

Marsh M, Marsh, L, Jacobsen D, Tofle C, Bakker JD. 2026. Nesting success of the Commodore Park Great Blue Heron Colony, 2024–2023. *Northwest Science* 99(2): *in press*.

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Nesting Success of the Commodore Park Great Blue Heron Colony, 2014-2023

Running footer: Great Blue Heron Nesting Success

2 Tables, 5 Figures

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Abstract

Long-term and consistent data are necessary to understand phenomena such as the timing and success of reproduction. A Pacific Great Blue Heron (*Ardea herodias fannini*) colony in Seattle, Washington, was studied from 2014 to 2023. Citizen scientists observed the usage of 120 nest locations repeatedly throughout each nesting season. Between 38 and 76 nests were active in any year. Incubation began in the colony between March 6 and 22, depending on the year (mean = March 15). The start of incubation in individual nests differed strongly within years, often by multiple months. Most measured variables differed much more strongly within years than among years. Compared to nests in which incubation began later, nests that began to be used in the first half of the season experienced an average of 5 more days of incubation and 12 more days of rearing. Early nests were also significantly more likely to successfully produce chicks, though they produced the same number of chicks per successful nest as late nests. Overall, early nests produced a disproportionate number of the colony's chicks each year (mean = 61%). Colony chick production was driven largely by the number of nests in a year. Nest locations used in multiple years were significantly more likely to be selected early in the season and to be successful. Pacific Great Blue Herons appear to recognize differences in nest quality and to select locations with a high likelihood of success. This study also demonstrates the value of citizen science and long-term monitoring.

Key Points

- When Pacific Great Blue Herons began to incubate their eggs varied significantly among years, as did the length of the rearing period, but chick production per successful nest did not.

- Nests that began to be used early in the season were more likely to be successful than those that began to be used later in the season.
- Nests used in multiple years were more likely to be used early in the season and to be successful.

Keywords: *Ardea herodias fannini*, chick, incubate, nest, citizen science

Introduction

The Pacific Great Blue Heron (*Ardea herodias fannini*) is a nonmigratory subspecies of Great Blue Heron found on the Northwest coast of North America, particularly in the Salish Sea bioregion from Puget Sound, Washington through the Strait of Georgia, British Columbia. This subspecies is smaller than inland subspecies and nests earlier in the spring. Its population status is being monitored by British Columbia, where there has been a slow decline in fledgling production since the 1970s (Butler and Baudin 2000), and by Washington State, where the population declined in the early 2000s after increasing during the 1980s and 1990s (Stabins et al. 2006). In British Columbia, it is listed as a Species of Special Concern. In Washington, it is a Priority Species, with published management recommendations (Azerrad 2012).

Pacific Great Blue Herons usually nest in colonies of up to 500 pairs in trees close to nearshore feeding grounds; colony size has been observed to increase with the size of nearby eelgrass meadows (Butler 1997, Azerrad 2012). Colonial nesting can be risky for the population as reproductive effort is clumped and failure of a large colony can impact reproductive output for an entire subregion. Great Blue Heron colonies are dynamic, changing within and between years.

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In recent decades, a trend of fewer and larger Pacific Great Blue Heron colonies has been noted (Eissinger 2007) which appears to be driven at least in part by bald eagle (*Haliaeetus leucocephalus*) predation (Vennesland and Butler 2004, Jones 2013, Goulet et al. 2021).

When a colony is abandoned, the surviving birds are forced to nest elsewhere. Although human disturbance can result in colony abandonment (Carlson and McLean 1996, Vennesland & Norman 2006), Matsunaga (2018) noted three cases in which Grey Herons (*Ardea cinerea*) on Hokkaido, Japan, established new nesting colonies in more urban areas after disturbance by predators. Similarly, Butler (1997) noted instances in British Columbia of herons moving colonies to areas with human activity. Perhaps a lower predation risk in these urban areas compensated for human disturbances, or shoreline development reduced the herons' nesting and foraging habitat in undisturbed areas.

Colony dynamics are strongly affected by nesting success. For example, colony size can relate to the number of chicks fledged from successful nests in the previous year (Forbes et al. 1985), and fledging success is positively correlated with colony persistence (Butler et al. 1995). Nesting success can depend on factors such as when incubation begins and how much time the adults devote to incubation and to rearing. Earlier incubation results in more time within the season for adults to care for their offspring. Post-fledging parental care has been found to increase fledgling survival after independence (Grüebler & Naef-Daenzer 2010, López-Idiáquez et al. 2018).

Pacific Great Blue Herons, when first capable of flight, are not fed by the parents at foraging areas, though Butler (1997) reported fledglings returning on their own or following their parent back from foraging areas to be fed at the nest. Juvenile herons are significantly less efficient at

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foraging than adults, and continued feeding should help them maintain condition while they acquire skill.

Stabins et al. (2006) documented 13 colonies in western King County, Washington, in 2000. The study reported here began after apparent predation by juvenile bald eagles led to the abandonment of one of these colonies in April 2013. This colony consisted of 86 nests in the Kiwanis Memorial Wildlife Preserve, a deep, wooded, undeveloped ravine bordered by quiet residential neighborhoods of Seattle. Many of the herons that abandoned the Kiwanis colony joined a small colony (7 nests) 200 m away in Commodore Park; 55 new nests were built in this colony within two weeks of the abandonment of the Kiwanis colony. Commodore Park overlooks the Hiram M. Chittenden Locks on the Seattle Ship Canal, the busiest shipping lock in the United States and a Seattle tourist attraction. The colony occupies a grove of mature red alder (*Alnus rubra*) trees on a steep bluff rising from a seawall promenade, 120 m from the lock wall. The colony is visible to the public from the top of the rise, and the herons seem oblivious to foot traffic, so a citizen science effort was established to monitor nesting success in this urban colony.

This study was initiated by retired biologist Michael Marsh, PhD, and another individual, both of whom collected data throughout the study (2014–2023). Between 2015 and 2021, there were two to six volunteer citizen scientists per year. Interest spiked after the pandemic and there were 15 volunteers in 2022. Six of these individuals returned in 2023, for a total of 17 volunteers that year. Without these volunteers, we could not have gathered enough data for this study.

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Citizen scientists observed the usage of individual nests regularly throughout the nesting season and followed a monitoring protocol to record data. We drew on the frequency and detail of these observations to consider nest usage patterns and productivity for Pacific Great Blue Herons.

Specifically, in this paper we asked three questions: 1) How does the start of incubation differ among years and among nests? 2) How does the start of incubation relate to incubation period, rearing period, nesting success, and chick production, and do these patterns differ among years? 3) Do long-term nest usage patterns relate to the timing of incubation and to nesting success?

Methods

Field Observations

The Commodore Park colony is located in a 3.9-acre public park on the shoreline of Salmon Bay in Seattle, Washington. The colony was monitored using a variant of the protocol reported by Vennesland and Norman (2006). Nests and trees were recognized from photographs taken at 5 standard positions before full leaf out, with each tree and nest numbered on the photographs for reference by observers. In 2014, trees were designated with letters and nests were numbered consecutively. In subsequent years, nests were identified by their tree letter and a number assigned consecutively from lowest to highest branch. New photo maps were necessary each year because trees fell or were removed, branches broke, English ivy (*Hedera helix*) was removed, nests were lost, and new nests were built. The most dynamic period was February and March, when early-arriving birds gathered sticks by pulling them from undefended nests, so that several nests were completely destroyed each year. Later arriving herons often built new nests where previous nests had been destroyed. As far as possible, each nest position within a tree retained the same ID from year to year. In 2021, all photo maps used to date were closely

examined and compared, and we identified 6 instances in which nest position IDs had been transposed between years. In response, a tracking table was built with a record of each position, showing its field ID for each year it was used and assigning a unique database ID for reference in all years. Overall, 120 unique nest locations were tracked for a total of 600 nest-years between 2014 and 2023.

Observations began in early spring, when adult herons were observed around the nests, and ended about 6 months later, when no chicks remained in the nests (Table 1). Volunteers worked individually or with a partner, choosing a day of the week and recording data for every nest in the colony each time they came, unless interrupted by weather. When an observer could not come, another volunteer often substituted for them within one day of their usual day.

Observations took more than two hours during peak activity in the colony. In some instances, particularly in 2022 and 2023, there were morning and afternoon observations on the same day. On average, there were 95 observations per year and 1.9 days between observations (Table 1). A small proportion of intervals exceeded 4 days (4.7%; $n = 44$); the maximum interval was 9 days. Longer intervals were more common in the first two years of the study, when there were fewer volunteers.

