



*Avian Behavior, Ecology, and Evolution*

## Apparent survival and return rate in the Saffron Finch *Sicalis flaveola*, a species with age-related phenotypes

### Supervivencia aparente y tasa de retorno del Jilguero dorado *Sicalis flaveola*, una especie con fenotipos relacionados con la edad

Andrés G. Palmerio<sup>1</sup>  and Viviana Massoni<sup>1,2</sup> 

**ABSTRACT.** We studied the return rate, apparent survival, and probability of recapture of the Saffron Finch (*Sicalis flaveola pelzelni*), a thrupid with sexual dichromatism and age-related male feather phenotypes; the second-year males are dull and indistinguishable from females to humans and conspecifics alike, whereas the after second year males are golden yellow. The study spanned six breeding seasons. We found that adult plumaged males and females did not differ in the return rate, but immature plumaged males had lower return rates than older plumage males. Return rates did not vary with previous nesting success. Apparent survival rate of all males combined and females was almost equal, but we found important differences when we compared both types of males, as older males had a higher apparent survival rate than younger ones. The recapture probability was sex and age related with females having higher probability of recapture than males, and older males a higher probability of recapture than young males. Finally, we compared the apparent survival of Saffron Finches to those of published studies on thrupids and found it to be close to the family average.

**RESUMEN.** Estudiamos la tasa de retorno, la supervivencia aparente y la probabilidad de recaptura del Jilguero dorado (*Sicalis flaveola pelzelni*), un tráupido con dicromatismo sexual y fenotipos del plumaje masculino relacionados con la edad; los machos del segundo año son opacos e indistinguibles de las hembras tanto para los humanos como para sus congéneres, mientras que los machos mayores de dos años son de color amarillo dorado. El estudio abarcó seis temporadas reproductivas. Hallamos que los machos y hembras con plumaje adulto no difirieron en la tasa de retorno, pero los machos con plumaje inmaduro tuvieron tasas de retorno más bajas que los machos con plumaje adulto. Las tasas de retorno no variaron con el éxito de nidificación previo. La tasa de supervivencia aparente de todos los machos combinados y de las hembras fue casi igual, pero encontramos diferencias importantes cuando comparamos ambos tipos de machos, ya que los machos mayores tuvieron una tasa de supervivencia aparente más alta que los más jóvenes. La probabilidad de recaptura estuvo relacionada con el sexo y la edad, teniendo las hembras una mayor probabilidad de recaptura que los machos, y los machos mayores una probabilidad de recaptura más alta que los machos jóvenes. Finalmente, comparamos la supervivencia aparente de Jilgueros dorados con aquellas de estudios publicados sobre tráupidos y resultó ser similar al promedio de la familia.

**Key Words:** *apparent survival; delayed plumage maturation; return rate; Sicalis flaveola; thrupid*

#### INTRODUCTION

Breeding site fidelity is the tendency to return to a previously occupied location (Switzer 1993). In birds, it provides benefits to the returning birds, e.g., an increased knowledge of the location of key resources (Rappole and Jones 2002), improved chances of maintaining a breeding territory and securing a mate (Pärt 1994), and reducing the predation risk by being familiar with the environment (Shutler and Clark 2003). Site fidelity is estimated by the return rates, i.e., the proportion of captured (marked) individuals that return to the site and are re-captured in subsequent seasons, and is, therefore, a function of detection probability and survival (Martin 1995).

Survival is a key trait of the life history strategy of a species (Stearns 1992) and is associated with other traits through trade-offs (Martin 2004), e.g., with body size (Linstedt and Calder 1976, meta-analysis by Scholer et al. 2020), or weight (Sæther 1989), age, and sex patterns (Sanz-Aguilar et al. 2017), etc. A seminal proposal by Trivers (1972) states that there are sex-specific costs of reproduction: after breeding, females may survive less than males because they usually perform most parental care related

tasks (e.g. egg production, incubation, chick feeding) and therefore incur higher reproductive costs. Despite this hypothesis of a trade-off between reproductive effort and survival having been abundantly studied, it remains controversial and has received both support (e.g., Cruz-Flores et al. 2021, meta-analysis by Santos and Nakagawa 2012) and rejection (e.g., Wojczulanis-Jakubas et al. 2020, meta-analysis by Chang et al. 2024).

