Timing and nest aggression in Purple Martins (*Progne subis*)

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A thesis submitted to the Department of Biological Sciences, University of Manitoba,

in partial fulfilment of the requirements for the course

BIOL 4100 (Honours Thesis)

for the degree of

Bachelor of Science (Honours)

Abstract

Earlier arrival at the breeding grounds after migration can confer advantages for migratory songbirds, including access to higher food abundance and to better compete for desirable territories. Selection for one sex to arrive before the other is often due to intrasexual competition for territories and mates, though the link between early female arrival (protogyny) and female-female competition is unclear from lack of research on female territoriality and nest aggression. I explored timing and aggression in the cavity nesting species Purple Martin (*Progne subis*), where males are known to defend nest cavities and compete aggressively toward other males though display protogyny, but these patterns have not been investigated in females. I investigated whether early arrival timing has selected for higher levels of aggression, competition for territory, and nest defense between females. I conducted a behavioural experiment at nesting colonies of Purple Martin in Winnipeg, Manitoba, where levels of aggression were assessed with simulated territorial intrusion using taxidermy mounts of female martins. I found that early nesting and age were positively associated with aggression, affirming that older birds that arrive and nest earlier are likely more experienced and in better condition to defend cavities. Sex had no significant effect on aggression, suggesting shared duty of defending nests by both members of the social pair regardless of the sex of the intruder. Females defended most aggressively after eggs were laid, which supports the parental investment hypothesis, where higher aggression is associated with higher nest investment. Overall, this study provides new insight on the role of age and timing on female aggression and nest defense in a migratory songbird, which will be valuable to further explore as migration timing advances with climate change.

Acknowledgements

This project would not have been possible without the help of my advisor, Dr. Kevin Fraser, whose support was invaluable every step of the way. I am also extremely to the members of my advisory committee, Dr. Gail Davoren and Dr. Jane Waterman, who volunteered their time to provide their expertise and feedback. Additionally, I could not have conducted this study without the generosity of University of Manitoba Faculty of Science who funded my research. Special thanks to fellow students Vinuri Mendis, Yantong Tan, and Avital Shalev for their help in collecting data and aid throughout the project.

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Introduction

Over the past 55 years, many species of migratory birds have been experiencing population declines ("The State of Canada's Birds Report" 2024). A key factor contributing to these declines is climate change, which disrupts the timing of migration to breeding sites in unfavourable ways. Many birds are unable to adjust their migration timing and the shift in temperature causes food abundance to peak earlier before the birds reproduce, causing a shortage of food to feed their young (Both et al. 2006). Other birds are advancing their migration times in step with the rapid progression of climate change, demonstrating a level of phenotypic plasticity in response to their changing environment (Both and Visser 2001; Gienapp et al. 2007). There are many benefits to earlier arrival times outside of avoiding mismatches with their food sources, as an earlier arrival also allows birds to claim territories with higher food abundance and safer nesting sites (Petit and Petit 1996). These early birds tend to be of higher phenotypic quality, which attracts other high-quality mates leading to higher offspring survival (Sergio et al. 2007).

Earlier breeding is also associated with higher reproductive success. Clutches that were laid earlier in the season tend to be larger as they are closer to peak food abundance, allowing the parent to feed more young (Perrins 1965; Brown and Roth 2002). Hatchlings from earlier clutches are also more likely to survive past their first year and join the breeding population (Hochachka 1990; Brown and Roth 2002).

Despite early nesting benefitting both parents' reproductive success, sometimes selection favours early arrival more in one sex over the other. This phenomenon is called protandry when males arrive at breeding grounds earlier and protogyny when females arrive earlier (Morbey and Ydenberg 2001). Protandry and protogyny have been well studied in species where one sex is

more dominant and must compete intrasexually for territory and mates. For example, male warblers that arrive earlier are more territorial and better competitors (Francis and Cooke 1986). Males of polygynous species that arrive earlier are also more likely to engage in extra-pair mating, increasing their reproductive success (Hasselquist 1998; Canal et al. 2012). There are potential costs for females of protandrous species that could offset reproductive advantages, such as poorer weather or unfavourable temperatures compared to later-arriving females which would reduce selection for protandry (Møller 1994; Møller et al. 2009). In species where females compete for territories, the females also arrive before males to out-compete other females, thus displaying protogyny (Oring and Lank 1982; Reynolds et al. 1986). Protogyny is far less studied than protandry as intrasexual competition between females is not well-explored in birds, and the sexes in protogynous species are harder to differentiate. To add, sex-based discrepancies in timing have also been observed in socially monogamous species without a clear reason, leaving potential questions for researchers (Turcotte-van de Rydt et al. 2023).