Data were recorded on standard field data forms. During each visit, the number of adults was noted and their actions documented (coded options when present: standing in or near nest, copulation, exchange of adults at nest, bringing sticks to build/repair nest, incubation, feeding young). Most nests could be viewed at a shallow enough angle to see the back or head of a heron in the incubation posture, or at least the tip of a beak. If chicks were present, they were counted

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and their age estimated based on field observations and illustrations in Vennesland and Norman (2006); behavior was not tracked for chicks. In addition to adult actions and young presence, coded options for nest status in the data form allowed observers to record that a nest was empty or gone, or ‘Other.’ A comment field allowed further notes. We did not have the resources or permissions to band the herons as would be required to track individuals.

Phenology Calculations

The data gathered by volunteers provide a detailed record of activities over time in each nest-year. These data were combined with natural history knowledge of Pacific Great Blue Herons to estimate when incubation began, eggs hatched, and chicks fledged for each nest-year.

Inconsistencies in the record were examined individually, particularly for nest-years where these events coincided with intervals of five or more days between observations. The resulting dates were used to calculate the lengths of the incubation and rearing periods as described in the ‘Data Analysis’ section below.

It takes an average of 95 days from when a Pacific Great Blue Heron egg is laid until the resulting chick has fledged (Vennesland and Norman 2006). Females can lay an egg every 2 days; the usual clutch size is 4 eggs. Eggs hatch after about 27 days of incubation, but the overall incubation period can be longer than this due to staggered laying (e.g., 35 days for a clutch of 4 eggs), cold weather slowing chick development, and re-nesting attempts (Vennesland and Norman 2006, Ahmad and Li 2023). Chicks fledge after having been reared for 50 to 60 days (Stabins et al. 2006, Vennesland and Norman 2006).

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Start of Incubation—While we were unable to confirm the presence of eggs in the nest, we drew on observer comments about, for example, herons taking the incubation posture briefly during nest building, and used the recorded pattern of adult behavior to judge when eggs had been laid.

Key indicators of incubation were when a heron was settled low in the nest in an incubation posture, and when the second adult no longer stood near the nest. During incubation, these indicators were evident during most observations. To be conservative in our assignment of first incubation dates, early records coded as incubation were altered to ‘sitting’ if it was more than 5 days before the next incubation record and there were at least two subsequent observations of adults standing or bringing sticks.

Hatching—Hatching is difficult to observe as heron chicks are not large enough to stretch their heads above the nest edge until they are at least a week old, and do not stand until they are three weeks old. Some authors have used the presence of eggshells under nests to determine if chicks have hatched (Vennesland and Norman 2006), but we could not do so because of the colony’s location on a steep slope and because it would have been impossible to know which nest in a tree the shells came from. Chicks began calling shortly after hatching, but it was not possible to associate audible calls with individual nests. On a few dates, we knew hatching had already occurred because a downy chick was observed through a gap in the nest, an adult was observed bringing food even though we couldn’t see a nestling, or an adult was observed removing shell material. To assign a hatching date for each nest-year, we reviewed the record of activities over time, focusing on dates 27-37 days after incubation began. The hatching date was often (66% of nest-years) designated based on behavioral indicators such as an adult that had been incubating but was now standing. Less commonly (19% of nest-years), the hatching date was designated as

the first date on which chicks were observed. In the other 15% of nest-years, the hatching date was designated as the last date on which incubation was noted.

Rearing—We counted the number of chicks visible at each visit. Chicks usually could not be seen when lying down, but were often standing 3 weeks after hatching and, after 4 weeks, spent an increasing amount of time standing, including on the edge of the nest or nearby branches.

When an adult brought food to a nest, all the chicks in it usually squabbled to be fed, and were easy to count. Some nests were obscured by leaves from most angles, and it was necessary for an observer to move around to obtain a view. This was more a function of constraints on the ground than the nests' positions in the colony, and is not believed to introduce a bias. For 30 nest-years, incubation occurred but no young were recorded. The causes of these failures are unknown, as we could not climb trees to examine nests and the terrain prevented a search for evidence on the ground. In other cases, chicks were no longer observed in a nest when they were too young to have fledged, and were assumed to have died. To be conservative in our assignment of last rearing date, late records of young in a nest-year were changed to 'fledglings' if the nest had previously been coded as empty for 21 days. In making this change, we assumed that the nest was no longer attended by an adult heron.

Data Analysis

Data were cleaned and loaded into a PostgreSQL database, PostgreSQL 17.6 on x86_64-windows, compiled by msvc-19.44.35217, 64-bit. Table definitions and queries were written in the database management tool DBeaver, version 25.3.0.202511301802. The database was queried for the coded nest events analyzed in the figures and tables. To simplify calculations of

date ranges, all calendar dates were expressed as days since January 1; these are referred to here as day of year (DOY).

Our first observation of incubation was unlikely to be the moment incubation began. Instead, we assumed that incubation began halfway between this observation and the previous observation. For example, if we observed incubation on DOY 100 but had not observed it on DOY 96, we assumed that incubation began on DOY 98. This date was calculated for each nest-year, and the start of incubation for the colony in any year was the earliest date at which incubation began in one of the nests. The incubation period for each nest-year was calculated as the difference between its start of incubation and hatching date. Although our assigned hatching date was unlikely the moment at which hatching occurred, we chose not to adjust this date relative to the observations around it because these calculations only changed the balance between incubation and rearing and not the overall time spent by adults. In addition, as noted below, the calculated incubation and rearing periods are reasonable based on the natural history of the species.

As with incubation, our last observation of rearing was not necessarily the date at which rearing ended; we calculated the end of the rearing period for a nest-year as the date halfway between the last observation of young at the nest and the date of the next observation. The rearing period for each nest-year was calculated as the difference between its hatching date and end of rearing. Including half of the interval between observations into the calculation of incubation and rearing periods reduces the impact of long intervals between observations on these periods. Additional consideration of these intervals is provided in Appendix S1.

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Following Stabins et al. (2006), we evaluated chick production and nesting success 50 days after hatching. By this point in rearing, most mortality has occurred (Pratt and Winkler 1985) but few chicks have fledged and left the nest. The database was queried for successful nests, defined as a nest with one or more chicks present ≥ 77 days after first incubation or 50 days after one or more chicks were observed in the nest.

All data summaries, analyses, and graphics were prepared in R (version 4.5.2; R Core Team 2025). Data manipulation used the tidyverse (version 2.0.0; Wickham et al. 2019), and graphics were created using the ggplot2 package (version 4.0.0; Wickham 2016). Analyses used the lm function in base R, lme4 package (version 1.1-37; Bates et al. 2015), and lmerTest package (version 3.1-3; Kuznetsova et al. 2017). Since we had no reason to expect a linear trend over time, we coded year as a factor. Statistically significant ($\alpha = 0.05$) effects of year and its interaction with timing of incubation were subject to *post-hoc* comparisons as coded in the emmeans package (version 2.0.0; Lenth 2025). When analyses used nest-years as the sampling unit, we included the database ID for each nest as a blocking term to account for the fact that some nests were used in multiple years.

Question 1—We used ANOVA to test whether the start of incubation of individual nests differed among years.

Question 2—We created a ‘timing of incubation’ factor by denoting whether the start of incubation for each nest was before or after the year’s median incubation start date. We used the median date for this calculation so that the two groups would be equally sized. We used ANOVA

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to test whether incubation period differed with timing of incubation (Early or Late), year, and the interaction between these factors. We also used ANOVA to test whether rearing period differed with timing of incubation, year, and the interaction between these factors. Nest failure was most likely to occur during the rearing stage, so we also analyzed the length of the rearing period for successful nests.

We used a generalized linear model (GLM) to test whether nesting success (yes or no; binomial distribution) varied with timing of incubation, year, and the interaction between these factors.

We then subset the data to successful nests and used GLM to test whether the number of chicks 50 days after hatching (poisson distribution) differed with timing of incubation, year, and the interaction between these factors. Finally, we tallied the number of chicks produced by early-nesting and late-nesting herons in each year to determine the relative importance of timing of incubation.

Question 3—We calculated how many years each nest location was used, how often it was successful, and the average date on which incubation started at that nest location. We graphically explored the relationship between nest usage and success, and used GLM to test whether success rate (binomial distribution, weighted by number of years nest was used) related to average incubation start date.

