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Effects of Aging on the Reproductive Success of Female Saltmarsh Sparrows (Ammospiza caudacutus) in Maine and New Hampshire

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Honors Thesis

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Abstract: The saltmarsh sparrow (*Ammospiza caudacutus*) is a ground-nesting specialist in coastal salt marshes of the Northeast. Rising sea-levels increase the loss of offspring due to tidal flooding, reducing nest success and resulting in a sharp population decline. In other avian species, age has been shown to affect nest success through altering fertility, behavior, and the number of young produced, favoring older individuals. I investigated age effects on nest success of female saltmarsh sparrows using nest monitoring data collected at four sites of a long-term demographic monitoring project: Chapman's Landing (Stratham, NH), Eldridge Marsh (Wells, ME), Popham Beach (Phippsburg, ME), and Maquoit Bay (Brunswick, ME). Reproductive success was measured categorically, based on whether a nest failed entirely or fledged at least one chick, and quantitatively, based on the number of chicks fledged per nest. The causes of failure (flooding or predation) were also observed. Female age was reconstructed using historical banding data. I predicted that older females will have greater quantitative and qualitative reproductive success than younger individuals due to their higher experience level. Similarly, I predict that younger females will be more prone to flooding due to their inexperience. Findings showed a correlation between the age and reproductive success of female saltmarsh sparrows with older females losing a higher proportion of nests to flooding while in the egg stage but fledging a higher proportion of nestlings than younger females. With increased understanding of the effects of aging, demographic surveys could better estimate fecundity and prioritize conserving populations with the greatest growth potential.

Introduction

Vertebrate species tend to show a correlation between reproductive success and age (Clutton-Brock, 1989), though there have been few occasions where age has not had an observable effect. These scenarios are often associated with reptiles and amphibians (Olsson and Shine, 1996; Halliday and Verrell, 1988) but have also been seen to a lesser degree in birds such as tree swallows and wood ducks (De Steven, 1980; Hepp and Kennamer, 1993). The more commonly seen and generally accepted correlation is that age increases the reproductive success of an individual, though the underlying factors tied to this are numerous. Existing hypotheses include Selection, Constraint, Restraint, and Senescence with various levels of overlap and support across the categories. Essentially, the Selection Hypothesis credits variation in reproductive success to individual quality or fitness, Constraint refers to an individual's ability/skill/experience, Restraint to maximizing the time an animal has left in its life to reproduce, and Senescence to the deterioration in physiology or investment enabling an individual to reproduce (Dugdale et al., 2011).

Many of the studies investigating these hypotheses do so through the female of the species, though some breeding systems, such as polygynandrous badgers (*Meles meles*), monogamous sparrowhawks (*Accipiter nisus*), and variably monogamous cardinal fish (*Apogon doederleini*) and sunfish (*Lepomis macrochirus*) do support a similar positive connection between male age and offspring production (Dugdale et al., 2011; Newton et al., 1981; Okuda et al., 1998; Cargnelli and Neff, 2006). Breeding and social systems also play a role in determining what factors are tied to age that could benefit reproduction. For example, in species with a social hierarchy, such as mountain goats, older individuals often attain higher levels of dominance which afford them greater access to mates and resources (Côté and Festa-Bianchet, 2001). Social dominance, and therefore age, are then also closely tied with body condition and size, both of which have been tied to increased levels of reproductive success (Olsson and Shine, 1996; Halliday and Verrell, 1988). Interestingly, these papers show that, when mass is accounted for, age may have less of an impact than originally hypothesized, though both studies focus on herpetology. For birds, one study investigating breeding experience and age showed that, when the other variable was controlled for, both experience and age showed an increase in nest success (Harvey et al., 1985).

In avian species, the most frequent hypotheses supporting a positive correlation between age and nest success are Senescence and Constraint (Wooller et al., 1990; Hamer and Furness, 1991; Wheelwright and Schultz, 1994). In lesser snow geese, older females (across age classes) produce larger clutches of eggs and raise more young (Rockwell et al., 1993). Their success is attributed to an increase in the experience of obtaining more of the nutrients required to produce more eggs (Rockwell et al., 1993). In prothonotary warblers, older (than one year) females produced larger clutch sizes, initiated egg-laying earlier, and had a significantly higher number of fertile eggs than younger females (Blem et al., 1999). Similarly, when comparing inexperienced vs. experienced (first nesting season vs. later) incubation behaviors in female hooded warblers, older individuals visited their nests more often to incubate nestlings on cold mornings and, in doing so, maintained a higher and more stable nest temperature than inexperienced females, supporting greater hatching success (Williams et al., 2019). Additionally, experienced females chose nest sites that had higher minimum temperatures, which likely aided in maintaining a consistent temperature (Williams et al., 2019). While most studies use the number of eggs, nestlings, or fledglings produced to quantify nest success, Cichoñ (2003) found no significant difference between these factors but instead in the size and mass of chicks.