Along with arrival time, the level of territoriality may also change depending on the level of investment, which changes throughout the breeding season. Parental investment involves any action that increases their offspring's survival such as feeding or guarding at the cost of investing in other offspring (Trivers 1972). As the breeding season progresses, offspring become more valuable as parents have invested more of their time and energy to care for them. Parents tend to defend nests more intensely against predators the more nests are developed (from incubation to hatching to young growing) regardless of early or late breeding (Bjerke et al. 1985; Tryjanowski and Goławski 2004; Shew et al. 2016).

Purple Martins (*Progne subis*) are a long-distance migratory swallow and aerial insectivore. They are colony nesters that nest exclusively in man-made houses, foraging for

insects relatively close to nesting sites (Brown et al. 2021). Mature birds that have returned to breed more than once (after second year or ASY birds) exhibit sexual dimorphism, with females lacking the metallic blue ventral plumage of males (Brown et al. 2021). During breeding season, returning males select cavities that attract females, with pairs remaining socially monogamous for the season and sharing nest-building and young provisioning duties, though during incubation and brooding females usually stay in the nest while males defend the cavity (Allen and Nice 1952). Physical altercations over cavities between members of the same sex have been observed in this species before, but intrasexual competition and defense behaviours of females have not been described or studied in depth (Allen and Nice 1952; Johnston and Hardy 1962).

Purple Martins, like many songbirds, are often described as protandrous, as males are perceived as more dominant and territorial and arrive at breeding sites earlier, though newer evidence suggests females are advancing their migration times to be similar or earlier than males (Morton and Derrickson 1990; Turcotte-van de Rydt et al. 2023; Smith and Fraser 2024). Their colonial nesting sites with limited spaces create competition for cavities as higher cavities that are further from ground predators are chosen first by competitive, earlier arriving birds that also tend to be the oldest (Morton and Derrickson 1990). Additionally, early egg-laying dates are associated with higher fledging success and thus parental fitness (Brown and Roth 2002). It is possible that selection for early arrival in female Purple Martins could be driven by sexual selection or intrasexual competition in the same way that protandry is selected for, though information on female aggression and protogyny in general is scarce (Kokko et al. 2006). There is a need for more research on sex-based differences in timing and nest site competition in Purple Martins, as well as for female songbirds in general.

I aim to discover a link in Purple Martins between early nesting and intrasexual aggression. I hypothesize that aggressive behaviour is driven by intrasexual competition to claim the best territory earlier in the breeding season, thus increasing reproductive success by nesting earlier. Alternatively, birds could be more aggressive later in the season when offspring have hatched due to increased investment into reproduction and caring for offspring. I predict that female birds would be more aggressive to female intruders compared to males due to intrasexual competition, which also drives selection for protogyny. I also predict that more aggressive birds will claim higher quality (i.e. physically higher) cavities and will be most aggressive prior to nests being built.

Methods

Study system

Purple Martins are excellent subjects for behavioural study for a few reasons. Their colonial nesting and housing make nesting sites easily accessible and concentrated in one area, allowing for many individuals to be sampled in a shorter timeframe. It is also easy to identify males and females as well as their rough age (second year/SY or after second year/ASY) by their plumage, so no handling is required to gather age and sex data. ASY males are most easily identified, and SY males and females can be differentiated from ASY females by speckles of blue feathers under the tail and throat and pale undertail coverts respectively (Brown et al. 2021). Research took place at 3 established field research sites located in or near Winnipeg: the University of Manitoba Fort Garry campus; Fort Whyte Alive; and Oak Hammock Marsh. Each

site contained two artificial nest houses with 14 nest cavities each of varying heights. Sites were located near bodies of water where insect abundance is high. The methods used for this research have been approved by the University of Manitoba Animal Care Committee (Protocol #F2025-006, AC11969).