Results

Question 1—On average there were 59 active nests per year in the colony, with a minimum of 38 nests in 2018 and a maximum of 76 nests in 2021 (Table 2). Across years, incubation of the first

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nest began as early as March 6 (DOY 66; in 2016) and as late as March 22 (DOY 81; in 2014), with an average of March 15 (DOY 74). When all nests were considered, the start of incubation varied significantly among years ($F_{9,462} = 13.1$; $P < 0.001$) and was later in 2017 and 2019 than in most other years (Figure 1). The start of incubation varied substantially among nests within years; in almost every year there were 3-4 months between the first and last nests to be incubated.

Question 2—Early-nesting herons incubated their chicks an average of 5 days longer than late-nesting herons ($F_{1,452} = 40.4$; $P < 0.001$) (Figure 2A; Table S2). Inter-annual variation in incubation period was small; the mean incubation period ranged from 33 days in 2023 to 37 days in 2021 (mean = 35 days) (Table 2) and did not differ among years ($F_{9,452} = 1.6$; $P = 0.109$). The patterns for early- and late-nesting herons did not differ among years ($F_{9,452} = 0.5$; $P = 0.879$).

Early-nesting herons reared their chicks an average of 12 days longer than late-nesting herons ($F_{1,425} = 44.9$; $P < 0.001$) (Figure 2B; Table S3). The length of the rearing period differed significantly among years ($F_{9,425} = 4.9$; $P < 0.001$); rearing was shortest in 2018 (57 days) and longest in 2022 (72 days), with a mean of 63 days (Table 2). The patterns for early- and late-nesting herons did not differ among years ($F_{9,425} = 0.6$; $P = 0.717$). When unsuccessful nests were excluded from analysis, the differences between early- and late-nesting herons and among years remained significant (Figure S3).

Early-nesting herons were successful 94% of the time while late-nesting herons were successful 75% of the time ($\chi^2(1) = 21.2$; $P < 0.001$) (Figure 3A; Table S4). The percentage of nests that

were successful varied significantly among years (χ^2 (9) = 21.9; P = 0.009), though *post-hoc* contrasts did not identify pairs of years that differed in success. The interaction between timing of incubation and year was not significant (χ^2 (9) = 12.2; P = 0.201).

Fifty days after hatching, successful nests contained an average of 2.7 chicks per nest. Chick production did not differ between successful nests of early- and late-nesting herons (χ^2 (1) = 1.2; P = 0.278) (Figure 3B; Table S5). Similarly, chick production of successful nests did not differ among years (χ^2 (9) = 6.6; P = 0.678), and the interaction between timing of incubation and year was not significant (χ^2 (9) = 2.3; P = 0.987).

Colony chick production ranged from 78 chicks in 2018 to 182 in 2023 (mean = 136) (Figure 3C). Early-nesting herons always produced more than half of the chicks, ranging from 54% of total chick production in 2017 to 67% in 2020 (mean = 61%).

Question 3—Some nests were used for a single year while others were used for all 10 years (Figure 4A). Nests that were more successful were also used more often. For example, every nest that was used for more than 4 years successfully produced chicks at least half of the time (Figure 4B). The earlier a nest began to be used in the season, the more likely it was to be successful (χ^2 (1) = 61.2; P < 0.001) (Figure 5; Figure S1; Table S6). The model fit to these data predicts that a nest location would have a success rate of 0.5 if incubation began in it on May 5 (DOY 125).

Discussion

We document substantial variation in when Pacific Great Blue Herons begin to incubate their eggs and how long incubation and rearing last. Despite inter-annual differences in some behaviors, there was no variation in chick production per successful nest among years. Intra-annual differences were more substantial than inter-annual differences: nests where incubation began early in the year were used longer and were more successful. Furthermore, intra-annual differences were consistent across years; nests that regularly began to be used early in the year were more successful than those that were not used until later.

Inter-annual Variation

The first observation of incubation within the colony differed by about two weeks among years. This date could be affected by many different factors. For example, disturbances could delay nest and mate selection. Food availability may be a trigger, as it is critical for egg production (Butler 1997). Butler (1993) reported that Great Blue Heron egg laying began shortly after fish abundance increased in eelgrass beds where they foraged. Fish abundance increases as the low tides shift from nighttime to daytime, the shallow waters warm, and the eelgrass produces new sprouts. After that, abundance varies with the migration or spawning of different fish species (Butler 1997). Anecdotal evidence suggests that the start of incubation differs between colonies, suggesting that it is not directly affected by weather conditions. However, we did not have the resources to analyze the many potential weather-related variables.

Although incubation began later in some years than others, mean incubation period did not differ among years (Figure S2; Table 2). Reduced variation in period length makes sense as there are strong biological controls on incubation rates and on the growth rates of chicks. Furthermore, the

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mean incubation period during this study (35 days) is identical to the time that Vennesland and Norman (2006) reported between when a clutch of 4 eggs begins to be laid and when those eggs hatch, suggesting that our procedures for estimating the start of incubation and hatching yielded reasonable values.

The mean rearing period during this study (63 days) is similar to the value reported in the literature (60 days; Vennesland and Norman 2006). The length of this period varied by about two weeks among years (Table 2), perhaps reflecting differences in food availability. The year 2022 was notable because the rearing period was several days longer than for any other year.

We note that our dataset contains some unfortunately long intervals between observations (Table 1), generally from times when few citizen scientists were involved in the study. While these intervals could affect estimates of incubation period and rearing period among years, we feel for several reasons that they do not bias our estimates greatly (see Appendix S1 for additional details). First, the only intervals that affect these period lengths are those at the start or end of a period. Second, we minimized the impact of these intervals by assuming that incubation began halfway between our first observation of it and the previous observation, and that rearing began halfway between our last observation of it and the next observation. As a result, the impact of an observation interval is half of its actual length. Third, most of the longer observation intervals occurred during 2014 and 2015, but the incubation and rearing periods of these years were not unusual compared to other years. Finally, we note that incubation periods did not differ among years and that the overall effect of year on rearing period was small compared to that between early and late nesting herons.

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Nest success varied significantly among years, though differences were small enough that *post-hoc* contrasts did not identify pairs of years that differed in success. Chick production per successful nest did not vary among years. Our overall production rate of 2.7 chicks per successful nest falls within the range of values reported by other studies (Forbes et al. 1985; Pratt and Winkler 1985). Nine years exceeded the threshold of 2.5 chicks per successful nest identified by Forbes et al. (1985) for colony growth, and no year fell below the threshold for colony decline (2.3 chicks per successful nest). However, an assessment of colony dynamics would require comparable data from multiple colonies and therefore was beyond the scope of our study. A larger dataset would also be required to study carry-over effects between years.

The year 2017 was unusual because incubation started later than in most years, most nests were successful (91%), late nests had their highest success rate (86%), and young were observed in nests as late as September 22 (DOY 264). We speculate that the high success rate that year, particularly of late nests, reflects reduced predation on heron chicks. In other years, we regularly observed bald eagle predation on heron chicks. For example, a neighbor observed a pair of eagles taking heron chicks to their nest 0.8 km from the colony. In 2017, the eagle nest appeared to have failed: the pair of eagles continued to frequent the nest area but no eagle fledglings were observed. Failure of the eagle nest would have reduced their food demands. In addition, citizen scientists observed a bald eagle being harassed in August 2017 by an osprey (*Pandion haliaetus*) teaching its chick to hunt below the locks. Interestingly, despite the high success rate this year, colony-wide chick production was average.

In 2013, the year that the Kiwanis colony was abandoned, the Commodore Park colony was estimated to have fledged 87 young herons. The colony produced more than this during most years of this study, and produced its highest numbers during the last few years (2021-2023) (Figure 3C). These numbers are promising for the colony and possibly for the subspecies, though comparable data from other colonies would be required to assess regional dynamics. Colony chick production can be conceptualized as the product of the number of nests, probability of nest success, and production per successful nest. Since production per successful nest did not differ among years and nest success was not strongly significant – no pair of years clearly differed – colony chick production is driven largely by the number of nests in a year.

Intra-annual Variation

Nesting success was strongly dependent on when incubation began within the year. This was true when comparing early- and late-nesting herons within years (Figure 3A) and when considering overall usage patterns across years (Figure 5). Stabins et al. (2006) reported significantly higher nesting success for herons that began incubation before April 17 than after that date. Our results are consistent with this: nests that began to be used by April 17 (DOY 107) were successful 79% of the time (Figure 5). Early-nesting herons produced most of the chicks in the colony in any year (Figure 3C), indicating that these nests are particularly important for the persistence of the colony.

