Benitez Saldivar, M. J., and V. Massoni. 2025. Sex differences in nest attention against simulated conspecific intrusions in the Saffron Finch (*Sicalis flaveola pelzelni*). Journal of Field Ornithology 96(2):1. https://doi.org/10.5751/JFO-00632-960201

Avian Behavior, Ecology, and Evolution

Sex differences in nest attention against simulated conspecific intrusions in the Saffron Finch (*Sicalis flaveola pelzelni*)

Diferencias entre sexos en la atención de nidos en contra de intrusiones conespecíficas simuladas en el Pinzón Azafrán (*Sicalis flaveola pelzelni*)

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ABSTRACT. Nest attention has a strong effect on nestling survival and is essential for the reproductive success of the parents. Secondary cavity nesters compete intensively for access to cavities and face high risk of nest usurpation by conspecifics. We describe nest attention by both sexes in the Saffron Finch (*Sicalis flaveola pelzelni*), and compare rates of nest attention in response to experimental territorial intrusions of live male and female conspecifics. During the incubation and brooding periods, in response to intrusions by other females or males, both natural and experimental, the attending females arrived at the nest immediately. Females also stayed close to the nest during egg laying and "old" 8–9 days old nestlings' periods, but never attacked the intruders. Attending males took more time to approach the nest but spent a lot of time close to it, during the egg laying, incubation, and "young" 4–5 days old nestling periods, especially during simulated intrusions by other males. Focal males kept intruders of both sexes at bay and physically attacked the male intruders. The observed responses could be elicited by the perceived risk of mate or cavity loss before raising a brood. This study on a multi-brooded subtropical obligate secondary cavity nester reveals sex differences of nest attention in response to the sex of conspecific intruders.

RESUMEN. La atención de nidos tiene un efecto fuerte en la sobrevivencia de los polluelos y es esencial para el éxito reproductivo de los padres. Aves que anidan en cavidades secundariamente compiten intensamente por el acceso a cavidades y enfrentan un alto riesgo de usurpación de nidos por conespecíficos. Describimos la atención de nidos por ambos sexos en el Pinzón Azafrán (*Sicalis flaveola pelzelni*), y comparamos las tasas de atención de nidos en respuesta a intrusiones territoriales experimentales de conespecíficos machos y hembras vivos. Durante los periodos de incubación y cría, en respuesta a intrusiones por otras hembras y machos, tanto naturales como experimentales, las hembras asistentes arribaron al nido inmediatamente. Las hembras también se quedaron cerca al nido durante los periodos de puesta de huevos y el periodo de polluelos "viejos" de 8-9 días de edad, pero nunca atacaron a los intrusos. Los machos asistentes tomaron más tiempo en acercarse al nido pero pasaron mucho tiempo cerca a él, durante los periodos de puesta de huevos, incubación, y el periodo de polluelos "jóvenes" de 4-5 días de edad, especialmente durante intrusiones simuladas por otros machos. Los machos focales mantuvieron a raya a los intrusos de ambos sexos y atacaron físicamente a los intrusos machos. Las respuestas observadas podrían ser provocadas por el riesgo percibido de pérdida de pareja o cavidad antes de criar pichones. Este estudio de un ave subtropical de múltiples crías que anida en cavidades secundariamente, revela la diferencia entre sexos en la atención de nidos en respuesta al sexo de intrusos conespecíficos.

Key Words: *intraspecific competition; nest attention; secondary cavity nester; Sicalis flaveola pelzelni; simulated territorial intrusions; Thraupidae*

INTRODUCTION

Aggressive behavior entails costs that are worth bearing if individuals succeed in ensuring benefits essential to their survival and reproduction by excluding competitors from the use of key resources (Lopez-Sepulcre and Kokko 2005, Duckworth 2006). Aggression and territoriality are necessarily frequent at the intraspecific level, given that conspecifics share limiting resources (Newton 1994). In socially monogamous species, both sexes are expected to participate in the territorial exclusion of conspecifics (Canoine and Gwinner 2005, Hall and Peters 2009).

In birds, both males and females are usually more aggressive toward a same-sex than to an opposite-sex intruder (Mays and Hopper 2004, Marshall-Ball et al. 2006, Gill et al. 2008). Given that most monogamous birds exhibit extra-pair paternity (Griffith et al. 2002, Maldonado-Chaparro et al. 2018), the sexes differ in their interests and high intrasexual aggression has been interpreted in reference to sexual conflict and mate guarding (Busch et al. 2004, Hall 2004, Rogers et al. 2007). Indeed, although males are aggressive toward male intruders throughout the nesting cycle, aggression is intensified when their social partners are fertile as a response to increased risk of paternity loss (Tobias and Seddon 2000, Chuang-Dobbs et al. 2001). Males are less aggressive toward intruding females, perceived as potential social or extra-pair mates (Stutchbury 1998, Double and Cockburn 2000). However, males often show aggressive behavior toward females attempting to usurp males' territory (Stutchbury and Robertson 1987), destroy the eggs (Kasahara et al. 2014, Krieg and Getty 2016) or kill its offspring (Chek and Robertson 1991).

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Likewise, female-female intraspecific aggression influences the social and genetic mating system in several species (Sandell and Smith 1997, Rosvall 2011). Indeed, female aggressiveness is higher during egg-laying and incubation (Krieg and Getty 2016) than during the nestling period, either to avoid the settlement of other females, which may divert parental care away from their primary brood (Slagsvold and Lifjeld 1994, Krieg and Getty 2016) or because nests with eggs are more vulnerable than those with nestlings (Krist 2004).