Nest aggression trials

Like Lipshutz and Rosvall (2021) I used taxidermy mounts of female Purple Martins to simulate nest intrusion. I obtained mounts from the avian Biological Collections at the University of Manitoba. One, posed in a perched position, was attached to the house in front of a targeted cavity without blocking access to the cavity (Figure 1a). The other, lying on its belly, was attached to the inside of the cavity with just its beak outside, simulating a more aggressive intruder (i.e. female martins typically sit within the cavity entrance, effectively blocking the entrance for entry by others; Figure 1b). To determine whether any aggressive behaviours are truly in response to an intruding female rather than any object, control observations were taken using rolled up fabric approximately the same size as the mounts attached in the same positions as the mounts in separate trials (Figure 1c). Use of a control or mount as well as positioning it inside or outside the cavity was randomly decided (coin flip to decide mount or control, then again to decide inside or outside). Prior to setting up trials, cavities were first observed to ensure birds (particularly females) are present there, then checked for nest progress, recorded at one of the following stages: no nest; partial nest; completed nest; nest with eggs; nest with young. Along with nest progress, the date of the trial, position of the mount/control object, site location, exact cavity ID (unique across all sites), cavity height (numbered 1-4 with 1 being the highest), and ambient temperature were also recorded as variables.

For each trial, one mount was placed in its respective position at a cavity where at least one bird was seen going in and out during preliminary observation. Observations were recorded via video camera to be later analyzed. Observations were recorded from at least 10 meters away to prevent distractions or disturbance to the birds. Trials lasted 5 minutes beginning when the bird returns to the observed cavity and were seen within ~30 cm of the mount. Aggression was quantified by the total duration of aggressive behaviours observed during the 5 minutes rounded to the nearest second. Aggressive behaviours included swooping attacks, where the bird flew up above the house and dove into the mount to contact the mount (full time of positioning for dive and the dive itself were counted as aggressive). Aggressive pecking and clawing included the bird grabbing or contacting the mount with its feet or beak. For trials using the mount placed inside the cavity, time spent inside the cavity with the mount was also counted as aggressive. In trials where both the male and female were present, both birds' behaviours were recorded and quantified as separate observations under the same trial. The duration (seconds) of behaviours described above were summed for an overall 'aggression score.'

Of the birds present in each trial, I recorded their sex and age as well their leg band number if available as observed with a spotting scope to check for repeated observations, though most birds observed were unbanded. Sex and age were determined visually. As the birds settled and finish their nests, I recorded the date of the first egg laid by the birds at the cavity the trial took place.

Trials were repeated across the three study sites throughout June and July at different cavities, though occasionally cavities were repeated at different times. In total, I observed 48 individuals across 35 trials.

Statistical analysis

All statistical tests were conducted in R version 4.5.2. Normality of aggression scores was assessed with a Shapiro-Wilk test. To see if aggression scores from control observations differed significantly from experimental observations, I conducted a Wilcoxon rank-sum test. Control aggression scores were found to be significantly lower than in observations with the mounts ($W = 358$, $p = 0.001$), so they were removed from the dataset, leaving me with 25 trials and 35 observations. Aggression was not significantly different between mounts positioned inside or outside the cavity ($W = 118.5$, $p = 0.41$). For this reason, aggression scores from both mount positions were included and lumped together for analysis.

Effects of sex, age, cavity height, first egg date, and nest progress on aggression score were analyzed with generalized linear models created using the MASS package (see Table 1 for a list of models). Multiple models were run due to the small sample size, as more than three parameters would likely overfit the model. Mixed models with random effects were considered to account for non-independence due to some trials containing observations of both the male and female defending the cavity at the same time and some cavities observed more than once throughout the season, though variance components for cavity ID and trial ID were consistently near zero. For this reason and for avoiding non-convergence with a smaller dataset, I opted to only include fixed effects. Because there were many observations with an aggression score of 0, I ran the GLMs with a negative binomial distribution to account for overdispersion (Green 2021). After fitting the models, I checked for overdispersion by plotting residuals using the simulateResiduals function from the DHARMa package.

Results

Aggression scores were significantly impacted by the bird's age when controlling for sex and cavity height (p-value < 0.0001, Table 2) as well as when controlling for first egg date and cavity height (p-value = 0.0075, Table 3), where older (ASY) birds had higher aggression scores (Figure 2). Sex was not a significant predictor when paired with age and cavity height (p-value = 0.75, Table 2).

Cavity height also had a strong effect on aggression scores, with the 3rd highest cavities being associated with the highest aggression scores in all three models (Table 2,Table 3, andTable 4; Figure 2 and Figure 3). The 2nd highest cavities also predicted higher aggression scores when accounting for first egg date and nest progress in model 3 (p-value = 0.043, Table 4). Nest progress had some impact on aggression, though the only significant predictor was nests with eggs after accounting for first egg date and cavity height (p-value = 0.048, Table 4). Partial nests that were sampled never produced eggs so they were not included in this analysis. Nests with young had the widest range of aggression scores, varying from 0 to 219 (Figure 5), but when combined with first egg date and cavity height had an insignificant effect on aggression (p-value = 0.53, Table 4).