Our data do not permit us to determine why nesting success was affected by when incubation began, though we can speculate on possible reasons. Mortality could be higher later in the season if, for example, fewer nests containing chicks led to higher predation pressure on them from the

bald eagles in the vicinity. Another possibility is that adults who begin incubation earlier are more experienced at foraging. Food and other resources might be more readily available early in the season. Butler (1993) reported that fish abundance declined during the season to the point that when chicks were 26 to 44 days old there was barely enough food beyond the energy demands of the adults to feed 2 or 3 chicks.

Another intra-annual difference is in time spent raising chicks: the incubation period was an average of 5 days longer for early-nesting herons and the rearing period was an average of 12 days longer, meaning that the chicks in these nests received more than two weeks of additional parental effort. The rearing period ended when chicks died or fledged, suggesting that the shorter rearing period for late-nesting herons could be a result of chick mortality shortening the period of parental care. However, when the data were restricted to successful nests, the length of the rearing period remained significantly longer for early- than late-nesting herons (Figure S3). The longer this care extends beyond 50 days, the minimum age for fledging, the better chance the juvenile will maintain its body condition while learning to forage, thus increasing its likelihood of survival to adulthood.

To the best of our knowledge, no other study has related long-term use of individual nest locations to nesting success. Based on a decade of observations, we found that some nest locations are consistently more successful than others. Two lines of evidence suggest that herons recognize these locations. First, consistently successful nest locations were much more likely to be used repeatedly and, relatedly, no nest locations used in multiple years failed in all years (Figure 4B). Second, nests that were used repeatedly were more likely to be those in which

incubation began earlier in the season (Figure S1). One study of banded herons (Simpson 1984) reported that most did not return to the same nest in subsequent years, suggesting that the repeated use of nests that we observed was not due to nest fidelity by individual birds. Perhaps there is a general preference for the characteristics of these nests, either instinctively or as a learned behavior. We encourage future researchers to explore these issues.

Numerous state and local jurisdictions have instituted management guidelines to protect colonies from human disturbance by restricting activities within prescribed distances at particular times of the year (Vennesland & Norman 2006). For the Commodore Park colony in Seattle, current regulations include a year-round buffer (60 m, and all contiguous forest) where development is limited and larger, seasonal buffers in which excess noise is prohibited during a pre-nesting season (450 m, January 1 to March 31 (DOY 1 to 90)) and a nesting season (152 m, February 1 to August 31 (DOY 32 to 243)) (SDCI 2018). Our results indicate that the phenology of incubation and rearing changed minimally over this decade of monitoring, and that the designated nesting season includes all observed incubation periods during the study period and most, but not all, of the rearing periods for individual nests.

Conclusions

Pacific Great Blue Heron nesting begins at different dates both among and within years. Nests that begin to be used early in the season have longer incubation and rearing periods and are more likely to be successful, though they produce the same number of chicks as nests that begin to be used late in the season. Furthermore, nests used in multiple years were more likely to be selected early in the season and to be successful, suggesting that Pacific Great Blue Herons recognize

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differences in nest quality and preferentially use those with a high likelihood of success.

Frequent and detailed data collection over multiple years was necessary to understand nesting success. Citizen scientists led this study, and the involvement of multiple volunteers permitted the collection of much more data than would have been possible by one or two individuals. We encourage interested parties to conduct similar monitoring at other colonies and to share their findings so that future analyses can compare nesting success among sites and years. We also encourage the involvement of citizen scientists in other types of projects. Urban environments provide a convenient location in which citizen scientists can operate.

Acknowledgements

Mike Marsh led this project since its inception and oversaw the preparation of this manuscript, but passed away while it was in peer review. We thank the many individuals who assisted with observations over the years. We also thank Ruth Kalstad and several peer reviewers for comments that strengthened the final version of the manuscript.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data Availability Statement

The datasets used in this study can be found in the XZY repository (to be provided upon manuscript acceptance).

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Supplementary Materials

Supplemental material available online at (URL to be provided)

Author Contributions

M.M. contributed to all aspects of this project. L.M. contributed to fieldwork, data curation, and manuscript preparation. D.J. contributed to project conceptualization and manuscript preparation. C.T. contributed to fieldwork and manuscript preparation. J.D.B. contributed to data analysis and manuscript preparation.

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Figures

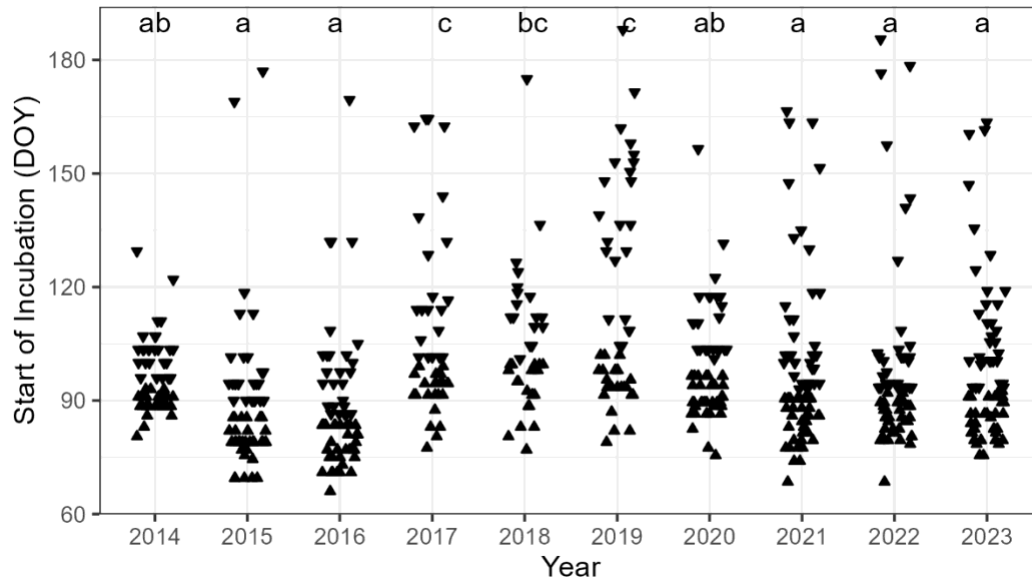


Figure 1. First day of year (DOY) at which incubation was noted, by year. Points are nests, jittered horizontally to show overlapping values. *Post-hoc* contrasts are reported near the top of the graph; years that share the same letter(s) are not statistically different from one another. Point shapes reflect whether values are below or above the median for each year, and are provided to link these data with timing of incubation (Early or Late) in Figures 2 and 3. Full statistical results are in Table S1.