Competition for nesting sites is strong in obligate secondary cavity nesters (Rosvall 2011, Moreno 2015) because the availability of cavities is often a limiting resource (Rosvall 2008), which may affect population size (Cockle et al. 2010). Consequently, both sexes are expected to react strongly toward potential usurpers of suitable nesting sites (Brazill-Boast et al. 2011, Cantarero et al. 2015).

Thraupidae is a species-rich family of songbirds endemic to the Americas, but remains understudied (Shogren et al. 2019, Bonaparte et al. 2024). The Saffron Finch, *Sicalis flaveola pelzelni*, P. L. Sclater 1872, is a multi-brooded thraupid, secondary cavity-nesting subspecies with sexual dichromatism and delayed plumage maturation. Females and second-year males have a whitish belly and an olive back streaked with black, while after-second year males are golden yellow. The occurrence of sexual dichromatism (Badyaev and Hill 2003), delayed plumage maturation (Hawkins et al. 2012, Vergara et al. 2013), and the need for pre-existing cavities suggest intense intrasexual competition for cavities among males, and, among females, for access to cavities defended by males. Although second year Saffron Finch males can reproduce successfully (Palmerio and Massoni 2009), to maximize parental investment, females should prefer dominant, more experienced mature-plumaged males (Hawkins et al. 2012, and references therein), given they show high temporal consistency in parental care (sensu Wang et al. 2023). Females co-build the nest, incubate and brood alone, and feed their nestlings at higher rates than males (Palmerio and Massoni 2011). Typical clutch size is 3.9 ± 0.05 eggs. Incubation lasts 13 days and nestlings fledge at 14–15 days (Palmerio and Massoni 2009). In a previous study in this subspecies, we found 31.8% of extra-pair offspring and 51.8% of broods with at least one extra pair nestling (Benítez-Saldívar et al. 2019). If both sexes seek extra-pair copulations away from the nest, they reduce nest attention.

Simple observations of nest attention can fail to detect the reactions to conspecifics because territorial intrusions are unpredictable and usually lead to short-term responses (Logue and Gammon 2004). An alternative is to conduct experimental intrusions using stuffed decoys (Préault et al. 2002, Murphy et al. 2009) or, as in this study, presenting live caged individuals (Busch et al. 2004, Van Dongen and Mulder 2008).

Here, we describe nest attention by males and females and evaluate the response of males and females to simulated (experimental) territorial intrusions (hereafter STIs) by live conspecifics of both sexes along the nesting period. We expect both sexes to react toward conspecific intrusion, particularly during the egg-laying period, when the risk of nest takeover is higher. We also expect individuals to be more aggressive toward same-sex than opposite-sex intruders.

METHODS

Sicalis flaveola pelzelni is distributed from southeastern Brazil and eastern Bolivia to central Argentina, south to La Pampa Province (Ridgely and Tudor 1989). Because second-year males are indistinguishable from females for humans (Benítez-Saldívar and Massoni 2018), we exclusively conducted observations of spontaneous nest attention and STIs on breeding pairs composed of females and after-second year yellow males raising the first brood of the season.

This study was carried out between December 2004 and March 2005 in a field system of 96 nestboxes separated by approximately 30 m from each other, mounted on metal poles between 1.3 and 1.7 m above the ground and attached to main fence wooden posts around cattle enclosures in an agricultural landscape of the province of Buenos Aires, Argentina (35°34'S, 58°01'W). Saffron Finches preferred to build nests in nestboxes that were close to buildings and trees like tala (*Celtis tala*), espinillo (*Acacia bonariensis*), and eucalyptus (*Eucalyptus* sp.).

We conducted the experiment with nests of four eggs. Nestboxes were monitored throughout the breeding season, daily from the beginning of the nest-lining stage to detect the onset of egg-laying, every two days during incubation, and daily from the day before the estimated date of hatching. Nestboxes were checked every two days until nestlings were 12 days old, when visits were interrupted to avoid premature fledging; visits were resumed one day after the expected departure date to record the number of successfully fledged nestlings.

The same observer made all the observations (n = 28) and recorded nest attention by both sexes during the hours of greatest activity (6:00 to 12:00 am) at egg-laying (n = 7), at day 5 of the incubation period (n = 7), at nests with young nestlings (4–5 days old, n = 7), and with old nestlings (8–9 days old nestlings; n = 7). The observer positioned 20 m away from the focal nestbox, used binoculars (10x50) and a voice recorder to register the activity for 30 min as soon as a member of the pair was seen at < 5 m from the nestbox. From the recordings, we registered: the sex that arrived first, the latency of each sex to approach within 5 m from the nestbox, and the proportion of time spent by each sex at < 5 m from the nest. Such variables have been used as a cue of aggressive disposition toward intruders in previous studies (Sandell and Smith 1997, Kleiber et al. 2007).

Following observations, the same observer conducted the STIs experiments using female or male live intruders. We decided to use live caged birds because stuffed models do not move. A stationary, non-interactive model does not contribute to the natural dynamic of interaction between live animals and this could be potentially perplexing to focal birds (Laidre and Vehrencamp 2007). Live model behaviors, however, may interact with that of focal birds in ways that make difficult the assessment of the response. Stuffed models have proved to be equally useful to prompt nest owners' reactions than real cuckoos (Tryjanowski et al. 2018) and tree swallows (Bentz et al. 2019). Therefore, we decided to avoid killing the individuals we used as intruders.