The date of the first egg laid also influenced aggression, with birds defending cavities with earlier-laid eggs being more aggressive overall (Figure 4 and Figure 5). This effect was significant in conjunction with cavity height and nest progress (p-value < 0.0001, Table 4), though not when age and cavity height were included (Table 3).

Discussion

This study explored female aggression and nest defense behaviour in a long-distance migratory songbird. Research on migration timing and nest defense has tended to focus on male behaviours leaving many research gaps regarding factors driving female protogyny. I explored these patterns in purple martins, finding that levels of aggression were most associated with timing of nesting, age, and level of parental investment. Earlier-nesting and older females tended to be more aggressive and defended nests most vigorously after eggs were laid, supporting the hypothesis that more invested nests would be defended more aggressively.

I found that females that arrived earlier had higher levels of aggression in behavioural trials than females that had later timing. Early arriving birds tend to arrive in better body condition, with higher fat stores and higher body mass that allows them to more easily defend territories in physical combat (Sergio et al. 2007; Filiberti and Perlut 2018). This difference in condition may explain the higher levels of aggression I observed in birds that had earlier nests and likely also arrived earlier after spring migration. Purple martin first egg dates tend to be associated with migration arrival timing, where the first to arrive have the earliest nests (Sturch et al. in prep.). While I found this pattern in both male and female martins, aggression in early-arriving Purple Martins had been previously unexplored in females.

Age played a significant role in predicting aggression scores, with the significantly higher aggression from ASY birds compared to SY (Figure 2). In most species of birds, including Purple Martins, older individuals tend to arrive at breeding grounds earlier, allowing them to claim more desirable territories and/or begin nesting and laying eggs earlier (Oring and Lank 1982; Francis and Cooke 1986; Morton and Derrickson 1990). If older birds are arriving at breeding sites in

better condition to defend and claim territories, it makes sense that their aggression scores were significantly higher than the younger birds. However, these patterns had previously only been described for male Purple Martins but my study demonstrates that earlier female timing is also associated with higher levels of nest aggression in Purple Martins.

I found that nest aggression levels were highest when young had hatched. The increasing level of aggression after nests were completed and birds had laid eggs is indicative of parents defending nests that they had put more investment into, supporting the parental investment hypothesis. This increase is similar to the pattern seen by Tryjanowski and Goławski (2004) where both male and female Red-Backed Shrikes (*Lanius collurio*) increased their aggressive behaviour towards predators as offspring increased in value. The similarities end here, as I did not find that nests with young predicted higher aggression scores when accounting for first egg-laying date, despite having some of the highest aggression scores (Figure 5). Date of first egg likely explained much of the variance in aggression scores, which shows that early nesters defend nests most vigorously, perhaps owing to the advantages of early arrival. It is also possible that later nesting birds failed to hatch any young during the scope of the study, leaving the most aggressive and early nesting birds overrepresented in the nest with young category which likely explains the non-significant coefficient for nests with young despite the high aggression score (Table 4). Trials ended prior to young fledging due to the widespread presence of ectoparasites (mites, fly larvae) in nests across all field sites, as transferring the mounts from one cavity to the next would spread parasites to otherwise less affected nests. Exposure to ectoparasites after egg-laying has detrimental effects on both the parent and offspring, contributing to higher mortality of young and higher provisioning requirements for parents (Richner and Heeb 1995). Early nesting young would have had less time exposed to the parasites, likely having higher survival

rates than later hatching young, contributing to higher fitness for parents that begin nesting sooner (Badyaev et al. 2006).

Acting more aggressively at the egg-laying stage of the breeding season contradicts my prediction that aggression would be highest before nesting because of competition for nesting sites. If birds display less territoriality prior to nesting than after nests are built unlike the findings of Rosvall (2008), early arrival in order to claim territory may not be a driver of aggression in Purple Martins. Instead, nest defence behaviour could just be a response of birds to any perceived intruder regardless of species with the presence of young being a larger factor in determining the level of aggression. Though I showed that the martins reacted to the mounts more aggressively than the control object, it is unclear if the birds in this study were reacting to the mount as if it was another martin or a different competing bird, perhaps due to the mounts' lack of movement or vocalizations. Limitations in mount realism and a lack of research on nest defense in Purple Martins prevent any definitive conclusions to be drawn on infanticide within this species or by another introduced species. Nonetheless, there is a clear pattern of higher aggression in order to protect future offspring when parental investment is high.