Overall, the reproductive success of species can often be shown with a senescence curve (inverted U-shape) such as in barnacle geese, which peak in productivity around age 11, though the average life span is about 9 years (Black and Owen, 1989). This pattern has also been shown in Great Tits and Goldeneye ducks, both focusing on the female parent (Perrins and Moss, 1974; Dow and Fredga, 1984). Since individuals may die before this 'peak,' they could be improving in reproductive success for their entire lives, with the oldest individuals of a population representing the greatest production of offspring.

Another factor correlating to nest success in birds is the timing of nest initiation. In American coots, increased age was tied to nesting later in the season with results showing increased reproductive success (Perdeck and Cave, 1992). Conversely, European blackbirds showed increased age leading to earlier nest initiation but still with higher success going to the older females, likely attributed to the younger females' inability to forage for food (Desrochers, 1992).

The saltmarsh sparrow (*Ammospiza caudacutus)* is the only passerine in the world that nests exclusively in salt marshes—habitats that are defined by their periodic flooding by the ocean's tides (Gjerdum et al., 2005). As ground-nesters, they must fit their 23–27-day nesting cycle within the 28-day lunar tide cycle or risk the drowning of their chicks or eggs. Since the breeding season spans roughly three tidal cycles, there are about three time periods available for nesting, or re-nesting, attempts. Evolutionarily, they have been selected to nest in portions of high elevation of mature marsh, the area flooded least frequently at only twice a month. Both habitat (vegetation structure) and behavioral (nest initiation) variables have been shown to affect nest success (Gjerdrum et al., 2005). Despite this high degree of specialization, between 60-80% of nest failure is due to flooding, with depredation responsible for only a small proportion of the remaining percentage (Shriver et al., 2007; Marshall et al., 2020). A key behavioral adaptation enhancing nest success in saltmarsh sparrows may be plasticity in nest characteristics. Benvenuti et al. (2018) investigated whether female saltmarsh sparrows altered their nesting behavior based on the success/failure of previous experiences. The authors found that females with nests failed due to flooding increased the height of their nests in subsequent attempts while those that failed due to predation lowered the height of their later nests (Benvenuti et al., 2018). Theoretically, this would suggest that older, and therefore more experienced, female saltmarsh sparrows would have the greatest nest success.

The effects of aging on the reproductive success of saltmarsh sparrows have never been directly studied, and they are a unique and important system under threat of extinction. Despite existing nesting adaptations, rising sea levels or alterations of tidal flow will have a devastating impact on nesting survival. Aside from flooding, the encroaching sea water shifts the distribution of grass species to more short *S. alterniflora*, which is a less favored nesting substrate than *S. patens* (Gjerdrum et al., 2005). Since this species is not territorial and shows high site fidelity with minimal dispersal (Hartley and Weldon, 2020), they provide an opportunity to study a polygynandrous mating system not often seen in birds. The female sparrows are the only contributors to nest success, suggesting that, by improving the scientific understanding of how age affects female saltmarsh sparrow reproductive success, demographic surveys could better inform restoration managers on which populations hold the greatest growth potential and therefore should be prioritized when making conservation decisions.

I predict older females will have greater reproductive success in terms of categorical nest outcome (success vs. failure) as well as the proportion of eggs hatched and chicks fledged per nest. Additionally, since flooding in a salt marsh can be considered a more frequent cause of nest failure than predation, and females have demonstrated plasticity with nest characteristics, I predict that younger females will be more prone to nest flooding than older females. Conversely, if experienced females raise the height of their nest to avoid flooding, then I predict older females are more likely to have nest depredation than younger females.

Methods

Study Sites

To investigate the age effects on nest success of female saltmarsh sparrows, I used nest monitoring data collected at four sites of a long-term demographic monitoring project: Chapman's Landing (Stratham, NH), Eldridge Marsh (Wells, ME), Popham Beach (Phippsburg, ME), and Maquoit Bay (Brunswick, ME) (Fig. 1). University of New Hampshire researchers in conjunction with the Saltmarsh Habitat and Avian Research Project have collected data at Chapman’s Landing (CL) from 2011-2016 and 2019-2022, Eldridge Marsh (EL) from 2011-2022, and Popham Beach (PB) and Maquoit Bay (MQ) in 2016, 2017, 2020, and 2022. All field activity occurred between May and August.