We performed female STIs during egg-laying (n = 7), incubation (n = 7), nests with younger nestlings (n = 7), and with older nestlings (n = 7); we also performed the same number of male STIs along the nesting period. We performed live intruder experiments in which the intruder was kept for 30 min in a standard cage (20x20x20 cm) hanging from the fence at 1 m above the ground and placed lateral to the focal nestbox at a distance of 1 m from it as in Sandell and Smith (1997). This placement provides nest owners with multiple perching sites and reduced inter-territory variance in visibility of the caged bird (Kleiber et al. 2007). The intruder birds were captured at a field site 120 km away. The intruder birds hopped between two perches within the cage or remained motionless; we did not detect measurable differences in the response of focal birds to those behaviors. Before carrying out the experiments, we performed molecular sexing to identify the sex of the drab intruder using the protocol of Fridolfsson and Ellegren (1999).

The sex of the first intruder was established at random. Two days after the first experiment, a subsequent STI was performed with an individual of the opposite sex. Between presentations, the live models were lodged in individual cages (20x30x50 cm) with food and water *ad libitum*, under conditions of visual but not acoustic isolation and a natural light-darkness regime. After experimentation, the intruder birds were released at the capture site.

Data was analyzed using non-parametric statistics given that assumptions of normality and equality of variances were not met in either original or transformed data sets. We used the McNemar test for dependent samples to compare the proportion of times the males and females returned first or together to the nestbox. We used the Wilcoxon test to compare the latency to approach of males and females at < 5 m of their nest during observations or male and female STIs at each nesting stage, and the proportion of time spent at < 5 m from the nestbox. Statistical analyses were performed with STATISTICA 8.0 software (StatSoft Inc).

RESULTS

The Saffron Finches at our study site made 44 reproductive attempts in the breeding season 2004–2005, during which they used 27% (26 of 96) of the total available nestboxes.

Nest attention: parental care observations

Half of the time, the pair approached the nest together during egg laying, and there was no difference between the sex that arrived first (McNemar $\chi^2 = 0.455$, $df = 1$, $P = 0.56$). During the incubation period, the pair arrived to the nest together 36% of the time (McNemar $\chi^2 = 3.84$, $df = 1\ 0\ P = 0.04$). During the young nestling period, 30% of the visits were made by both parents together, but females arrived first most of the time (McNemar $\chi^2 = 7.88$, $df = 1\ P = 0.009$). During egg laying and old nestling phases, both males and females took a while to approach at < 5 m from the nest, between 20.5 to 24.5 mins and 10 to 18.5 mins, respectively, and the pair did not differ on that behavior. (Fig. 1). During the incubation and young nestling periods males took significantly longer than females to approach the nest (Fig. 1). During the old nestling period, males showed a similar latency to approach the nest than females, arrived together with the female in 41% of visits, and there were no differences between sexes when arriving first (McNemar $\chi^2 = 0.455$, $df = 1$, $P = 0.34$). During the observations, the proportion of time males perched at < 5 m varied greatly (Fig. 2), and did not differ significantly from the amount of time females perched at < 5 m from nests (not shown).

Simulated territorial intrusions

We found no differences in which sex arrived first to the scene (McNemar $\chi^2 = 0.455$, $df = 1$, $P = 0.67$). When the intruder was a female, we found no differences in the latency to approach the nest between focal males and females during the egg-laying period. But males approached the nest sooner than females during the incubation and young nestlings' periods. Males and females showed no differences in latency to approach the nest during the old nestling period (Fig. 1). When the intruder was a male, there were no differences between males and females' latency to approach the nest at any stage of the nesting period (Fig. 1).

Females' proportion of time close to the nest was significantly different between female STIs and natural observations during the egg laying and old nestling periods and not different during the incubation and young nestling periods (Fig. 2). Females' response during male STIs was non-significantly different than during natural observations at any nesting period (Fig. 2). Females never evicted nor attacked the experimental intruders.

Males' proportion of time close to the nest was significantly different between female STIs and natural observations only during the incubation and young nestling periods, and not during the egg-laying and old nestling periods (Fig. 2). The same results were obtained during male STIs (Fig. 2). We had to stop male STIs twice because of the violence displayed by the focal males, who flapped their wings and attempted to peck the intruder male through the cage bars.

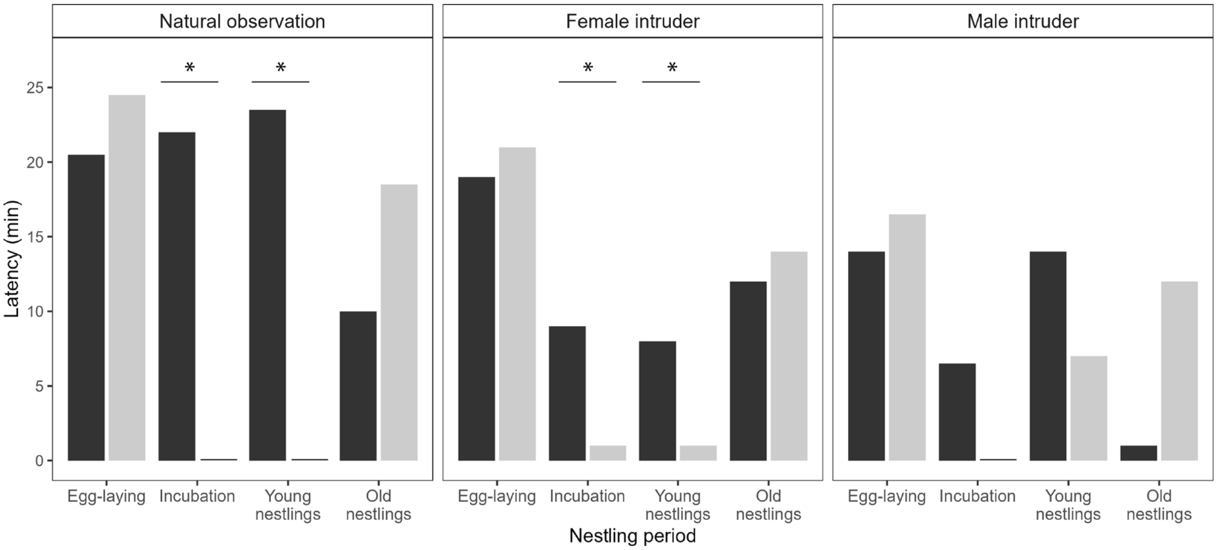
When non-experimental natural intrusions occurred (either females, drab males, or ASY males) in all cases the males evicted the intruder. The aggressive behavior consisted in flushing the birds away by supplanting them repeatedly from different perches. Females did not react to natural intruders.