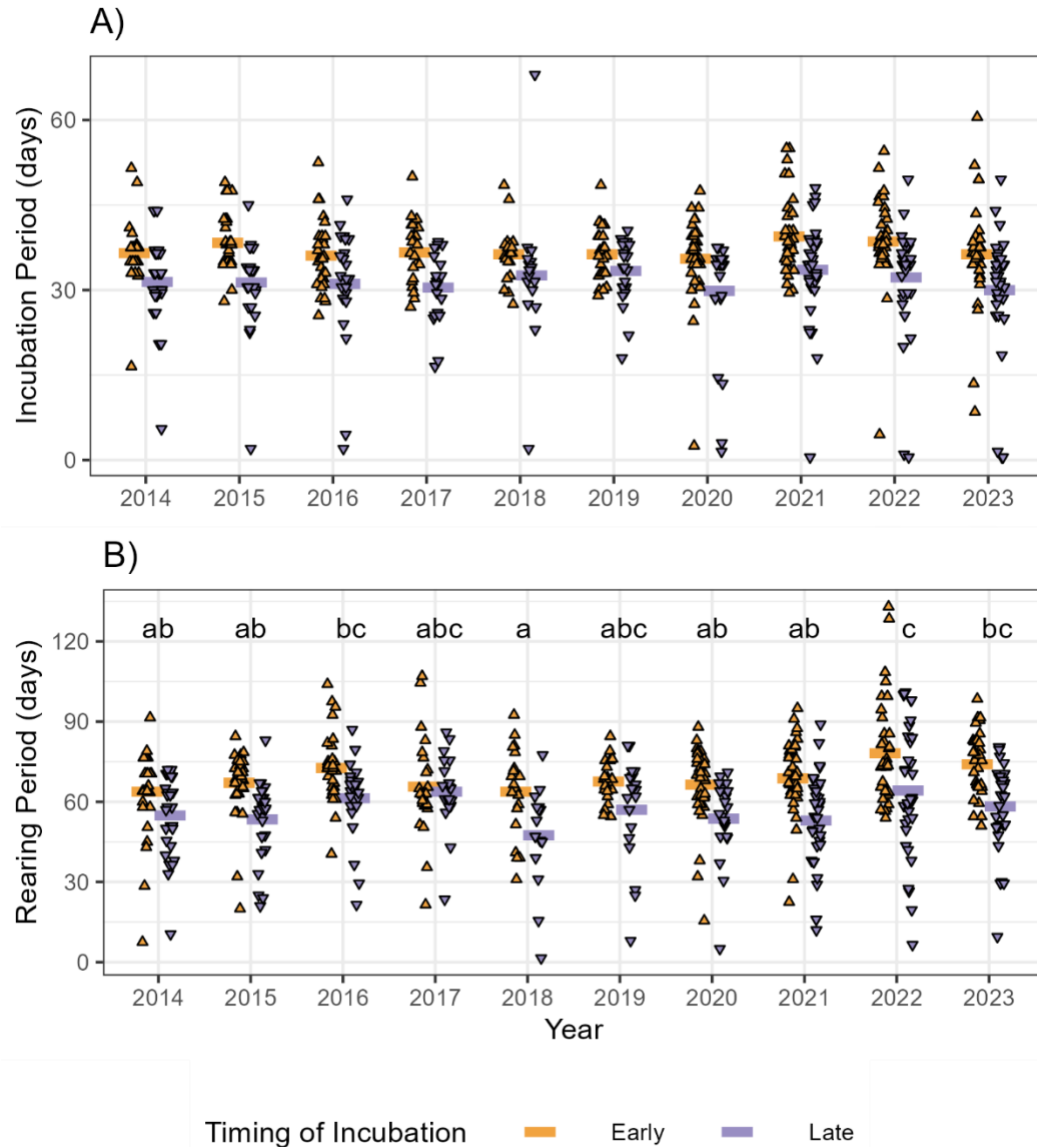


Figure 2. Length of the (A) incubation period and (B) rearing period. Colors and shapes distinguish nests initiated in the first or second half of the incubation period (Early or Late) in each year. Points are nests, jittered horizontally to show overlapping values. The thick lines denote mean values. Incubation period differed with timing of incubation ($P \leq 0.001$) but did not differ among years ($P = 0.109$) and the interaction was not significant ($P = 0.879$) (full statistical results in Table S2). Rearing period differed with timing of incubation and among years ($P \leq 0.001$) but the interaction was not significant ($P = 0.717$) (full statistical results in Table S3).

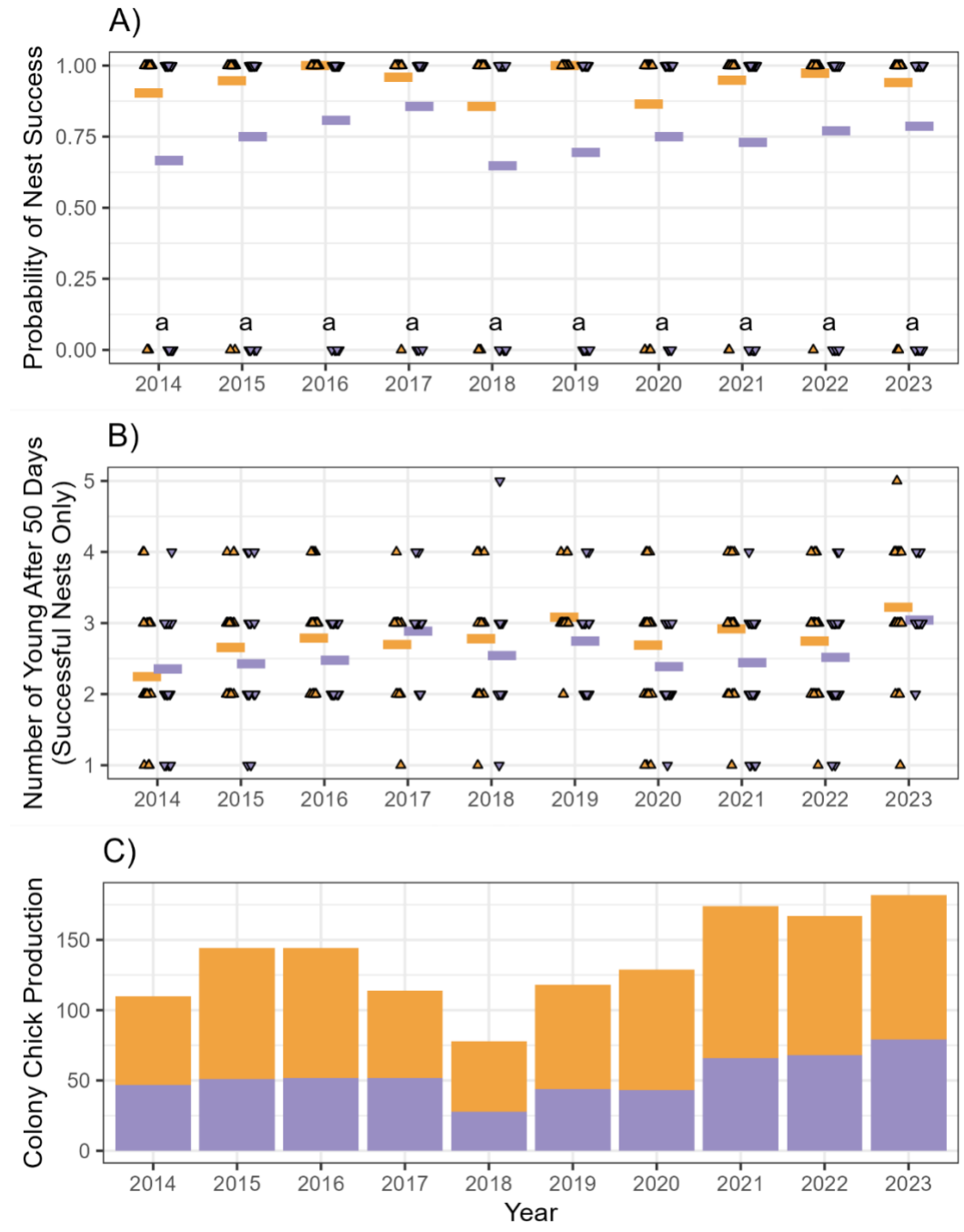
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Post-hoc contrasts are reported near the top of the graph of rearing period; years that share the same letter(s) are not statistically different from one another.

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Timing of Incubation Early Late

Figure 3. (A) Probability that a nest was successful, (B) number of chicks produced per successful nest, and (C) colony chick production. Colors and shapes distinguish nests initiated in the first or second half of the incubation period (Early or Late) in each year. In (A) and (B), points are nests, with horizontal jittering but numerous overlapping values. In (A), the main effects of timing of incubation and of year were significant ($P \leq 0.009$) but the interaction was not significant ($P = 0.201$) (full statistical results in Table S4). Although the effect of year was significant, *post-hoc* contrasts indicated that no years differed from one another as indicated by the identical lowercase letter at the bottom of the graph. In (B), no factors were significant ($P \geq 0.278$; full statistical results in Table S5). Colony chick production is the number of chicks produced from Early and Late nests in each year.