This experiment also yielded some unexpected results contradictory to initial predictions regarding comparisons between the sexes to explain protogyny in this species. The lack of effect of sex on aggression is surprising considering only female mounts were used in this study. There was no significant difference in aggression scores between males and females (Figure 4), coinciding with the findings of Lipshutz and Rosvall (2021), who also found that aggression did not differ between sexes of various bird species regardless of the sex of the mount. Though Lipshutz and Rosvall (2021) did not study a colonial cavity nester like the Purple Martin, they did show that the comparable cavity-nesting Tree Swallow (*Tachycineta bicolor*) had similar

aggression levels between the sexes. Tree swallows also have similar migration patterns to Purple Martins described by Turcotte-van de Rydt et al. (2023), with females migrating at faster rates than males (Gow et al. 2019). While social monogamy in Purple Martins would have predicted this outcome as both sexes compete for territory and mates, the similarities in aggression between the sexes does not coincide with protogyny observed in this species (Turcotte-van de Rydt et al. 2023). It is therefore likely that selection for territoriality in females is not what is driving their earlier arrival times compared to males as both parents defend their nests equally against any intraspecific intruder.

Though the similarity between the sexes fails to explain selection for protogyny in this system, it does give insight on the role of each parent in defending the nest. Nest defense during incubation and brooding was previously thought to be the male's job, though females could be sharing the role more than in the past as selection favours protogyny and female territoriality (Allen and Nice 1952; Turcotte-van de Rydt et al. 2023). Further analysis of the effect of both sex and nest progress on aggression could show whether females are equally as aggressive as males during incubation and brooding (nests with eggs and nests with young) or if previous observations are still accurate and females are actually more territorial during pre-egg laying stages.

Even though aggression was lower before nests were built, the time period of this study may not have captured the highest aggression scores from the earliest arriving birds, as cavities may have been claimed and defended weeks before nest-building began. Missing data from the early nesting stages of the earliest-arriving birds could explain the extremely low aggression scores from cavities without nests compared to even partially built nests. The earliest arriving birds could have already successfully claimed and defended their cavities shortly after their

arrival in late April, which was before research began, so the only peak in aggression that was recorded came after their young hatched. Since these early arriving birds were predicted to be more aggressive compared to most birds which arrive in May, their aggression scores may be skewed lower during the nest progress stages prior to nest building depending on how many individuals were not sampled earlier. This potential omission could also explain why lower cavities had higher aggression scores if later-arriving birds were still defending the less desirable cavities not claimed by the early birds.

Another unexpected result was lower cavity heights (particularly height 3) had higher aggression scores than higher cavity heights even when accounting for the other variables. Decreased aggression in higher cavities compared to lower cavities could mean that there is not competition for higher cavities, suggesting predation from ground predators is not a risk for the nesting birds in this study compared to those studied by Morton and Derrickson (1990). In contrast, competition from other species of cavity-nesting birds could be causing the lack of defense for higher cavities instead. House Sparrows (*Passer domesticus*) are known for their persistent territoriality towards Purple Martin homes, fighting martins for nesting cavities and removing their eggs and young (Brown 1977). House Sparrows have been shown to prefer higher cavities, displacing native birds and forcing them to nest in lower cavities (Cordero and Salaet 1988). Interspecific competition from other birds at high cavities alongside predation risk at lower cavities could explain why Purple Martins fought amongst themselves for the middle cavities where higher aggression scores were seen. For this study, I did not consider presence of interspecific competitors such as House Sparrows let alone assess interspecific competition for cavities, though the possible effects may warrant further research.

In conclusion, nest aggression in Purple Martins is driven by a variety of factors relating to individual traits and breeding ground nesting choices. Older birds acted most aggressive towards a perceived intruder, perhaps because of the better condition they arrived with that aided in arriving earlier. The selection pressure for early nesting is likely driving high aggression for early arriving birds as competition for cavities from other martins or other species is fierce with the limited space of colonial housing. The role of females in nest defense is also clearer, as both parents will attack intruders regardless of sex. Further studies on the effect of mate presence during a trial would require expanding the dataset for a proper repeated measures experiment, as sample size constrained analysis of many factors. More consistent repeated sampling of cavities throughout the breeding season across each stage of nesting would be better suited for mixed-effect modelling, including random effects for cavity and trial to account for non-independence without overfitting. Including mounts of male Purple Martins and mounts of competing species such as House Sparrows could also clarify the role of intersexual competition in Purple Martins as well as uncover the effect of interspecific competition on cavity selection. Aggression after egg-laying and hatching suggests a need to defend their nests from intruders that may be threatening their eggs and offspring, as infanticide is often perpetrated by competing species such as the House Sparrow who are known to toss martin eggs out of nests, but less often by other martins (Loftin and Roberson 1983). Additionally, future research on the reproductive success of more aggressive females (i.e. aggressive females fledge more young) could also show whether selection favours both early arrival and high aggression. Investigating these selection patterns would be especially important as climate change brings earlier springs, potentially causing changes in birds' timing and behaviour.