Field Methods

Adult birds were captured using mist nets in both passive and targeted efforts. For general demographics, arrays of seven nets were set up at varying locations within each marsh, dispersing efforts across entire sites and reducing number of repeated locations. Targeted efforts were used to specifically capture females and connect them to their nests, using two nets surrounding the nests of interest. Captured birds were banded with a uniquely numbered aluminum USGS band and color band coded to their site of capture. Band numbers and color patterns were recorded on all sparrows captured, including recaptured individuals. Females received an additional color band fastened with a PIT tag to aid in connecting them to nests throughout the season while being minimally invasive (using an RFID reader). Morphological measurements were also taken along with fecal, blood, and feather samples with varying consistency throughout the years. Bycatch (non-sparrow species) were recorded by species and released without bands and measurements.

Nests were searched for and monitored throughout the breeding season using Ruskin et al.'s (2017) protocol with patterned combing of habitat in combination with observing behavioral cues from females. Once nests were located, their GPS coordinates, dimensions, vegetation, and status (active, with eggs or nestlings, how many, etc…) were recorded and marked with a flag 2m from the nest in relation to a set reference point. Nests were monitored every 2-3 days to record the updated status and collect measurements of the nestlings (which were banded if possible) until the nest was completed (either through failure or success). At the end of the season, a nest fate was established to each nest based on the observations of the final nest check. Fates included: fledged (if at least one nestling was believed to have fledged), flooded (ex: if nest bowl was wet), depredated (ex: if chicks were missing or nest was damaged), unknown failure, or unknown (Ruskin et al., 2017).

Vegetation characteristics of nest sites and randomized locations were also collected but not utilized for this study.

Data Analysis

Available data records from 2011-2022 were compiled from the various databases into one Microsoft Excel sheet for analyses. Recorded captures were filtered using the appropriate study sites and removing males from the sample. Only nests with a confirmed connection to a female ID were used. These nests were then further filtered to include only those with known nest fates. Age was reconstructed for the remaining females using their band numbers and initial banding dates. For example, if a female was found nesting in 2019 and had been banded in 2018 as a nestling, that female was considered a one-year-old. Only females that were banded as nestlings or hatch-years were included in the study to ensure proper aging.

Statistical tests included linear regression and t-tests to test hypotheses about female age and reproductive success. Linear regression used the range of ages present as the independent variable (i.e. 1, 2, 3, 4) whereas t-tests used females grouped as either one-year-olds or older than one year.

Reproductive success was defined as whether a nest failed entirely (fail) or fledged at least one chick (success), as well as based on proportions, with higher eggs hatched and chicks fledged interpreted as successful.

Dependent variables were the proportions of each nest fate, proportions of each egg fate, and proportions of each nestling fate. Nest fates included hatched (if at least one egg hatched), fledged, flooded, or depredated, with proportions calculated out of total nests. Egg fates included hatched, flooded, or depredated, with proportions calculated out of an individual nest's maximum number of eggs and then averaged. Nestling fates included fledged, flooded, or depredated, with proportions calculated out of an individual nest's maximum number of nestlings and then averaged; nests that did not hatch were excluded from this analysis.

Results

Overall

A total of 1192 saltmarsh sparrow nests were recorded between 2011-2022 at the four sites. Of these, 846 nests were connected to a female, and 108 of the females associated with these nests were banded as hatch-years or nestlings. For hypothesis testing, my sample size was these 108 nests with known-aged females. Most of these nests were from CL (68 nests), followed by EL (30), PB (9), and MQ (1). The most common nest fate was fledged, followed by flooded (Fig. 2). There were 264 nestlings in the dataset, with 167 belonging to one year-old females and 95 to older females. Nestling fates similarly reflected the overall nest fates.

The age of females ranged from one to four years old, with most individuals in the youngest category (64 females), steadily decreasing in abundance with age (2: 29 females, 3: 14 females, 4: 1 female).

Linear Regression

The proportion of hatched nests increased significantly (at alpha value 0.05) with age while the proportion of hatched eggs decreased with age. The proportion of eggs flooded decreased significantly with age, and the proportion of nestlings fledged increased significantly with age. Due to a single female representing the four-year-old category, however, these results are difficult to assess with confidence.