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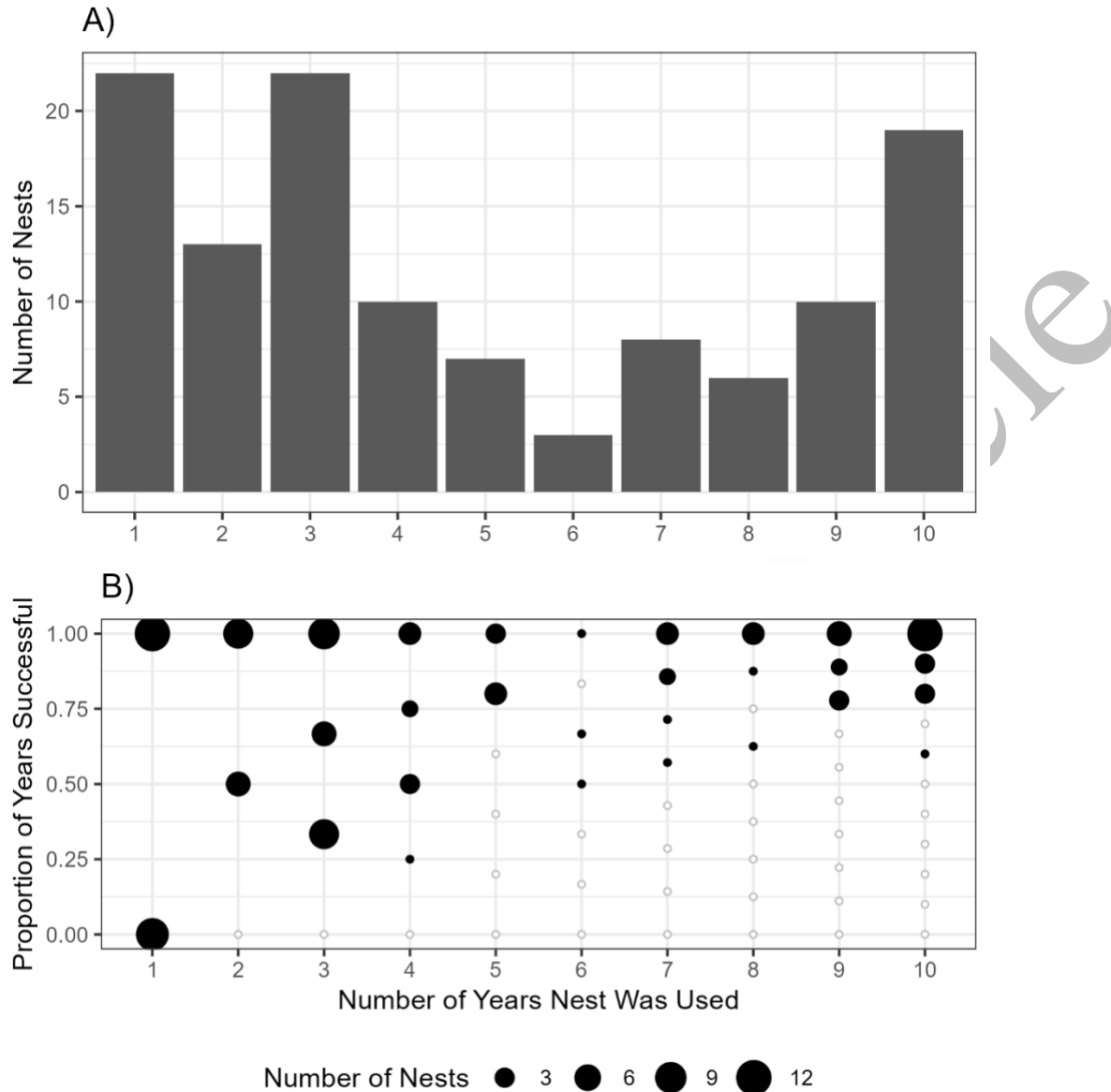


Figure 4. (A) Number of nests used for 1-10 years and (B) nesting success (proportion of years used in which the nest contained one or more chicks 50 days after hatching) as a function of the number of years in which a nest was used. In (B), point size reflects the number of nests with each combination of values; open grey points are combinations that did not occur.

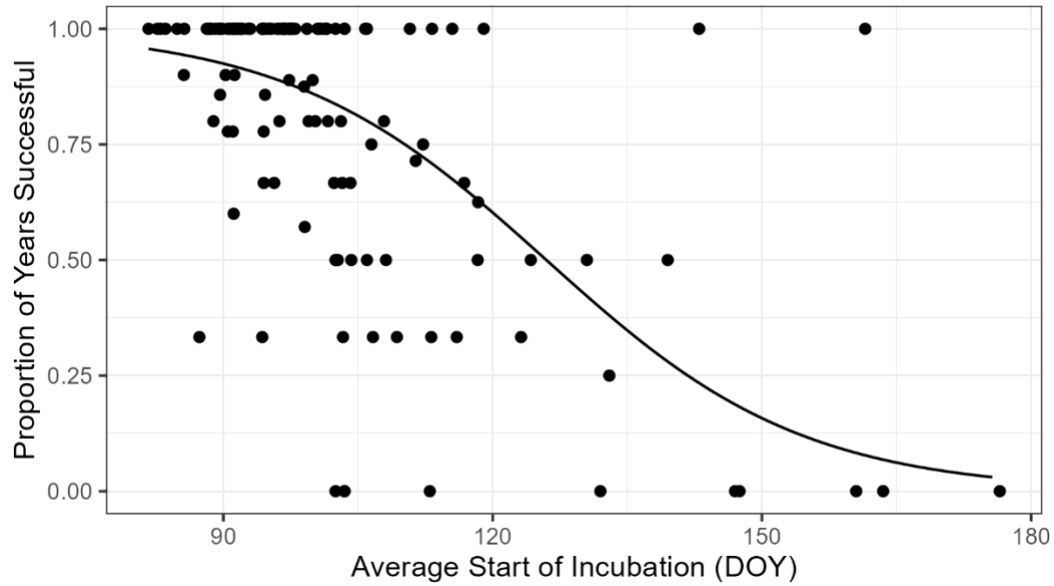


Figure 5. Nesting success (proportion of years used in which a nest contained one or more chicks 50 days after hatching) as a function of the average date that nest location first began to be used within the incubation season (DOY: day of year). Each point is a nest location ($n = 120$) and the curve is a logistic fit to the data ($P < 0.001$; full statistical results in Table S6). These data are also shown in Figure S1, with a separate graph for each number of years a nest was used.

Table 1. Summary information about the start and end of observations (Obs.: observation; DOY: day of year), length of observation period, observation frequency (number, number of days), and intervals between observations. The number of days observed is less than the number of observations because there were morning and afternoon observations on some days. Overall values are reported as mean \pm SD among years, and total values as the sum across years.

Year	First Obs. Date (DOY)	Final Obs. Date (DOY)	Obs. Period (days)	Obs. (#)	Days Observed (#)	Mean Obs. Interval (days)	Intervals > 4 Days (#)
2014	70	205	135	32	31	4.4	13
2015	48	211	163	51	47	3.3	10
2016	46	218	172	76	75	2.3	0
2017	26	272	246	114	98	2.2	9
2018	32	225	193	84	83	2.3	5
2019	68	252	184	91	87	2.0	0
2020	48	218	170	88	82	2.0	2
2021	51	211	160	82	75	2.0	0
2022	45	269	224	170	135	1.3	4
2023	49	225	176	160	133	1.1	1
Overall	48 \pm 14	231 \pm 25	182 \pm 32	95 \pm 43	85 \pm 33	1.9 \pm 0.9	4 \pm 5
Total			1823	948	846		44

Table 2. Summary information about number of active nests, first incubation date (DOY: day of year), lengths of the incubation and rearing periods, percentage of nests that were successful, and number of chicks (50 days after hatching) per successful nest. Incubation period, rearing period, and chicks per successful nest are reported as mean \pm SD among nests in each year. Overall values are reported as mean \pm SD among years.

Year	Active Nests (#)	First Incubation Date (DOY)	Incubation Period (days)	Rearing Period (days)	Successful Nests (%)	Chicks per Successful Nest (#)
2014	61	81	34 \pm 7	59 \pm 16	79	2.3 \pm 0.8
2015	65	70	35 \pm 7	61 \pm 15	86	2.6 \pm 0.7
2016	59	66	34 \pm 8	68 \pm 14	92	2.7 \pm 0.6
2017	45	78	34 \pm 7	65 \pm 17	91	2.8 \pm 0.6
2018	38	77	35 \pm 9	57 \pm 20	76	2.7 \pm 0.9
2019	47	79	35 \pm 5	63 \pm 15	85	3.0 \pm 0.6
2020	61	76	33 \pm 9	61 \pm 16	82	2.6 \pm 0.7
2021	76	69	37 \pm 8	61 \pm 18	84	2.7 \pm 0.8
2022	72	69	35 \pm 9	72 \pm 23	88	2.7 \pm 0.7
2023	67	76	33 \pm 11	66 \pm 17	87	3.1 \pm 0.7
Overall	59 \pm 12	74 \pm 5	35 \pm 1	63 \pm 4	85 \pm 5	2.7 \pm 0.2

1 **Supplemental Material**

2 Appendix S1.

3 Some intervals between observations were longer than desired (Table 1). This appendix
4 summarizes our assessment of whether large intervals, defined here as > 4 days, could bias the
5 calculation of incubation and rearing periods.

6 The incubation and rearing period lengths for a nest-year are only affected by the interval that
7 immediately preceded the first observation of incubation or that immediately followed the last
8 observation of rearing. We note that a single large interval could affect multiple nests if
9 incubation began or rearing ended at the same time in them. The effect of a large interval would
10 be consistent for all affected nests, unless the same interval affected the start of incubation of one
11 nest and the end of rearing of another nest.

12 Large intervals occurred in 2014, 2015, 2017, and 2018. Intervals in other years did not affect
13 critical nest event dates.

14

15 Incubation Period

16 There were large intervals immediately preceding the first incubation date of 15 nest-years: 1 in
17 2014, 11 in 2015, 1 in 2017, and 2 in 2018. All of these were late nests; they began to be
18 incubated after the median date when incubation began for the year. Thus, any effect of large
19 interval on incubation period would be most evident in the difference between early and late
20 nests in 2015.