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Table 1. Predictors for aggression score with negative binomial generalized linear model analysis.

Model	Predictors
1	Sex + Age + Cavity height
2	First egg date + Age + Cavity height
3	First egg date + Cavity height + Nest progress

Table 2. Results of negative binomial generalized linear model analysis for predicting aggression score from sex, age, and cavity height (Model 1). Reference groups were female for sex, after second year for age, and height 1 for cavity height.

Predictors	Coefficient	Std. error	z	p-value	
Male	-0.170	0.532	-0.320	0.75	
Second year	-3.798	0.727	-5.226	0.000	***
Height 2	1.436	0.768	1.869	0.06	
Height 3	2.183	0.658	3.321	0.001	***
Height 4	0.695	0.925	0.751	0.45	

***p-value < 0.001, **p-value < 0.01, *p-value < 0.05

Table 3. Results of negative binomial generalized linear model analysis for predicting aggression score from first egg date, age, and cavity height (Model 2). Reference groups were after second year for age and height 1 for cavity height.

Predictors	Coefficient	Std. error	z	p-value	
First egg date	-0.068	0.041	-1.688	0.09	
Second year	-2.158	0.807	-2.675	0.007	**
Height 2	0.876	0.767	1.143	0.25	
Height 3	1.684	0.709	2.374	0.018	*
Height 4	0.881	0.908	0.970	0.33	

***p-value < 0.001, **p-value < 0.01, *p-value < 0.05

Table 4. Results of negative binomial generalized linear model analysis for predicting aggression score from first egg date, cavity height, and nest progress (Model 3). Reference groups were height 1 for cavity height and no nest for nest progress.

Predictors	Coefficient	Std. error	z	p-value	
First egg date	-0.366	0.092	-3.969	0.000	***
Height 2	1.636	0.807	2.026	0.04	*
Height 3	1.791	0.678	2.641	0.008	**
Height 4	0.468	0.905	0.517	0.60	
Complete nest	1.420	1.894	0.750	0.45	
Nest with eggs	3.188	1.610	1.981	0.04	*
Nest with young	-1.180	1.916	-0.616	0.54	

***p-value < 0.001, **p-value < 0.01, *p-value < 0.05

Figure 1. Photos of mounts positioned A) outside a cavity, B) inside a cavity, and C) a control placed outside a cavity.