DISCUSSION

We characterized the natural nest attention of Saffron Finches and the responses of each sex to female and male simulated territorial intrusions along the nesting period. We found that females reacted more to intrusion by other females than to intrusions by males. Females arrived sooner than males to their nests during a female intrusion, especially during the incubation and young nestling periods, but never attacked the intruders. Males did not change the latency to arrive at the nest with either female or male experimental intruders. Males did increase the proportion of time spent close to both types of intruders, during incubation and young nestling periods. Occasionally, males violently attacked the experimental ASY male intruder, and also flew away the drab natural intruders.

Nest attention is frequently performed by both sexes in monogamous species. As reported for other obligate secondary cavity nesters (Rosvall 2008, 2011, Moreno 2015), we expected Saffron Finches to actively defend their cavity, in particular during the egg periods (Knight and Temple 1986, Krist 2004). However, we found that focal birds of both sexes did not reduce the latency to approach the nest during the egg-laying period. At the egg stage, nests are under high risk of destruction or usurpation by other cavity nesters like House Wrens *Troglodytes aedon*, White-rumped Swallows *Tachycineta leucorrhoa*, House Sparrows *Passer domesticus,* or by conspecifics (Palmerio and Massoni 2009).

Fig. 1. Median of the latency (min) to approach at < 5 m to the nest by male (dark grey) and female (light grey) Saffron Finches (*Sicalis flaveola pelzelni*), in the absence of simulated intrusions, and during female and male simulated intrusions along the nesting cycle. (*) denotes significant comparisons at P ≤ 0.05.



During the egg-laying period, females may move away from the nestboxes in search of additional nutrients (de Heij et al. 2006), or to actively pursue extra-pair fertilizations (e.g., Double and Cockburn 2000). In our study population, there is moderate extra-pair fertilization rate (Benítez Saldívar et al. 2019) and males may have performed mate-guarding during the fertile period, following their partners closely (Low 2005), therefore leaving the nestbox alone. As an indirect cue of mate guarding, the proportion of cases in which the pair returned together to the nestbox peaked during the egg-laying period. No direct observation of egg-destruction or nest usurpation by conspecifics have been registered so far in this species. Early ringing during nestbox choice and the experimental reduction of available and preferred nestboxes would help to quantify the extent of intraspecific competition in this species (Rosvall 2008, Jacot et al. 2009, Krieg and Getty 2016).

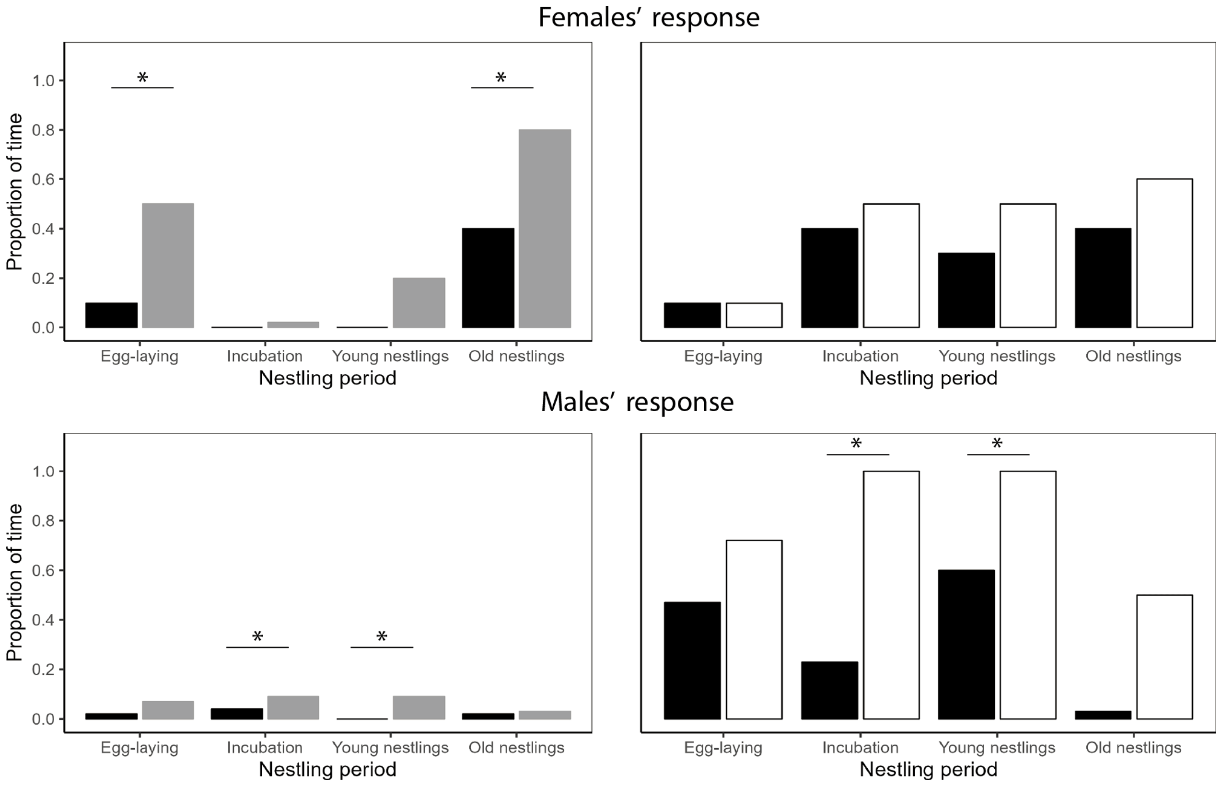
Males showed a relatively constant latency at the different nesting stages during observations. We have witnessed Saffron Finches engage in the defense of nestbox surroundings rather than in the defense of a multi-purpose territory (sensu Lack 1968), and have observed males flying over long distances away from and to the nestboxes to feed nestlings. The fact that they maintain similar latency along the nesting period suggest they may spend time within a given (fixed) distance from the nests.