T-tests

Contradicting the linear regression, older females hatched a lower proportion of nests but at a marginally significant level (p-value: 0.079). Also contrary to the regression, older females had a higher proportion of eggs with a flooded fate and with a significant p-value (0.031) (Fig. 3). The two remaining t-tests agreed with the regression results, with older females hatching a lower proportion of eggs (p-value: 0.008) (Fig. 4) and fledging a higher proportion of nestlings (p-value: 0.008) (Fig. 5).

Discussion

My initial hypotheses were that older females would overall have greater reproductive success than younger females, producing a higher proportion of hatched nests/eggs and fledged nests/chicks. Additionally, I expected younger females to be more prone to flooding as a cause of nest failure whereas older females would be more susceptible to nest predation.

Contrary to my hypotheses, older females hatched a significantly smaller proportion of their nests and eggs than younger females. Similarly, the eggs of older females were flooded at a higher proportion than those of younger females. This discrepancy in apparent 'success' may be attributed to nest timing. In order to fit their nests between the monthly high tides, saltmarsh sparrows must be able to time their nesting cycle within the narrow window to avoid flooding (Gjerdum et al., 2005). Other avian species have shown variation in timing of their nest initiation based on age (Perdeck and Cave, 1992; Desrochers, 1992). While older, more experienced birds should hypothetically be better attuned to this time period, rising sea levels could alter or shorten the window that these sparrows have to successfully raise a nest. Younger, inexperienced birds may then be at an advantage, since they have none of the learned behaviors that would encourage them to repeat what was previously successful. Older females, however, could actually be suffering from sticking to methods that are no longer applicable to the current tidal situation. This phenomenon has been described as an ecological or evolutionary trap (Schlaepfer, 2002).

While fewer of their eggs hatched and fewer of their nests yielded nestlings, older females did fledge a higher proportion of both total nests and individual nestlings. This pattern is consistent with results of previously mentioned studies (Wooller et al., 1990; Hamer and Furness, 1991; Wheelwright and Schultz, 1994). Interestingly, the paper by Wheelwright and Schultz (1994) also incorporates predation into their study design, simulating nest failure to investigate re-nesting attempts. While depredation was not a significant factor for the saltmarsh sparrows I studied, comparing the attempts of younger vs. older females to rebuild after a flooding failure may be a point of interest for future studies to investigate how long it takes to build the new nest and whether or not it was successful. This is especially important considering females in this study were labeled as one year old if they were found nesting the year after they were banded as a nestling, but this does not take into account any experience gained from multiple nest attempts within that season. Additionally, the monitoring of the fledged offspring for this study design ceases once they leave the nest which means survival to adulthood is unknown. Regardless, this result may provide support to my previously mentioned theory of nest initiation since these data suggest older females, once they are past the egg stage, do show increased reproductive success. Essentially, though they may get flooded out more in the early stages, the experience of older females enables them to provide better care for the offspring that do hatch and increase the likeliness that they will fledge. One related study on silvereyes has shown that the older females are more efficient foragers than their younger counterparts, improving nestling success (Jansen, 1990).

While only one of my hypotheses was supported by the data, the results still suggest a correlation between age and reproductive success in female saltmarsh sparrows with older individuals flooding out at early stages but fledging higher proportions of the young that survive. If older individuals are expected to be more productive in offspring, then a deviation from that pattern could be concerning as it could mean that even the most experienced of the population are suffering from the effects of outside forces. Without effective conservation methods, the future of species like the saltmarsh sparrow are bleak. Their population is declining at a rate of 9% a year, the highest of any passerine bird species in North America. At the current rate, complete extinction is predicted within the next 50 years, and some say sooner (Marshall et al., 2020). As of 2020, they are listed as globally endangered and are being considered for listing by the USFWS under the Endangered Species Act, but the decision was delayed until 2023 (Gifford, 2019). The preservation of the saltmarsh sparrow is important as it represents the conservation of salt marsh habitat as a whole.

Salt marshes are essential due to both their role as a habitat to the sparrows as well as economically valuable species of fish that use them as nurseries. Its provision of ecosystem services is also critical to humans. The dense vegetation helps protect the shoreline from waves, flooding, and erosion. In addition, they store carbon which helps mitigate the impacts of climate change, and limits pollution from human waste as well as through the removal of excess nutrients (Renzi et al., 2019).