Other factors can affect the apparent survival and return rates, such as climatic variables (Salewski et al. 2013), food availability during the non-breeding (Lahti et al. 1998) or breeding season (França et al. 2020), nesting habits (Martin and Li 1992), prior successful reproductive experience (Miño and Massoni 2017), age-related detection probability (Manes and Anderson 2013), and age-specific mortality and survival (Bouwhuis et al. 2012). The return rate and apparent survival of individuals may also be associated with the plumage phenotypes they carry (Pizarro-Muñoz et al. 2018).

Delayed plumage maturation is the delayed acquisition of definitive plumage coloration until after an individual's first potential breeding period (Hawkins et al. 2012). If minimum

<sup>1</sup>Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina, <sup>2</sup>Instituto de Ecología, Genética y Evolución - IEGEBA, Universidad de Buenos Aires, Buenos Aires, Argentina

conditions for reproduction are met, individuals with immature plumage may opportunistically reproduce, though frequently with lower success than older mature plumaged males (Hawkins et al. 2012 and references therein). Early reproduction could be costly if the fecundity or the survival of adults or offspring is reduced (Stearns 1992). The expectation is that when reproduction of young individuals is delayed, the individuals' apparent survival increases (Berggren et al. 2004).

The Neotropic zone is by far the richest realm of land bird species in the world, as it holds ~36% of all known species (Soares et al. 2023); the Thraupidae is a species-rich family of songbirds comprising 382 species endemics to the Americas. Although the number of studies providing estimates of survival rates of thraupids has recently increased (Shogren et al. 2019), this parameter is currently lacking for most of the species in this family. An interesting model in which to study the relationship between age-related traits and survival is the Saffron Finch (*Sicalis flaveola pelzelni*), a sedentary non-excavator, cavity-nesting thraupid ranging from southern Brazil and eastern Bolivia to central Argentina, south to La Pampa Province and Uruguay (Ridgely and Tudor 1989). This subspecies shows delayed plumage maturation; second year males (hereafter SY males) have a brown back and a whitish belly and, to humans and conspecifics alike, seem to be indistinguishable from females by color (Benitez-Saldivar and Massoni 2018), and are capable of breeding successfully (Palmerio and Massoni 2009); in contrast, after SY males (hereafter ASY males) are golden yellow with an olive back streaked with black. Second year male nests do not differ in reproductive variables from ASY male's nests in a nest-box system (Palmerio and Massoni 2009) and both plumage morphs have similar chick feeding rates (Palmerio and Massoni 2011). Females solely incubate the eggs and feed the offspring significantly more often than males (Palmerio and Massoni 2011).

Apparent survival, recapture probability, and return rates in this species are unknown; we aim to estimate and compare these parameters and rates and discern whether sexes and male plumage morphs differ in them. Here, we estimate the apparent survival ( $\phi$ ) and recapture probability (P) in relation to year, prior breeding success, and age class of Saffron Finch males and females (breeders and recruits), and describe the average life span of females, SY, and ASY males. We also investigate whether and to what extent rates are affected by prior reproductive success at the breeding site using a 6-seasons dataset. We expect that (1) females would have a lower apparent survival than males; (2) SY males would have less apparent survival than ASY males; and (3) prior breeding success to have an impact on their (females, SY males, and ASY males) apparent survival rate.

## METHODS

Data for this study were collected during the breeding season (December to March) from 2004 to 2010 in a nest-box system in an agricultural landscape within the Pampa biome, at Chascomús, Buenos Aires Province, Argentina (35°34'S, 58°01'W; Massoni et al. 2007). Between 96 and 113 nest boxes were available, 30 m apart, and distributed over ~63 ha (see Massoni et al. 2007 for further details). Each nest box had a lateral door that allowed monitoring of the nest's progress, and a "wigwag" trap to capture the breeding adults when they enter the box. The trap is activated by pulling a long piece of monofilament fishing line that is

attached to a swiveling piece of wood when the focal bird enters the box during the trapping period. Females were captured when incubating, and males were captured while feeding newly hatched nestlings, and their plumage coloration was recorded. Adults were attached with a numbered aluminum ring and a unique combination of colored plastic rings for further identification. All nests were inspected every 1–2 days until day 12 to avoid premature fledgling, which tends to occur at day 14 of age (Palmerio and Massoni 2009); a nest was considered successful if at least one nestling fledged. Families of fledglings and parents (the latter color ringed) remain in the area and fledglings are fed for a few days, so we were able to assert that there was nest success instead of failure (1/0) but we were uncertain of the number of fledglings.