21 We distinguished nests in 2015 from those in all other years combined. For each nest-year, we
22 calculated the length of the incubation period in three ways: without adjusting for the length of
23 the preceding interval, adjusting by half the length of the preceding interval, and adjusting by the
24 full length of the preceding interval. After calculating these intervals, we averaged them for early
25 and late nests in 2015 and in the other years. Finally, we calculated the difference between the
26 values for early and late nests.

Method	2015			All Other Years		
	Early	Late	Difference	Early	Late	Difference
No interval	37.1	29.3	7.8	36.0	30.6	5.4
Half interval	38.4	31.4	7.0	37.0	31.6	5.4
Full interval	39.6	33.4	6.2	37.9	32.7	5.2

27
28 Ignoring large intervals, the difference between early and late nests is 2.4 days longer in 2015
29 than in all other years (7.8 vs. 5.4). Fully incorporating the interval that preceded the start of
30 incubation reduced this difference between years to 1 day (6.2 vs. 5.2). The incorporation of
31 large intervals in 2015 reduces the difference between early and late nests by 1.6 days (7.8 vs.
32 6.2), whereas in years that contained few to no large intervals the difference between early and
33 late nests was largely unaffected by whether the interval was incorporated (5.4 vs. 5.2).
34 Incorporating half of the interval led to differences between early and late nests that were
35 intermediate between the extremes.

36

37 Rearing Period

38 There were large intervals immediately following the last rearing date for 91 nest-years: 54 in
39 2014, 29 in 2015, 5 in 2017, and 3 in 2018. Slightly more of these large intervals were for early
40 than late nests (52 vs. 39). Thus, any effect of large interval on rearing period would be most
41 evident in 2014 and 2015 but would not clearly be associated with the difference between early
42 and late nests.

Method	2014 and 2015	All Other Years
No interval	60.5	64.7
Half interval	63.0	65.8
Full interval	65.6	66.9

43

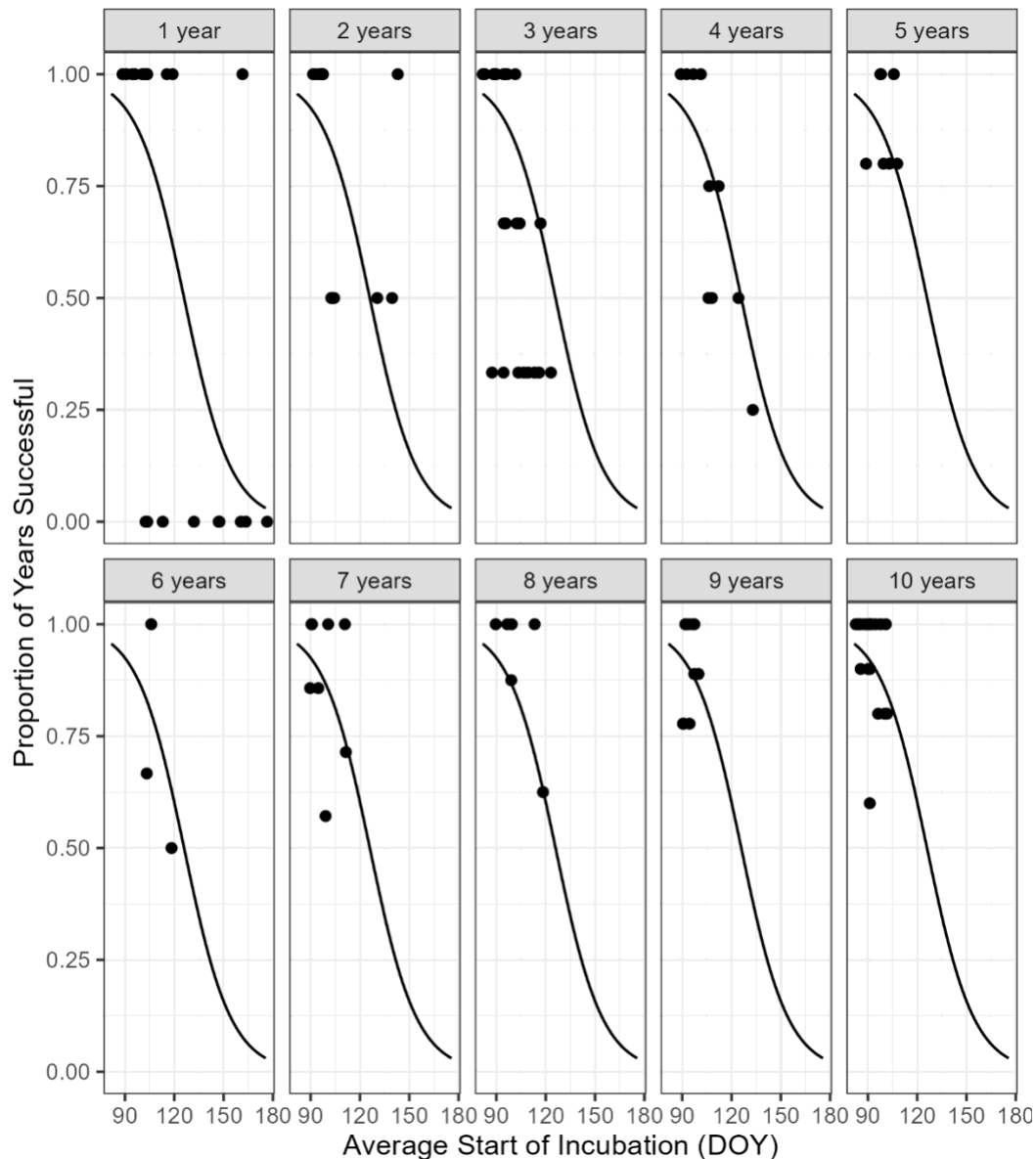
44 Ignoring large intervals, the length of the rearing period was 4.2 days shorter in 2014/2015 than
45 in other years (60.5 vs. 64.7). Fully incorporating the interval that followed the last observation
46 of rearing reduced this difference to 1.3 days (65.6 vs. 66.9). Incorporating half of the interval
47 led to a difference of 2.8 days (63.0 vs. 65.8).

48

49 Conclusion

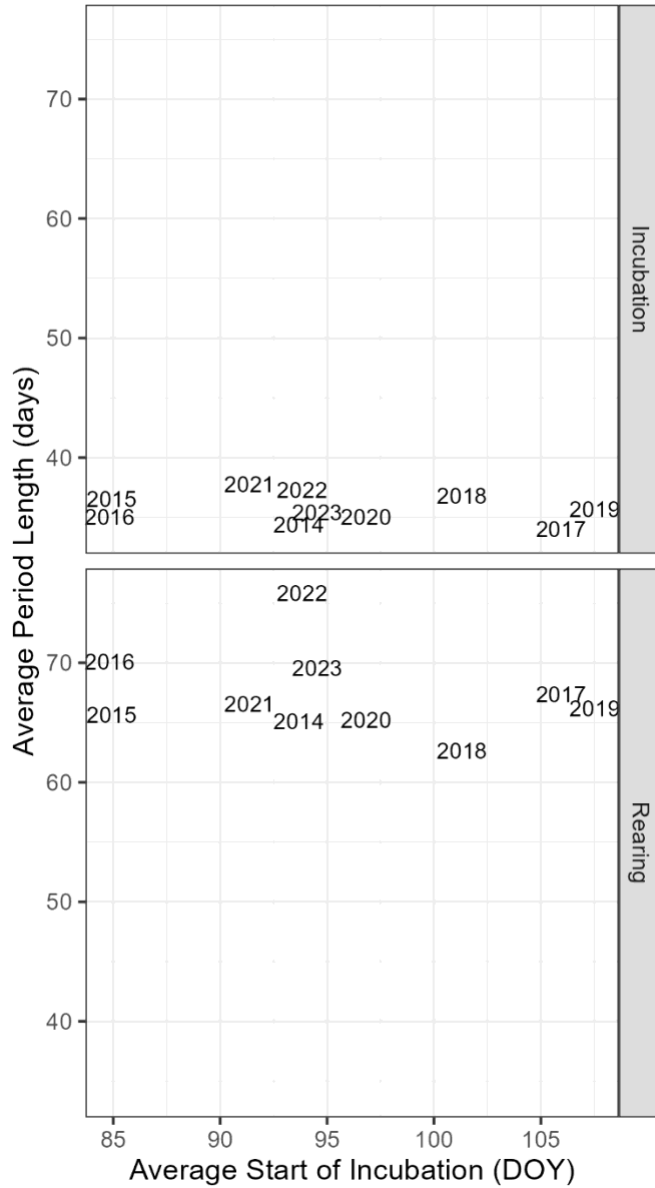
50 Our approach of incorporating half of the interval provides a reasonable balance between the
51 extremes of ignoring all large intervals and giving them full weight in the calculation of
52 incubation and rearing periods.