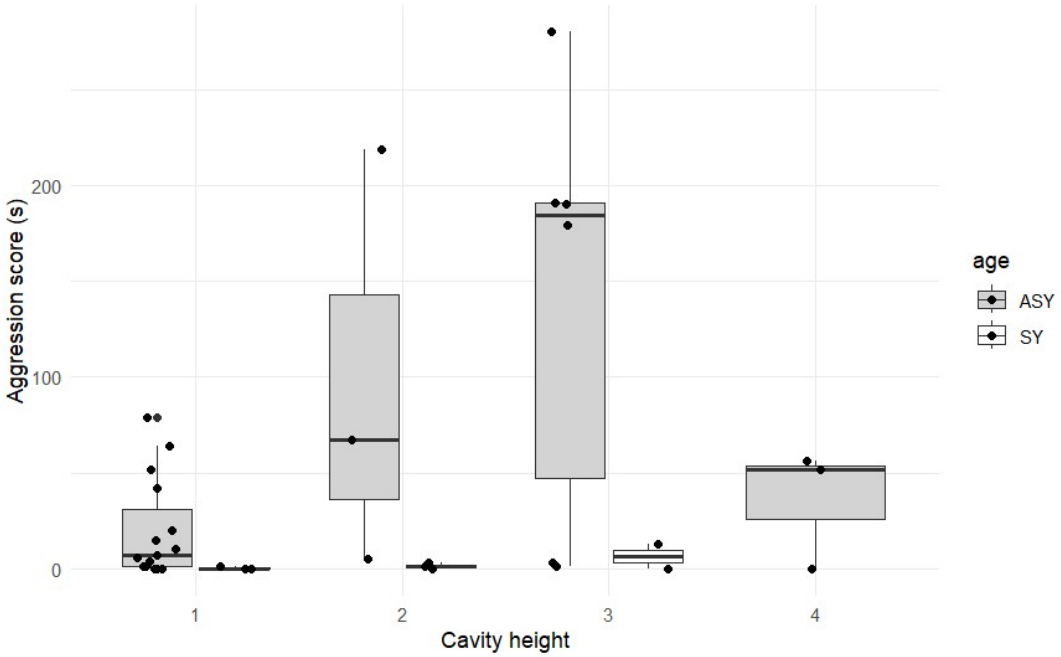

Figure 3. Boxplots for the number of seconds aggression was shown (aggression score) by Purple Martins (*Progne subis*) towards a simulated cavity intrusion by the height of cavity, where 1 is the highest and 4 is the lowest, and age (second year=white, after second year=shaded). (n = 25, 35 observations).

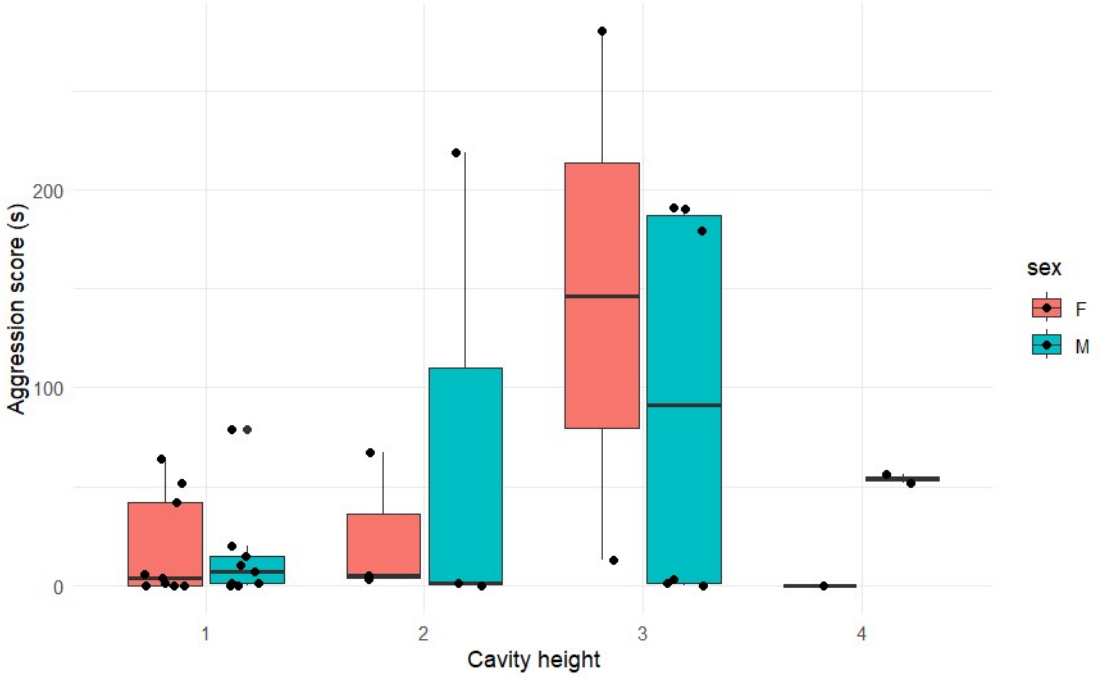

Figure 2. Boxplots for the number of seconds aggression was shown (aggression score) by Purple Martins (*Progne subis*) towards a simulated cavity intrusion by the height of cavity, where 1 is the highest and 4 is the lowest, and sex (female=red, male=blue). (n = 25, 35 observations).

