of 0%, all of which had relatively small TEND values. Reasons for clutch failures included one instance of predation, two instances of eggs failing to hatch, and one instance of nest abandonment. The latter three of these events had no visible causes and could be correlated with stress from exposure proximity to humans. These results thus support the prediction that reproductive success (through SR) is greater with further distance away from anthropogenic activities.

In comparison, the relationship between TEND and SR in 2017 was not statistically significant (Fig. 10). This inconsistency is perhaps again indicative that varying ecological conditions (that we were unable to account for during the study) can be more influential than human interference. Specifically, there were

five nests that had an SR of 0% in 2017. Unlike the previous year, however, these failed clutches were suspected to be not attributed to background patterns of human disturbance because all of the clutch losses were due to destruction from other birds or direct vandalism. As seen above, the data indicate that the monitoring of additional years is recommended to fully understand the relationship of these two variables across multiple breeding season.

Limitations of the Study

While the research revealed several statistical predictors of swallow reproductive success, the study's primary limitations stemmed from its small sample size both within and across breeding seasons. The unequal distribution of nests across different HDLs resulted in a data set that was necessary to be analyzed with conservative, non-parametric tests. Furthermore, without a means to exclude natural nest predators and competitors, varying levels of depredation and nest disruption between the two years of the study may have overshadowed the effects of our focal predictor variables. Finally, the shift towards later FCIDs in 2017, in addition to the statistical non-independence issue of individual birds potentially reusing the same nests across consecutive breeding seasons (Safran 2006), made it unsuitable to combine the two years' worth of data to increase statistical power in order to offset the small annual sample sizes.

Conclusions

Results from the 2016 season support our first prediction and reinforce findings by Safran (2006) that earlier nesting is a predictor of Barn Swallows' greater reproductive success via both ARO and SR. The putative mechanism is that there is a temporal cut-off date for producing second clutches, and pairs that produce second clutches produce more eggs than pairs that have time to lay only one clutch. Regarding anthropogenic effects, HDL was not found to directly influence Barn Swallow reproductive success in either season; except in 2017 when greater human interference was inversely related to the total number of eggs a Barn Swallow pair produced per season. However, HDL's generally small impact on other metrics of swallow reproductive success may have been overshadowed by other ecological factors, such as varying levels of nest depredation. The study implied that different types of predation in different HDLs may need to be explored in future studies. Finally, the results supported the hypothesis that larger TEND might positively affect Barn Swallow reproductive success through increased clutch survival rates.

Overall, despite the inconsistencies between the two years, this study contributes new insights into the various ecological and anthropogenic factors affecting annual reproductive success of Barn Swallows in shared greenspace and suggests several new directions for future studies.

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LITERATURE CITED

- Beyer Blinder Belle Architects & Planner LLP. 2000. *Fort Totten Battery: Historic Preservation & Interpretive Plan*. Bayside, NY
- Finch, D. M. 1990. Effects of predation and competitor interference on nesting success of House Wrens and Tree Swallows. *The Condor*, 92, 674–687.
- Hodson, J., Fortin, D., LeBlanc, M.-L., & Bélanger, L. 2010. An appraisal of the fitness consequences of forest disturbance for wildlife using habitat selection theory. *Behavioral Ecology*, 164, 73–86. doi: 10.1007/s00442-010-1691-4
- Kight, C. R. & Swaddle, J. P. 2007. Associations of anthropogenic activity and disturbance with fitness metrics of Eastern Bluebirds (*Sialia sialis*). *Biological Conservation*, 138, 189–197. doi:10.1015/j.biocon.2007.04.014
- Lowry, H., Lill, A., & Wong, B. B. 2011. Tolerance of auditory disturbance by an avian urban adapter, the noisy miner. *Ethology*, 117, 490–497. doi: 10.1111/j.1439-0310.2011.01902.x
- Marzano, M., & Dandy, N. 2012. Recreationist behaviour in forests and the disturbance of wildlife. *Biodiversity and Conservation*, 21, 2967–2986. doi: 10.1007/s10531-012-0350-y
- New York City Landmarks Preservation Commission. 1999. *Fort Totten Historic District: Designation Report*. Bayside, NY
- Osawa, T. 2015. Importance of farmland in urbanized areas as a landscape component for Barn Swallows (*Hirundo rustica*) nesting on concrete buildings. *Environmental Management*, 55, 1160–1167. doi: 10.1007/s00267-015-0457-5
- Ramstack, J.M., Murphy, M.T., & Palmer, M.R. 1998. Comparative reproductive biology of three species of swallows in a common environment. *Wilson Bulletin*, 110, 233–243.

- Al Rubaiee, Z., Al Murayati, H., & Møller, A. 2018. Arrival date and microorganisms in Barn Swallows. *Journal of Avian Biology*, 49, e01665. doi: 10.1111/jav.01665
- Safran, R. J. 2004. Adaptive site selection rules and variation in group size of Barn Swallows: individual decisions predict population patterns. *The American Naturalist*, 164, 121–131. doi: 10.1086/422198
- Safran, R. J. 2006. Nest-site selection in the Barn Swallow, *Hirundo rustica*: what predicts seasonal reproductive success? *Canadian Journal of Zoology*, 84, 1533-1539. doi: 10.1139/Z06-176
- Scordato, E. S., & Safran, R. J. 2014. Geographic variation in sexual selection and implications for speciation in the Barn Swallow. *Avian Research*, 5, 8. doi: 10.1186/s40657-014-0008-4
- Sirost, E. 2010. Should risk allocation strategies facilitate or hinder habituation to nonlethal disturbance in wildlife? *Animal Behaviour*, 80, 737-743. doi: 10.1016/j.anbehav.2010.07.014
- Wiebe, K. L., Koenig, W. D., & Martin, K. 2007. Costs and benefits of nest reuse versus excavation in cavity-nesting birds. *Annales Zoologici Fennici*, 44, 209-217.