Annual return rate was defined as the proportion of banded Saffron Finches in the year  $t$  that returned in the following years; individuals banded as nestlings were added to the dataset on the first year they were captured breeding at the study site. The average reproductive life-expectancy for each individual was calculated using the equation  $1 - ln^{-1}(\phi)$  (Stenhouse and Robertson 2005).

## Statistical analyses

Using contingency tables, we compared return rates of breeders between years. We also compared seasons regarding their average air temperature (in C°) and precipitation (in mm) from the National Weather Service (SMN, 2004–2010). The previous breeding experience, sex, and morph of the breeding males were compared using contingency tables in R Statistical environment (v4.1.2; R Core Team 2021). We ran models for live encounter data, corrected for the probability of encounter (P) to analyze adult survival; adult apparent survival ( $\phi$ ) and recapture (P) rates were estimated using Cormack-Jolly-Seber (CJS) open-population capture-recapture models in Program MARK 9.0 (White and Burnham 1999), following maximum-likelihood procedures and notation described by Lebreton et al. (1992). First, we tested whether the general model ( $\phi_{(y*s)} P_{(y*s)}$ ), (see below for symbol's meaning) fitted the data and assumptions underlying the CJS. We then used the median  $\hat{c}$  method (variance inflation factor) to estimate a value of  $c$  derived from a logistic regression analysis (Cooch and White 2006). We used this estimated  $\hat{c}$  value to correct AICc into QAICc. A set of 16 models alternating constancy  $(.)$ , year  $(y)$ , and sex  $(s)$  effects for  $\phi$  and P were developed:  $\phi_{(y*s)} P_{(y*s)}$ ,  $\phi_{(y*s)} P_{(y)}$ ,  $\phi_{(y*s)} P_{(s)}$ ,  $\phi_{(y*s)} P_{(.)}$ ,  $\phi_{(y)} P_{(y*s)}$ ,  $\phi_{(s)} P_{(y*s)}$ ,  $\phi_{(.)} P_{(y*s)}$ ,  $\phi_{(y)} P_{(s)}$ ,  $\phi_{(s)} P_{(y)}$ ,  $\phi_{(y)} P_{(y)}$ ,  $\phi_{(s)} P_{(y)}$ ,  $\phi_{(.)} P_{(y)}$ ,  $\phi_{(s)} P_{(s)}$ ,  $\phi_{(y)} P_{(.)}$ ,  $\phi_{(s)} P_{(.)}$ , and  $\phi_{(.)} P_{(.)}$ .

Another set of models were used to analyze separately, the apparent survival and ( $\phi$ ) and the recapture rates of males that reproduced in Chascomús for the first time as SY or ASY males, alternating constancy  $(.)$ , year  $(y)$ , and age category  $(a)$  effects for  $\phi$  and P were developed using  $\phi_{(y*a)} P_{(y*a)}$  as the general model:  $\phi_{(y*a)} P_{(y*a)}$ ,  $\phi_{(y*a)} P_{(y)}$ ,  $\phi_{(y*a)} P_{(a)}$ ,  $\phi_{(y*a)} P_{(.)}$ ,  $\phi_{(y)} P_{(y*a)}$ ,  $\phi_{(.)} P_{(y*a)}$ ,  $\phi_{(y)} P_{(a)}$ ,  $\phi_{(a)} P_{(y)}$ ,  $\phi_{(y)} P_{(y)}$ ,  $\phi_{(.)} P_{(y)}$ ,  $\phi_{(a)} P_{(a)}$ ,  $\phi_{(a)} P_{(.)}$ ,  $\phi_{(y)} P_{(.)}$ ,  $\phi_{(.)} P_{(a)}$ , and  $\phi_{(.)} P_{(.)}$ . Akaike's Information Criterion (AIC) weighted for sample size (AICc) and overdispersion (QAICc) were used for model ranking and selection (Anderson et al. 2000). Models with the lowest QAICc values were retained as the best compromise between high proportion of deviance explained and a low number of parameters. We also analyzed the apparent survival rate and probability of recapture of females

banded as nestlings that returned to the colony to breed on subsequent years. The mean adult life-expectancy for all groups was calculated using the same equation as before, i.e.,  $1 - \ln^{-1}(\phi)$  (Stenhouse and Robertson 2005).