Human modification has resulted in the loss of over half the tidal wetland area in the United States (Gjerdrum et al., 2005). An additional threat to the saltmarsh habitat includes ditching for mosquito control, which affects natural drainage, encourages erosion, and will likely never become vegetated without intervention (Redfield, 1972). The surge of invasive species, which alters the plant community, shoreline development, which affects nutrient and salinity levels, overfishing, pollution, and oil spills are also topics of concern (Renzi et al., 2019).

Saltmarsh sparrows serve as an indicator species for marsh health, but healthy numbers are required for accurate assessments. In order to monitor and address the numerous threats of marsh degradation, better understanding of the factors affecting sparrow population dynamics and nesting success are needed. With increased knowledge of the effects of aging on the reproductive success of saltmarsh sparrows, demographic surveys could better estimate fecundity and prioritize conserving populations with the greatest growth potential.

Relevant Figures

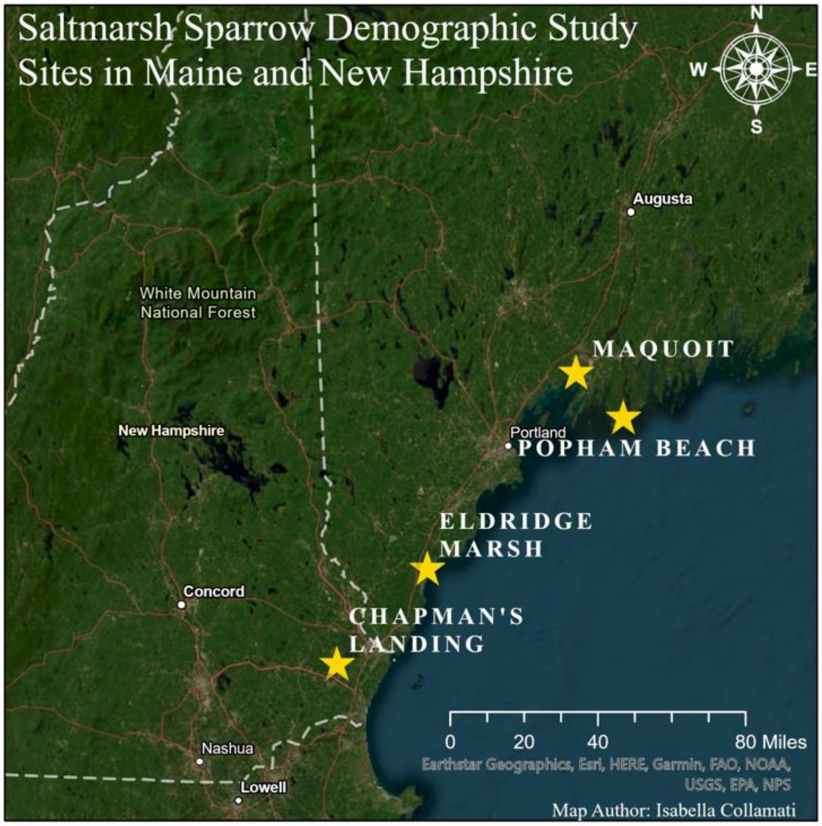

Figure 1. ArcGIS Map of Maine and New Hampshire, depicting locations of four study sites used for this project (Maquoit Bay, Popham Beach, Eldridge Marsh, and Chapman's Landing).

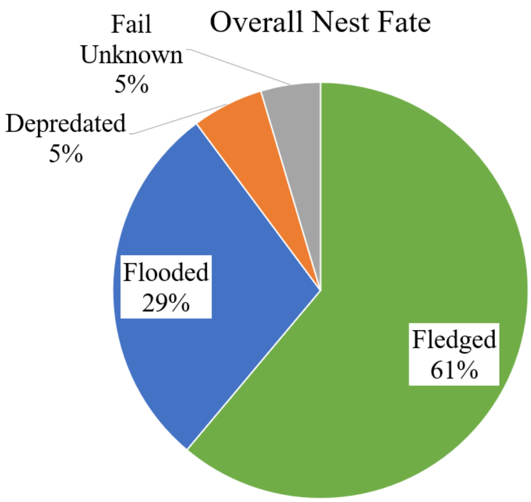

Figure 2. Overall nest fates of the 108 nests monitored over the 2011-2022 study period. Values are compiled between the four sites (Chapman's Landing, Eldridge Marsh, Popham Beach, and Maquoit Bay) and across all age groups. Fledged fates are nests with at least one chick leaving the nest.