Not surprisingly, given that they incubate and brood the chicks alone (Palmerio and Massoni 2011), females approached sooner than males and spent more time inside the nestbox during incubation and when nestlings were young. Females partially reduced their association with the nestbox when nestlings grew older, until matching that of males. It is possible that during this period females recover physically, considering that parental care is female-biased and shows high temporal consistency (sensu Wang et al 2023). Saffron Finches produce an average of 1.7 broods and up to three successful broods per season (Palmerio and Massoni 2009). Recovery of body condition at the end of the first breeding attempt is essential to produce a second brood and to increase the chance of survival to the next breeding season.

As expected for cavity nesters (Botero-Delgadillo et al. 2015, Cantarero et al. 2015) both sexes of the Saffron Finch increased their nest attendance in response to a simulated territorial intrusion. Despite the fact that during the studied period Saffron Finches only used 28% of the available nestboxes, they clearly preferred those placed in the vicinity of buildings and forest borders over those inside the forest or placed in the open pampas, making intraspecific competition for such nestboxes very likely (Massoni, *unpublished data*). During the simulated intrusions both males and females responded and, contrary to the natural observations, there was no difference in the sex that arrived first. However, the response of residents varied depending on the sex of the intruder, as is frequently the case in socially monogamous birds (Fernández and Azkona 1994, Zilberman et al. 2001). In fact, several species are more aggressive toward same-sex than opposite-sex intruders (Marshall-Ball et al. 2006, Gill et al. 2008).

Saffron Finch females seemed more attentive (i.e., showed shorter latencies) than males to detect intrusions; they spent more time at < 5 m from the nests in response to female STIs during the egg-laying period than during natural observations (Brylawski and Whittingham 2004, Rosvall 2011). During egg-laying, the resident female is at risk of being actively displaced by another female, thus precluding any chance of reproduction (Jacot et al. 2009, Rosvall 2011). Females may also suffer egg dumping (Kleiber et al. 2007) or intraspecific brood parasitism (Lyon and Eadie 2008). Indeed, at the same study site, Saffron Finch females can raise nestlings other than their own: six females were excluded as mothers of the offspring in the nest that they attended (4.0% of the analyzed nestlings, 11.1% of the studied broods; Benítez-Saldívar et al. 2019). Therefore, a heightened response to female

Fig. 2. Proportion of time spent by male and female Saffron Finches (*Sicalis flaveola pelzelni*), at a distance < 5 m from the nest during spontaneous nest attention (black) and during female (light grey) and male (white) simulated intrusions along the nesting cycle. (*) denotes significant comparisons at P ≤ 0.05.



intrusion during the egg-laying period might be aimed at minimizing rearing of unrelated offspring or avoiding nest and mate usurpation. Females instantly approached the nest during the incubation and young nestling periods. This is in line with expectations, given that females incubate and brood alone, therefore requiring frequent and long bouts for the embryos and nestlings to grow and thrive (Palmerio and Massoni 2011).

Females also spent a great amount of time at < 5 m from the nestbox during female intrusions when nestlings were closer to fledge. This could be explained by the importance of guarding the nestbox as a resource to raise a second brood within the same reproductive season (Czapka and Johnson 2000). Although females reduced the latency to approach the nest during the young nestling period, they did not do so during the old nestling period. We currently have no explanation for this difference. Females also remained close to the nestboxes during male intrusions when nestlings were older, suggesting that males are also perceived as potential cavity usurpers. Alternatively, male intruders could be viewed as potential social or genetic partners for a subsequent breeding attempt within the season. However, females did not solicit copulation from caged males, in contrast to that observed in the Reed Warbler *Acrocephallus scirpaceus* (Hoi et al. 2013). Finally, females may especially attend the old nestlings because the probability of survival until reproduction is higher in older offspring than in younger ones (Dawkins and Carlisle 1976, Andersson et al. 1980).

Males are expected to be particularly involved in territorial defense if they are more efficient at deterring intruders of the same or different species. Saffron Finch males spent longer at the nest when conspecifics of both sexes intruded, a behavior that was also observed in Marsh Harriers *Circus aeruginosus* (Fernández and Azkona 1994), Orange-tufted Sunbirds *Nectarinia osea* (Zilberman et al. 2001), and in contrast to Zenaida Dove *Zenaida aurita* (Quinard and Cézilly 2012). Intrasexual aggression among males throughout the nesting cycle has already been reported in other species, particularly during the fertile period of the female (Tobias and Seddon 2000).