## RESULTS

Over the study period, Saffron Finches occupied between 26% and 55% of available boxes. We captured and banded with aluminum and a unique combination of color rings 90 different females and 77 different males, i.e., a total number of 167 individuals. We also banded 720 nestlings. Thirty-six nestlings banded at the site (5%) returned to breed in subsequent years (24 females, 10 SY males, and 2 ASY males). All male local recruits ( $N = 10$ ) were seen as breeding SY males and none were first seen as a breeding ASY male. Eighteen females were found breeding at the first year of life and six returned to breed two years after hatching.

The groups did not differ significantly in return rates of breeders between years. We recaptured 11 of 19, 12 of 22, 12 of 27, 18 of 31, and 17 of 25 females that returned in 2005, 2006, 2007, 2008, and 2009, respectively ( $\chi^2 = 4.0$ ,  $P = 0.5$ ,  $N = 124$ ). We recaptured 0 of 2, 5 of 9, 3 of 11, 4 of 14, and 3 of 13 SY males that returned in 2005, 2006, 2007, 2008, and 2009, respectively (SY males:  $\chi^2 = 0.9$ ,  $P = 0.4$ ,  $N = 60$ ). We recaptured 6 of 11, 7 of 10, 10 of 11, 11 of 14, and 12 of 14 ASY males that returned in 2005, 2006, 2007, 2008, and 2009, respectively (ASY males:  $\chi^2 = 0.7$ ,  $P = 0.6$ ,  $N = 49$ ). Overall, 51.1% of females, 36.4% of SY males, and 51.4% of ASY males were caught the following year, yielding a general return rate for Saffron Finches of 49.6 %.

The success or failure of the previous year breeding attempt did not affect the return rate of females: 45.3% of successful (24 of 53) and 48.6% (18 of 37) of unsuccessful females returned the following year ( $\chi^2 = 19.3$ ,  $P = 0.1$ ,  $N = 90$ ) and 42.6% of successful (21 of 49) and 40% (8 of 20) of unsuccessful males returned the following year ( $\chi^2 = 0.03$ ,  $P = 0.85$ ,  $N = 69$ ). The previous nesting success seems not to affect the returning rate: for SY males, 37.2% (13 of 35) of successful males and 41.3% (6 of 14) of unsuccessful ASY males returned the following year ( $\chi^2 = 3.2$ ,  $P = 0.26$ ,  $N = 49$ ); for ASY males 40.3% (13 of 32) of successful males and 44.1% (12 of 28) of unsuccessful males returned to breed in Chascomús the following year ( $\chi^2 = 6.9$ ,  $P = 0.34$ ,  $N = 60$ ).

When inspecting the variables affecting survival rates of Saffron Finches, only one model was within the two  $\Delta$ QAICc from the top model ( $\phi_{(.)}$ ,  $P_{(.)}$ ), suggesting a possible effect of sex in the apparent survival of Saffron Finches (Table 1a) and a constant recapture probability rate. The third ranked model had less support, with  $\Delta$ QAICc barely surpassing 2, indicating a possible effect of sex in both apparent survival and recapture rates. This model did not result in higher deviance of the estimates than that obtained by the two better-ranked models. The overall estimate under the top model resulted in a life expectancy of 2.68 years for Saffron Finches breeding at this site. The model averaging showed that the estimated survival of each sex was contained within the 95% confidence intervals of the overall estimate (Table 2a), and were almost identical. The recapture probability of females was 12% larger than that of males. The models including “year” as explanatory variable were not selected, indicating that the apparent survival and recapture rates of females and males were similar throughout the study.

**Table 1.** Results of Cormack–Jolly–Seber recapture models executed in the program MARK 9.0 arranged by  $\Delta$ QAICc values including (a) constant ( $\cdot$ ), year ( $y$ ), and sex-varying ( $s$ ) apparent survival ( $\phi$ ) and recapture probability ( $P$ ) in Saffron Finches (*Sicalis flaveola pelzelni*) and (b) constant ( $\cdot$ ), year ( $y$ ) and age ( $a$ ) apparent survival ( $\phi$ ) and recapture probability ( $P$ ) in Saffron Finch males. Differences in QAICc values from the top model ( $\Delta$ QAICc), Akaike’s model weights ( $w_i$ ), number of parameters ( $k$ ), and deviance are shown. Last line in (a) and (b) corresponds to the full parameterized model.