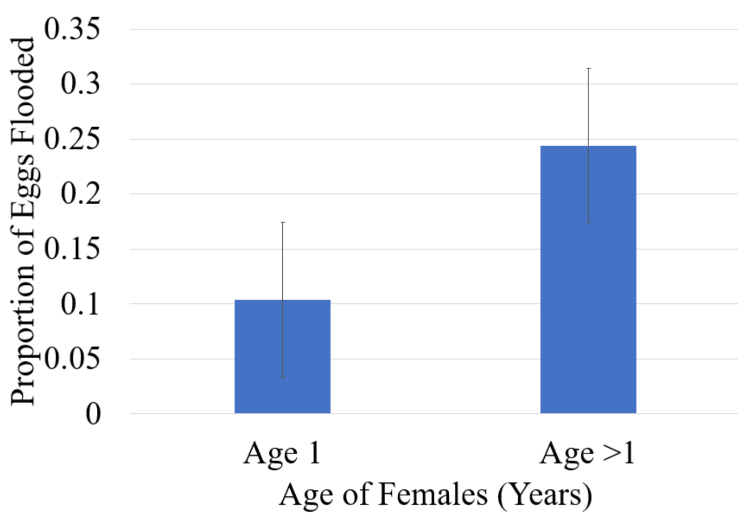

Figure 3. Bar graph comparing the average proportion of flooded eggs in nests of one-year-old females to nests of older females. Error bars included depict standard error and do not overlap, showing a significant t-test outcome of older females losing a higher proportion of eggs to flooding than younger females. Data collected from 2011-2022 between four sites (Chapman's Landing, Eldridge Marsh, Popham Beach, and Maquoit Bay).

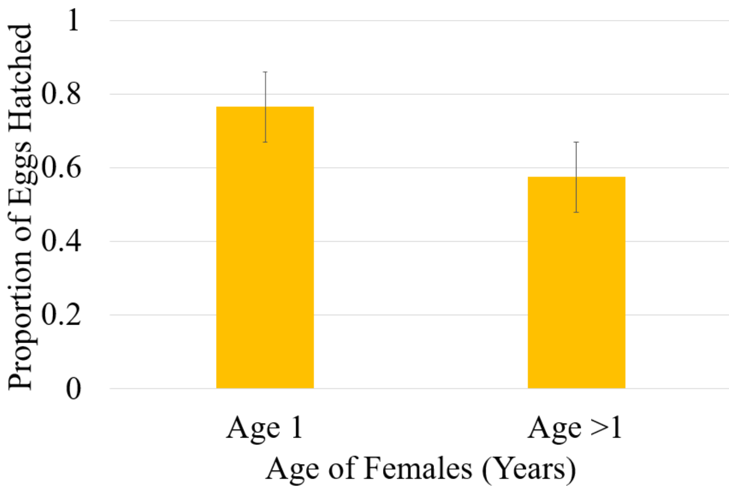

Figure 4. Bar graph comparing the average proportion of eggs hatched in nests of one-year-old females to nests of older females. Error bars included depict standard error and do not overlap, showing a significant t-test outcome of younger females hatching a higher proportion of eggs than older females. Data collected from 2011-2022 between four sites (Chapman's Landing, Eldridge Marsh, Popham Beach, and Maquoit Bay).

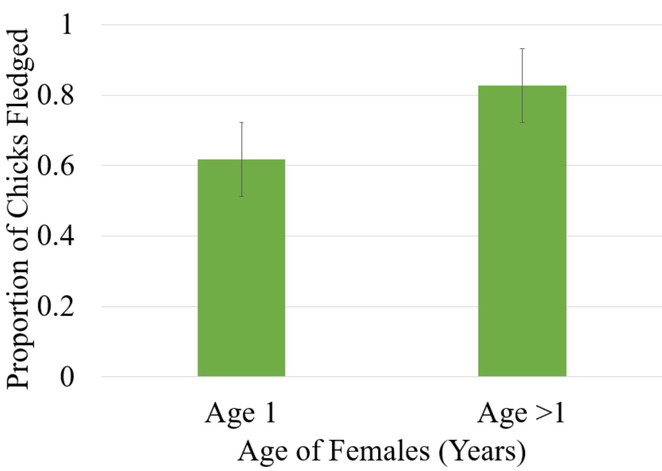

Figure 5. Bar graph comparing the average proportion of fledged nestlings in nests of one-year-old females to nests of older females. Error bars included depict standard error and do not overlap, showing a significant t-test outcome of older females fledging a higher proportion of nestlings than younger females. Data collected from 2011-2022 between four sites (Chapman's Landing, Eldridge Marsh, Popham Beach, and Maquoit Bay).

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