Resident males also spent a greater proportion of time close to the nest with male than female intruders, unlike Zenaida Doves, in which males and females differ in the frequency rather than in the intensity of the responses (Quinard and Cézilly 2012). In fact, only Saffron Finch males displayed aggression toward caged intruders in the form of pecking attempts and wing flapping, with these behaviors being exclusively directed against same-sex, after-second year males. In addition, we occasionally observed adult-plumaged males engaged in violent and even lethal confrontations in our study area (Massoni, *unpublished data*). These highly aggressive contests and our results indicate the existence of very strong intrasexual male competition in the Saffron Finch, as we expected for a dichromatic obligate secondary cavity nester with delayed plumage maturation.

This study demonstrates the occurrence of sex differences in nest attention against conspecific intruders in the Saffron Finch and completes previous results (Palmerio and Massoni 2011) showing division of parental duties. Overall, males are more involved in nest attention than females (they reacted to both female and male STIs). In this regard, future studies should be focused on quantifying the trade-off between foraging far away from the nest and the efficiency of male mate guarding behavior to avoid or reduce extra-pair fertilization in this species.

Acknowledgments:

We are thankful to one anonymous reviewer for thoughtful advice on the manuscript. We thank Andrés G. Palmerio for helping in data collection and authorities and personnel of the Instituto Tecnológico de Chascomús (INTECH-CONICET) for permission to work and reside. We thank Carolina I. Miño for constructive criticism and proofreading our manuscript.

Data Availability:

Code sharing is not applicable to this article because no code were analyzed in this study.

LITERATURE CITED

Andersson, M., C. G. Wiklund, and H. Rundgren. 1980. Parental defence of offspring: a model and an example. Animal Behaviour 28:536-542. https://doi.org/10.1016/S0003-3472(80)80062-5

Badyaev, A. V., and G. E. Hill. 2003. Avian sexual dichromatism in relation to phylogeny and ecology. Annual Review of Ecology Evolution and Systematics 34:27-49. https://doi.org/10.1146/annurev.ecolsys.34.011802.132441

Benítez Saldívar, M. J., and V. Massoni. 2018. Lack of conspecific visual discrimination between second-year males and females in the Saffron Finch. PLoS ONE 13(12):e0209549. https://doi.org/10.1371/journal.pone.0209549

Benítez Saldívar, M. J., C. I. Miño, and V. Massoni. 2019. Genetic mating system, population genetics and effective size of Saffron Finches breeding in southern South America. Genetica 147:315-326. https://doi.org/10.1007/s10709-019-00072-4

Bentz, A. B., K. J. Philippi, and K. A. Rosvall. 2019. Evaluating seasonal patterns of female aggression: case study in a cavity-nesting bird with intense female-female competition. Ethology 125:555-564. https://doi.org/10.1111/eth.12881

Bonaparte, E. B., C. Cuatianquiz Lima, H. D. Ferreira-Xavier, J. S. da Hora, F. G. Di Sallo, F. G. López, K. L. Cockle, and M. G. Núñez Montellano. 2024. Ecology and conservation of cavity-nesting birds in the Neotropics: recent advances, future directions, and contributions to ornithology, Ornithological Applications 126(4):duae042. https://doi.org/10.1093/ornithapp/duae042

Botero-Delgadillo, E., Y. Poblete, and R. A. Vásquez. 2015. Nestling mortality as a consequence of interspecific competition between secondary cavity nesters in the sub-Antarctic forests of Chile. Wilson Journal of Ornithology 127:131-134. https://doi.org/10.1676/14-073.1

Brazill-Boast J., E. Van Rooij., S. R. Pryke, and S. C. Griffith. 2011. Interference from long-tailed finches constrains reproduction in the endangered Gouldian finch. Journal of Animal Ecology 80:39-48. https://doi.org/10.1111/j.1365-2656.2010.01756.x

Brylawski, A. M. Z., and L. A. Whittingham. 2004. An experimental study of mate guarding and paternity in house wrens. Animal Behaviour 68:1417-1424. https://doi.org/10.1016/j.anbehav.2004.02.016

Busch, D. S., J. C. Wingfield, and I. T. Moore. 2004. Territorial aggression of a tropical passerine, *Zonotrichia capensis*, in response to a variety of conspecific intruders. Behaviour 141:1173-1188. https://doi.org/10.1163/1568539042664605

Canoine, V., and E. Gwinner. 2005. The hormonal response of female European Stonechats to a territorial intrusion: the role of the male partner. Hormones and Behaviour 47:563-568. https://doi.org/10.1016/j.yhbeh.2004.12.007

Cantarero, A., T. Laaksonen, P. E. Järvistö, D. Gil, J. López-Arrabé, A. J. Redondo, and J. Moreno. 2015. Nest defence behaviour and testosterone levels in female Pied Flycatchers. Ethology 121:946-957. https://doi.org/10.1111/eth.12407

Chek, A. A., and R. J. Robertson. 1991. Infanticide in female Tree Swallows: a role for sexual selection. Condor 93:454-457. https://doi.org/10.2307/1368967

Chuang-Dobbs, H. C., M. S. Webster, and R. T. Holmes. 2001. The effectiveness of mate guarding by male Black-throated Blue Warblers. Behavioural Ecology 12:541-546. https://doi.org/10.1093/beheco/12.5.541

Cockle, K. L., K. Martin, and M. C. Drever. 2010. Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. Biological Conservation 143:2851-2857. https://doi.org/10.1016/j.biocon.2010.08.002