Model	$\Delta$ QAICc	$w_i$	$k$	Deviance
(a) $\phi_{(.)} P_{(.)}$	0.00	0.39	2	78.10
$\phi_{(s)} P_{(.)}$	1.28	0.21	3	77.33
$\phi_{(s)} P_{(s)}$	2.04	0.14	3	78.09
$\phi_{(s*y)} P_{(s*y)}$	17.35	<0.01	18	60.31
(b) $\phi_{(.)} P_{(.)}$	0.00	0.44	2	71.06
$\phi_{(.)} P_{(a)}$	1.03	0.27	3	69.97
$\phi_{(a)} P_{(.)}$	1.86	0.18	3	70.81
$\phi_{(.)} P_{(y)}$	4.11	0.06	6	66.47
$\phi_{(a*y)} P_{(a*y)}$	17.88	<0.01	17	52.33

**Table 2.** Estimates of apparent survival ( $\phi$ ) and recapture probability ( $P$ ) for the top and average models in program Mark for (a) Saffron Finches (*Sicalis flaveola pelzelni*) and (b) Saffron Finch male phenotypes. Estimated parameter values  $\pm$  standard error (se), lower and upper limits of 95% confidence intervals, and lifespan.

Model	Parameter	Estimate $\pm$ se	95% CI		Lifespan	
			Lower	Upper		
(a) $\phi_{(.)} P_{(.)}$	$\phi$	0.689 $\pm$ 0.034	0.618	0.752	2.68	
	$P$	0.689 $\pm$ 0.048	0.587	0.775		
	Model-averaging	$\phi$ males	0.692 $\pm$ 0.048	0.590	0.778	2.71
	$\phi$ females	0.687 $\pm$ 0.045	0.594	0.767	2.60	
	$P$ males	0.649 $\pm$ 0.067	0.509	0.767		
(b) $\phi_{(.)} P_{(.)}$	$\phi$	0.708 $\pm$ 0.052	0.596	0.800	2.90	
	$P$	0.637 $\pm$ 0.073	0.486	0.765		
	Model-averaging	$\phi$ ASY males	0.735 $\pm$ 0.072	0.572	0.852	3.25
	$\phi$ SY males	0.688 $\pm$ 0.067	0.545	0.802	2.67	
	$P$ ASY males	0.711 $\pm$ 0.053	0.491	0.859		
	$P$ SY males	0.574 $\pm$ 0.094	0.387	0.874		

In the second set of models, which evaluated the effect of males’ age, two models were within two  $\Delta$ QAICc from the top model ( $\phi_{(.)}$ ,  $P_{(.)}$ ) indicating a possible effect of males’ age in the apparent survival or recapture rate of Saffron Finch males (Table 1b). The third model explained a slightly greater deviance of the estimated value and the next model had little support (almost doubled the  $\Delta$ QAICc). Both the apparent survival and recapture probability of ASY males were 46% larger than those of SY males (Table 2b). Models including “year” as explanatory variable were never selected, indicating that the apparent survival and recapture probabilities of SY and ASY males were similar throughout the study.

The overall apparent survival and recapture rates of males under the top model resulted in an estimated life expectancy of 2.90 for

males at our study site. The model averaging showed that the estimated apparent survival and recapture probabilities of ASY males were larger than that of SY males (Table 2b).

## DISCUSSION

This study reports, for the first time, the apparent survival rate and recapture probabilities of Saffron Finch breeders and finds clear differences in apparent survival between ASY and SY males, and a small difference between the sexes. We discuss the implications of our findings in light of the data reported for other Thrupids.

As mentioned earlier, breeding at familiar habitat carries several advantages, such as knowledge of the location of food (Stamps and Swaisgood 2007), efficient movement throughout the breeding area (Stamps and Swaisgood 2007), and effective escape from predators (Shutler and Clark 2003). Dispersing from the natal site is costly because of a lack of familiarity with the location of key resources (Rappole and Jones 2002), a lower probability of holding territory or a mate (Pärt 1994), and higher predation rates due to the exposure to unfamiliar environments (Shutler and Clark 2003).

The natal philopatry of Saffron Finches in this study (5%) is low but within the range observed across passerine species (Weatherhead and Forbes 1994). In most birds, the natal philopatry of females is less than that of males because females are, frequently, the dispersing sex (Clarke et al. 1997). An unexpected finding from this study was that the rate of natal philopatry of females doubled that of males. However, we must take this result with caution because of the low sample size of recruits, which prevents further conclusions.