53 Figure S1. Nesting success (proportion of years used in which the nest location contained one or
54 more chicks 50 days after hatching) as a function of the average date the nest location first began
55 to be used within the incubation season (DOY: day of year). The curve is a logistic fit to all of
56 the data ($P < 0.001$), repeated in facets to highlight the number of years (1 to 10) in which nests
57 were used. Each point is a nest location ($n = 120$ across all years). Figure 5 shows the same data
58 but without differentiating the number of years each nest location was used. Statistical results are
59 in Table S6.



61 Figure S2. Average length of incubation and rearing periods as a function of the average start of
62 incubation (DOY: day of year) in each year. The value for each year is the center of its label.

63

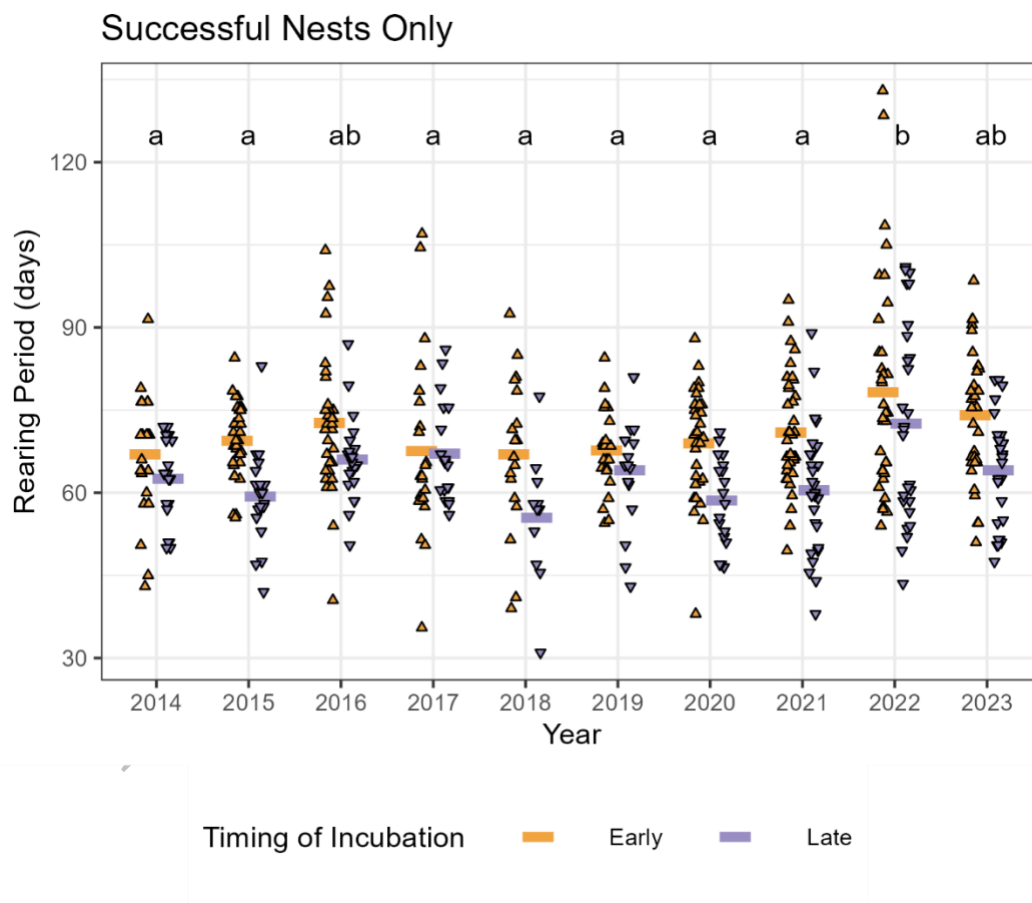


64

65

66

67 Figure S3. Length of the rearing period for successful nest-years (n = 503). Colors and shapes
68 distinguish nests initiated in the first or second half of the incubation period (Early or Late) in
69 each year. Points are nests, jittered horizontally to show overlapping values. The thick lines
70 denote mean values. The main effect of timing of incubation was highly significant ($F_{1,374} =$
71 29.6; $P \leq 0.001$) as was that of year ($F_{9,374} = 5.3$; $P \leq 0.001$) but the interaction was not
72 significant ($F_{9,374} = 1.0$; $P = 0.407$). The R^2 for this model is 0.362. *Post-hoc* contrasts among
73 years are reported near the top of the graph; years that share the same letter(s) are not statistically
74 different from one another.
75



76

77

78 Table S1. Results of ANOVA testing whether the first day of incubation varies among years. The
79 model included a unique Nest ID to account for the fact that some nest locations were used in
80 multiple years. The R^2 for this model is 0.467. The data associated with this analysis are shown
81 in Figure 1.

82

Term	df	SS	<i>F</i>	<i>P</i>
Nest ID	119	83716	2.41	<0.001
Year	9	34263	13.05	<0.001
Residual	462	134769		

83

84

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85 Table S2. Results of ANOVA testing whether length of incubation period differed with timing of
86 incubation (Early vs. Late), year, and the interaction between timing of incubation and year. The
87 model included a unique Nest ID to account for the fact that some nest locations were used in
88 multiple years. The R^2 for this model is 0.364. The data associated with this analysis are shown
89 in Figure 2A.

90

Term	df	SS	<i>F</i>	<i>P</i>
Nest ID	119	11249	1.67	<0.001
Timing of Incubation	1	2285	40.40	<0.001
Year	9	821	1.61	0.109
Timing of Incubation× Year	9	251	0.49	0.879
Residual	452	25568		

91

92

93 Table S3. Results of ANOVA testing whether length of rearing period differed with timing of
94 incubation (Early vs. Late), year, and the interaction between timing of incubation and year. The
95 model included a unique Nest ID to account for the fact that some nest locations were used in
96 multiple years. Thirty nest-year combinations were omitted as we were unable to determine
97 when rearing ended. The R^2 for this model is 0.422. The data associated with this analysis are
98 shown in Figure 2B.

99

Term	df	SS	<i>F</i>	<i>P</i>
Nest ID	116	50681	1.85	<0.001
Timing of Incubation	1	10585	44.94	<0.001
Year	9	10292	4.85	<0.001
Timing of Incubation× Year	9	1466	0.69	0.717
Residual	425	100110		

100

101

102

103 Table S4. Results of GLM testing whether probability of nesting success (binomial distribution)
104 differed by timing of incubation (Early vs. Late), year, and the interaction between timing of
105 incubation and year. The model included a unique Nest ID for each nest to account for the fact
106 that some nest locations were used in multiple years. The data associated with this analysis are
107 shown in Figure 3A.
108

Term	df	Deviance	Residual df	Residual Deviance	<i>P</i>
NULL			590	497.4	
Nest ID	119	217.6	471	279.8	<0.001
Timing of Incubation	1	21.2	470	258.6	<0.001
Year	9	21.9	461	236.7	0.009
Timing of Incubation × Year	9	12.2	452	224.5	0.201

109

110

111 Table S5. Results of GLM testing whether number of chicks per successful nest (poisson
112 distribution) differed by timing of incubation (Early vs. Late), year, and the interaction between
113 timing of incubation and year. The model included a unique Nest ID for each nest to account for
114 the fact that some nest locations were used in multiple years. The data associated with this
115 analysis are shown in Figure 3B.
116

Term	df	Deviance	Residual df	Residual Deviance	P
NULL			502	111.8	
Nest ID	109	27.8	393	84.0	1.000
Timing of Incubation	1	1.2	392	82.9	0.278
Year	9	6.6	383	76.2	0.678
Timing of Incubation × Year	9	2.3	374	74.0	0.987

117

118

119 Table S6. Results of GLM testing whether nest success rate (binomial distribution, weighted by
120 number of years nest location was used) varies with the average date on which incubation began.
121 Each point is a nest location, averaged across the years in which it was used. The data associated
122 with this analysis are shown in Figures 5 and S1.

123

Term	df	Deviance	Residual df	Residual Deviance	<i>P</i>
NULL			119	217.6	
Average Start of Incubation	1	61.2	118	156.4	<0.001

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Accepted Article