Czapka, S. J., and L. S. Johnson 2000. Consequences of mate sharing for first-mated females in a polygynous songbird, the House Wren. Wilson Bulletin 112:72-81. https://doi.org/10.1676/0043-5643(2000)112[0072:COMSFF]2.0.CO;2

de Heij, M. E., P. J. van den Hout, and J. M. Tinbergen. 2006. Fitness cost of incubation in Great Tits (*Parus major*) is related to clutch size. Proceedings of the Royal Society Series B 273:2353-61. https://doi.org/10.1098/rspb.2006.3584

Dawkins, R., and T. R Carlisle. 1976. Parental investment, mate desertion and a fallacy. Nature 262:131-133. https://doi.org/10.1038/262131a0

Double, M., and A. Cockburn. 2000. Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens. Proceedings of the Royal Society B: Biological Sciences 267:465-470. https://doi.org/10.1098/rspb.2000.1023

Duckworth, R. A. 2006. Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. Behavioural Ecology 17:1011-1019. https://doi.org/10.1093/beheco/arl035

Fernández, C., and P. Azkona, 1994. Sexual differences in conspegific territorial defense of Marsh Harriers (*Circus Aeruginosus*). Journal of Raptor Research 28:23-26.

Fridolfsson, A. K., and H. Ellegren. 1999. A simple and universal method for molecular sexing of non-ratite birds. Journal of Avian Biology 30:116-121 https://doi.org/10.2307/3677252

Gill, S. A., L. M. Costa, and M. Hau. 2008. Males of a single-brooded tropical bird species do not show increases in testosterone during social challenges. Hormones and Behavior 54:115-124. https://doi.org/10.1016/j.yhbeh.2008.02.003

Griffith S. C., I. P. F Owens, and K. A. Thuman. 2002. Extra pair paternity in birds : a review of interspecific variation and adaptive function. Molecular Ecology 11:2195-2212. https://doi.org/10.1046/j.1365-294X.2002.01613.x

Hall, M. L. 2004. A review of hypotheses for the functions of avian duetting. Behavioural Ecology and Sociobiology 55:415-430. https://doi.org/10.1007/s00265-003-0741-x

Hall, M. L., and A. Peters. 2009. Do male paternity guards ensure female fidelity in a duetting fairy-wren? Behavioral Ecology 20:222-228. https://doi.org/10.1093/beheco/arn139

Hawkins G. L., G. E. Hill, and A. Mercadante. 2012. Delayed plumage maturation and delayed reproductive investment in birds. Biological Reviews 87:257-274. https://doi.org/10.1111/j.1469-185X.2011.00193.x

Hoi, H., J. Krištofík, and A. Darolová. 2013. Experimentally simulating paternity uncertainty: immediate and long-term responses of male and female Reed Warblers *Acrocephalus scirpaceus*. PLoS One 8(4):e62541. https://doi.org/10.1371/journal.pone.0062541

Jacot, A., M. Valcu, K. van Oers, and B. Kempenaers. 2009. Experimental nest site limitation affects reproductive strategies and parental investment in a hole-nesting passerine. Animal Behaviour 77:1075-1083. https://doi.org/10.1016/j.anbehav.2009.01.012

Kasahara, S., Y. Yamaguchi, O. K. Mikami, and K. Ueda. 2014. Conspecific egg removal behaviour in Eurasian Tree Sparrow *Passer montanus*. Ardea 102:47-52. https://doi.org/10.5253/078.102.0110

Kleiber, D., K. Kyle, S. M. Rockwell, and J. L. Dickinson. 2007. Sexual competition explains patterns of individual investment in territorial aggression in Western Bluebird winter groups. Animal Behaviour 73:763-770. https://doi.org/10.1016/j.anbehav.2006.09.012

Knight, L., and S. A. Temple. 1986. Why does intensity of avian nest defense increase during the nesting cycle? Auk 318-327. https://doi.org/10.1093/auk/103.2.318

Krieg, C. A., and T. Getty. 2016. Not just for males: females use song against male and female rivals in a temperate zone songbird. Animal Behaviour 113:39-47. https://doi.org/10.1016/j.anbehav.2015.12.019

Krist, M. 2004. Importance of competition for food and nest-sites in aggressive behaviour of Collared Flycatcher (*Ficedula albicollis*). Bird Study 51:41-47. https://doi.org/10.1080/0006365-0409461331

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London, UK.

Laidre, M. E., and S. L. Vehrencamp, 2008. Is bird song a reliable signal of aggressive intent? Behavioral Ecology and Sociobiology 62:1207-1211. https://doi.org/10.1007/s00265-007-0539-3

Logue, D. M, and D. E. Gammon. 2004. Duet song and sex roles during territory defence in a tropical bird, the Black-bellied Wren, *Thryothorus fasciatoventris*. Animal Behaviour 68:721-731. https://doi.org/10.1016/j.anbehav.2003.10.026

Lopez-Sepulcre, A., and H. Kokko. 2005. Territorial defense, territory size, and population regulation. American Naturalist 166:317-329. https://doi.org/10.1086/432560

Low, M. 2005. Factors influencing mate guarding and territory defence in the stitchbird (hihi) *Notiomystis cincta.* New Zealand Journal of Ecology 29:231-242.