Contrary to our expectations, we did not find differences between ASY males and females in their apparent survival rates (51.1% and 51.4%, respectively) and modeling did not detect significant effects of sex. One explanation for this could be that the greater parental effort of females would be compensated for by a higher rate of surveillance and nest defense, costly behaviors performed by males (Gibson and Moehrenschrager 2008) that would reduce their apparent survival. We do not have estimates on the costs of nest box acquisition and protection, but we witnessed three intense fights among ASY males that ended in the death of one of the competitors. The competition for nest boxes or mates is, therefore, risky, costly, and of interest for future studies.

In line with our expectation, we found that the return rates of SY breeding males (34%) was lower than that of the ASY males. A possible explanation for this difference is that SY male breeders suffer greater mortality than ASY males because young individuals are less experienced in avoiding predators. Another possibility is that the low return rates of SY males mirrors the costs of intrasexual competition with ASY males for food resources, nesting cavities, or mates (Hawkins et al. 2012). Finally, it could be the result of losing the opportunity to trap the SY male by confusing it with a female and ruining the capture event to which these birds are sensitive. When that occurred, we made another attempt at capture and, if that failed, the nest was not used. Nonetheless, the return rate of SY males that did not breed remains unknown, preventing further discussion.

Contrary to our expectations, the previous reproductive outcome of a given individual seems not to affect the return rates of Saffron Finches as it occurs in several species (Miño and Massoni 2017,

and references therein). A possible explanation is that Saffron Finches do not use their own experience to actively return to the nesting site but, rather, prioritize reducing the risk of dispersing to a lower quality site and facing the risks associated to not being able to access key resources. In addition, the availability of nesting cavities at the study site (see below), which are normally scarce and for which Saffron Finches usually compete (Massoni, *personal observation*), could mask the effect of the outcome of the previous reproductive attempt on return rates. Saffron Finches breeding in Chascomús occupied ~25%–50% of the available nest boxes, so competition for this resource is relatively low because it is the only species breeding in our nest box assemblage during the summer, and would not explain the differences in return rates found in this study. Experimental evidence on competition for nest boxes would allow us to explore whether the winners belong to a specific age category.

In a previous study, Palmerio and Massoni (2009) did not find significant differences in body size or in weight between SY and ASY males, which may suggest that ASY males do not monopolize food resources (seeds or arthropods). Future experimental studies on competition for food between Saffron Finch males of different ages would help gather evidence to test this hypothesis.

As for competition for mates, in previous studies we found that females that mated with ASY males are larger and heavier than females that mated with SY males (Palmerio and Massoni 2009), and that there is assortative mating by physical condition between SY males and their mates (Benítez Saldivar and Massoni 2018). However, we lack knowledge about mate choice in this species. Male ASY Saffron Finches show less aggression toward SY males than toward each other: the aggressive and even deadly battles occur between ASY males (Massoni, *personal observation*). This could be because, to conspecifics, the plumage coloration of SY males is indistinguishable from females (Benítez Saldivar and Massoni 2018) and, as long as they do not sing, SY males go unnoticed by ASY males. Because the return rate is the product of apparent survival and the probability of detection, our results may be a result of any of these factors or a combination of both.

Survival estimates obtained for each sex show that males have about 7% higher survival rate than females (Table 2a), and that the estimated life expectancy is very similar in both sexes (about 2.6 years). The probability of recapture of females was 12% greater than that of males. This difference could be due to differential capturing times: females were caught during incubation, when they remain inside the nest box longer, whereas males were only trapped after hatching of nestlings, when they make short feeding visits to the nest, therefore lowering capture probabilities especially for SY males because of their female-like color, which would bias for human error.

We also found that the survival of older ASY males is 18% greater than that of younger SY males and this difference generates a greater life expectancy of ASY males (3.25 years) vs. that of SY males (2.67 years). Thus, potentially, ASY males could live for a third breeding season, increasing their total reproductive success. We have to bear in mind, however, that we do not know the apparent survival of SY and ASY males that forego early reproduction, thus our results do not allow us to achieve the real value of these parameters.

The recapture probability of ASY males was 21% higher than that of SY males; this lower capture rate of SY males could be due to the easiness of detecting yellow males compared to SY males, which are indistinguishable from females to humans and conspecifics alike, and remain undisclosed until they sing (Benítez Saldívar and Massoni 2018). Finally, we have to bear in mind that the apparent survival of SY males that reproduce outside the nest-box assemblage remains unknown, although there is no reason to assume it would be higher than that observed in this study.