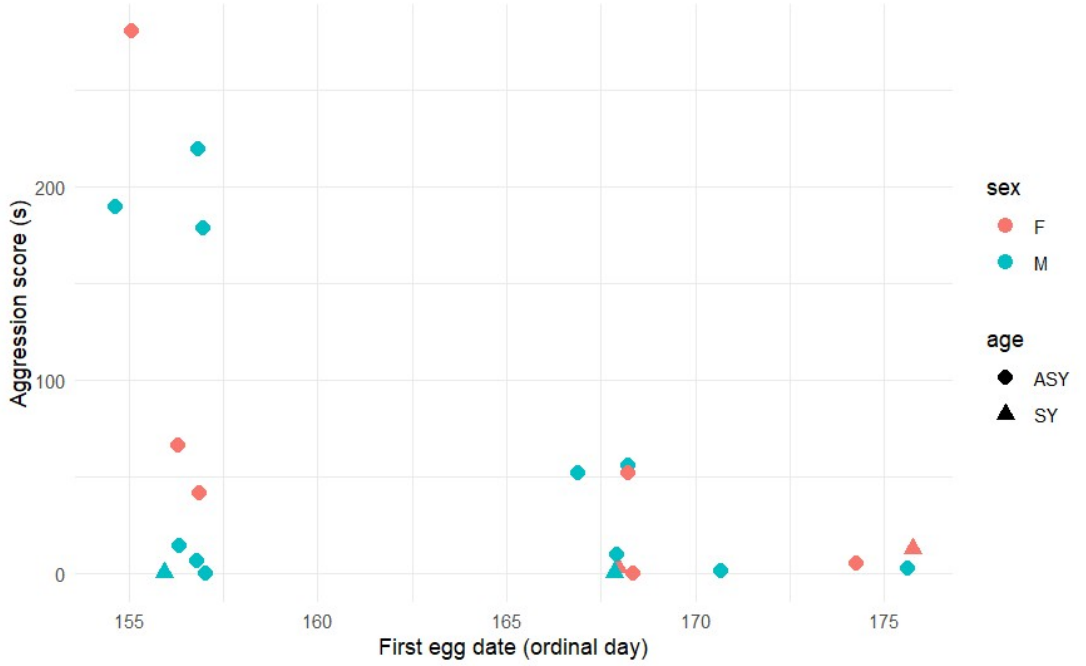

Figure 4. Plot of aggression score by the date an egg was first laid in the nest (ordinal day). Sexes are separated by colour (females red and males blue) and ages separated by shape (second year are triangles, after second year are circles). Observations from cavities where eggs were never laid are not shown.

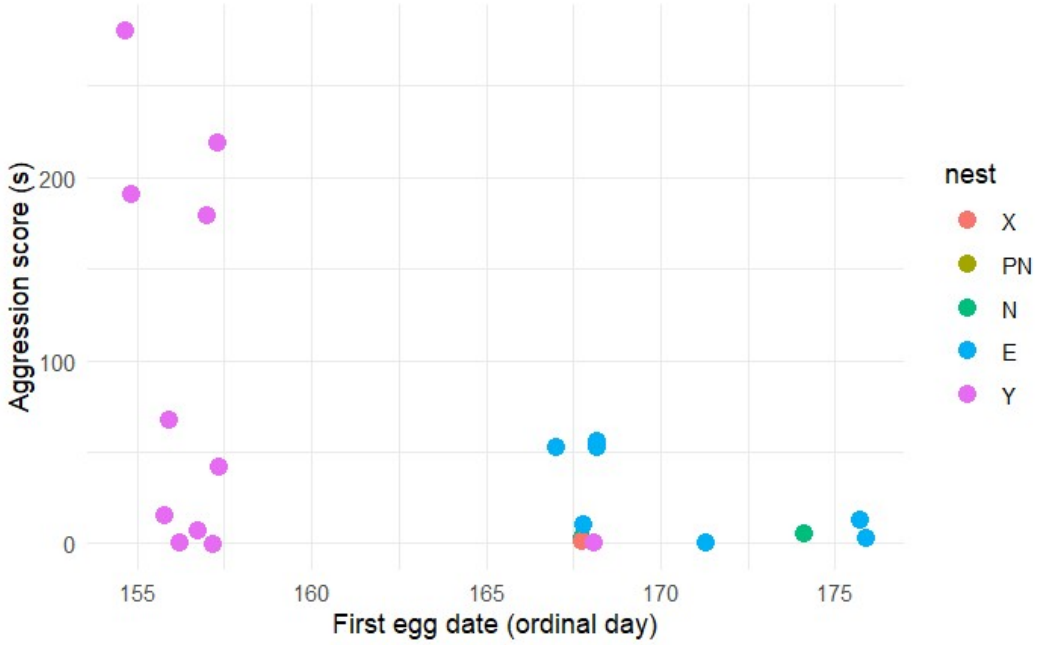

Figure 5. Plot of aggression score by the date an egg was first laid in the nest (ordinal day). Nest progress separated by shape, where X is no nest (circle), PN is partial nest (triangle), N is fully built nest (square), E is eggs present (cross), and Y is young present (box). Observations from cavities where eggs were never laid are not shown.