Lyon, B. E., and J. M. Eadie. 2008. Conspecific brood parasitism in birds: a life-history perspective. Annual Review of Ecology, Evolution, and Systematics 39:343-363. https://doi.org/10.1146/annurev.ecolsys.39.110707.173354

Maldonado-Chaparro, A. A., P. O. Montiglio, W. Forstmeier, B. Kempenaers, and D. R. Farine. 2018. Linking the fine-scale social environment to mating decisions: a future direction for the study of extra-pair paternity. Biological Reviews 1559:1558-1577. https://doi.org/10.1111/brv.12408

Marshall-Ball L., N. Mann, and P. J. B. Slater. 2006. Multiple functions to duet singing: hidden conflicts and apparent cooperation. Animal Behaviour 71:823-831. https://doi.org/10.1016/j.anbehav.2005.05.021

Mays, H. L., and K. R. Hopper. 2004. Differential responses of Yellow-breasted Chats, *Icteria virens*, to male and female conspecific model presentations. Animal Behaviour 67:21-26. https://doi.org/10.1016/j.anbehav.2003.01.003

Moreno, J. 2015. The incidence of clutch replacements in the Pied Flycatcher *Ficedula hypoleuca* is related to nest-box availability: evidence of female-female competition? Ardeola 62:67-80. https://doi.org/10.13157/arla.62.1.2015.67

Murphy, T. G., D. Hernández-Muciño, M. Osorio-Beristain, R. Montgomerie, and K. E. Omland. 2009. Carotenoid-based status signaling by females in the tropical streak-backed oriole. Behavioral Ecology 20:1000-1006. https://doi.org/10.1093/beheco/arp089

Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biology and Conservation 70:265-276. https://doi.org/10.1016/0006-3207(94)90172-4

Palmerio, A. G., and V. Massoni. 2009. Reproductive biology of female Saffron Finches does not differ by the plumage of the mate. Condor 111:715-721. https://doi.org/10.1525/cond.2009.080044

Palmerio, A. G., and V. Massoni. 2011. Parental care does not vary with age-dependent plumage in male Saffron Finches *Sicalis flaveola*. Ibis 153:421-424. https://doi.org/10.1111/j.1474-919X.2011.01103.x

Préault, M., S. Derégnaucourt, G. Sorci, and B. Faivre. 2002. Does beak coloration of male Blackbirds play a role in intra and/or intersexual selection? Behavioural Processes 58:91-96. https://doi.org/10.1016/S0376-6357(02)00004-9

Quinard, A., and F. Cézilly. 2012. Sex roles during conspecific territorial defence in the Zenaida Dove, *Zenaida aurita*. Animal Behaviour 83:47-54. https://doi.org/10.1016/j.anbehav.2011.09.032

Ridgely, R.S., and G. Tudor. 1989. The Birds of South America. Vol. 1: The Oscine Passerines. Oxford University Press, Oxford.

Rogers, A. C., N. E. Langmore, and R. A. Mulder. 2007. Function of pair duets in the Eastern Whipbird: cooperative defense or sexual conflict? Behavioral Ecology 18:182-188. https://doi.org/10.1093/beheco/arl070

Rosvall, K. A. 2008. Sexual selection on aggressiveness in females: evidence from an experimental test with Tree Swallows. Animal Behaviour 75:1603-1610. https://doi.org/10.1016/j.anbehav.2007.09.038

Rosvall, K. A. 2011. Maintenance of variation in sexually selected traits in females: a case study using intrasexual aggression in Tree Swallows *Tachycineta bicolor*. Journal of Avian Biology 42:454-462. https://doi.org/10.1111/j.1600-048X.2011.05322.x

Sandell, M. I., and H. G. Smith. 1997. Female aggression in the European Starling during the breeding season. Animal Behaviour 53:13-23. https://doi.org/10.1006/anbe.1996.0274

Shogren, E. H., M. A. Jones, B. K. Sandercock, and W. A. Boyle. 2019. Apparent survival of tropical birds in a wet, premontane forest in Costa Rica. Journal of Field Ornithology 90(2):117-127. https://doi.org/10.1111/jofo.12290

Slagsvold, T., and J. T. Lifjeld. 1994. Polygyny in birds: the role of competition between female for male parental care. American Naturalist 143:59-94. https://doi.org/10.1086/285596

Stutchbury, B. J. M. 1998. Extra-pair mating effort of male Hooded Warblers, *Wilsonia citrina.* Animal Behaviour 55:553-561. https://doi.org/10.1006/anbe.1997.0641

Stutchbury, B. J. M., and R. J. Robertson. 1987. Behavioral tactics of subadult female floaters in the Tree Swallow. Behavioural Ecology and Sociobiology 20:413-419. https://doi.org/10.1007/BF00302984

Tobias, J., and N. Seddon. 2000. Territoriality as a paternity guard in the European Robin, *Erithacus rubecula*. Animal Behaviour 60:165-173. https://doi.org/10.1006/anbe.2000.1442

Tryjanowski, P., F. Morelli, Z. Kwiecinski, P. Indykiewicz, and A. P. Møller. 2018. Birds respond similarly to taxidermic models and live cuckoos *Cuculus canorus*. Journal of Ethology 36:243-249. https://doi.org/10.1007/s10164-018-0554-z

Van Dongen, W. F. D., and R. A. Mulder. 2008. Male and female golden whistlers respond differently to static and dynamic signals of male intruders. Behavioral Ecology 19:1025-1033. https://doi.org/10.1093/beheco/arn061

Vergara, P., J. Martínez-Padilla, and J. A. Fargallo. 2013. Differential maturation of sexual traits: revealing sex while reducing male and female aggressiveness. Behavioral Ecology 24:237-244. https://doi.org/10.1093/beheco/ars159

Wang, D., W. Zhang, S. Yang, and. X. L. Richter.2023. Sex differences in avian parental care patterns vary across the breeding cycle. Nature Communications 14:6980. https://doi.org/10.1038/s41467-023-42767-5

Zilberman, R., B. Moav, and Y. Yom-Tov. 2001. Territoriality and mate guarding in the Orange-tufted Sunbird (Nectarinia osea). Israel Journal of Zoology 47:275-286. https://doi.org/10.1560/X352-Q3PD-MV63-UNB3