Last, the apparent survival of Saffron Finches is close to the average survival reported for other thraupids (Table 3). Saffron Finches are cavity nesters and this could lead to an increased survival rate compared to open-cup nesting species, which might be more exposed to predators or nest damage by external factors (e.g., unsuitable weather). Phylogenetically controlled meta-analyses comparing apparent survival of thraupid species with different nesting habits would help gain insights into this.

**Table 3.** Apparent survival of Thraupidae species in phylogenetic order.

Species	Apparent survival	
<i>Cyanerpes caeruleus</i>	0,489	Johnston et al. (1997)
<i>Coereba flaveola</i>	0,647	Johnston et al. (1997)
<i>Melopyrrha portoricensis</i>	0,722	Faaborg and Wiewel (2022).
<i>Loriotus luctuosus</i>	0,644	Johnston et al. (1997)
<i>Coryphospingus pileatus</i>	0,546	Tavares-Damasceno et al. (2017)
<i>Tachyphonus surinamus</i>	0,679	Tavares-Damasceno et al. (2017)
<i>Tachyphonus rufus</i>	0,606	Macario et al. (2017)
<i>Kleinothraupis atropileus</i>	0,349	Scholer et al. (2019)
<i>Sphenopsis melanotis</i>	0,697	Scholer et al. (2019)
<i>Thlypopsis ornata</i>	0,790	Tinoco et al. (2019)
<i>Conirostrum cinereum</i>	0,520	Tinoco et al. (2019)
<i>Sicalis flaveola pelzelni</i>	0,689	this study
<i>Catamenia inornata</i>	0,860	Tinoco et al. (2019)
<i>Diglossa cyanea</i>	0,730	Tinoco et al. (2019)
<i>Diglossa baritula</i>	0,596	Scholer et al. (2019)
<i>Diglossa humeralis</i>	0,730	Tinoco et al. (2019)
<i>Chlorospingus flavigularis</i>	0,433	Scholer et al. (2019)
<i>Iridosornis jelsk</i>	0,402	Scholer et al. (2019)
<i>Dubusia taeniata</i>	0,800	Tinoco et al. (2019)
<i>Anisognathus igniventris</i>	0,860	Tinoco et al. (2019)
<i>Thraupis palmarum</i>	0,678	Johnston et al. (1997)
<i>Stilpnia cayana</i>	0,405	Câmara and França (2017)
<i>Tangara gyrola</i>	0,742	Johnston et al. (1997)
Average	0,642	

#### Acknowledgments:

We are grateful to Carolina I. Miño for helpful comments on previous versions of this manuscript and to Reviewer 1 who pointed out valuable improvements to the manuscript.

#### Data Availability:

The data code that support the findings of this study are openly available at <https://doi.org/10.6084/m9.figshare.25594839>, <https://doi.org/10.6084/m9.figshare.25594842>, <https://doi.org/10.6084/m9.figshare.25594845>. Ethical approval for this research study was granted by CONICET; [5875]; [1122; 0090100880]; [11220130100342CO]; Universidad de Buenos Aires; [X-140]; [X-462]; [20020090200160]; [20020130100772].

#### LITERATURE CITED

- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wild Management* 64(4):912-923. <https://doi.org/10.2307/3803199>
- 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>
- Berggren, Å., D. P. Armstrong, and R. M. Lewis. 2004. Delayed plumage maturation increases overwinter survival in North Island robins. *Proceedings of the Royal Society B: Biological Sciences* 271:2123-2130. <https://doi.org/10.1098/rspb.2004.2846>
- Bouwhuis, S., R. Choquet, B. C. Sheldon, and S. Verhulst. 2012. The forms and fitness cost of senescence: age-specific recapture, survival, reproduction, and reproductive value in a wild bird population. *American Naturalist* 179(1):15-27. <https://doi.org/10.1086/663194>
- Câmara, T. P., and F. França. 2017. Demografia de *Tangara cayana* (Aves: Thraupidae) em um fragmento de restinga no extremo Norte de distribuição da Mata Atlântica. Dissertação. Centro de Biociências, Universidade Federal do Rio Grande do Norte, Natal, Brasil.
- Chang, C., M. Moiron, A. Sánchez-Tójar, P. T. Niemelä, and K. L. Laslowski. 2024. What is the meta-analytic evidence for life-history trade-offs at the genetic level? *Ecology Letters* 27(1): e14354. <https://doi.org/10.1111/ele.14354>
- Clarke, A. L., B.-E. Sæther, and E. Røskraft. 1997. Sex biases in avian dispersal: a reappraisal. *Oikos* 79:429-438. <https://doi.org/10.2307/3546885>
- Cooch, E., and G. White. 2006. Program MARK: a gentle introduction. Eighth edition. <http://www.phidot.org/software/mark/docs/book>
- Cruz-Flores, M., R. Pradel, J. Bried, J. González-Solís, and R. Ramos. 2021. Sex-specific costs of reproduction on survival in a long-lived seabird. *Biological Letters* 17:20200804. <https://doi.org/10.1098/rsbl.2020.0804>
- Faaborg, J., and A. Wiewel. 2022. Puerto Rican Bullfinch (*Melopyrrha portoricensis*), version 2.0. in T. S. Schulenberg and J. Gerbracht, editors. *Birds of the world*. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.purbull.02>
- França, L. F., R. D. Costa Morais, S. S. Henrique de Brito, M. R. Bezerra Dias, L. Vieira de Paiva, and C. A. de Souza Oliveira. 2020. Constant or varied survival? Effects of seasonal and unpredictable factors on bird survival in a Neotropical semi-arid region. *Journal of Arid Environments* 182:104278. <https://doi.org/10.1016/j.jaridenv.2020.104278>
- Gibson, K. W., and A. Moehrensclager. 2008. A sex difference in the behavioural response of nesting Mountain Bluebirds (*Sialia currucoides*) to a mounted predator. *Journal of Ethology* 26 (1):185-189. <https://doi.org/10.1007/s10164-007-0045-0>
- Hawkins, G. L., G. E. Hill, and A. Mercadante. 2012. Delayed plumage maturation and delayed reproductive investment in birds. *Biological Reviews* 87(2):257-274. <https://doi.org/10.1111/j.1469-185X.2011.00193.x>

- Johnston, J. P., W. J. Peach, R. D. Gregory, and S. A. Stewart. 1997. Survival rates of tropical and temperate passerines: a Trinidadian perspective. *American Naturalist* 150(6):771-789. <https://doi.org/10.1086/286093>
- Lahti, K., M. Orell, S. Rytikkönen, and K. Koivula. 1998. Time and food dependence in Willow Tit winter survival. *Ecology* 79(8):2904-2916. [https://doi.org/10.1890/0012-9658\(1998\)079\[2904:TAFDIW\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2904:TAFDIW]2.0.CO;2)
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67-118. <https://doi.org/10.2307/2937171>
- Linstedt, S. L., and W. A. Calder. 1976. Body size and longevity in birds. *Condor* 78:91-94. <https://doi.org/10.2307/1366920>
- Macario, P., M. Pichorim, P. F. Doherty Jr., G. S. Toledo-Lima, T. M. Oliveira-Júnior, T. P. F. Câmara, S. Macjane Melo, J. L. S. Silveira, J. C. Araújo, and L. F. França. 2017. Apparent survival and cost of reproduction for White-lined Tanager (*Tachyphonus rufus*, Thraupidae) in the northern Atlantic Rainforest, Brazil. *PLoS ONE* 12(10):e0185890. <https://doi.org/10.1371/journal.pone.0185890>
- Maness, T. J., and D. J. Anderson. 2013. Predictors of juvenile survival in birds. *Ornithological Monographs* 78:1-55. <https://doi.org/10.1525/om.2013.78.1.1>
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65(1):101-27. <https://doi.org/10.2307/2937160>
- Martin, T. E. 2004. Avian life-history evolution has an eminent past: does it have a bright future? *Auk* 121:288-301. <https://doi.org/10.1093/auk/121.2.289>
- Martin, T. E., and P. Li. 1992. Life history traits of open vs. cavity nesting birds. *Ecology* 73(2):579-592. <https://doi.org/10.2307/1940764>
- Massoni, V., F. Bulit, and J. C. Rebores. 2007. Breeding biology of the White-rumped Swallow *Tachycineta leucorrhoa* in Buenos Aires Province, Argentina. *Ibis* 149:10-17. <https://doi.org/10.1111/j.1474-919X.2006.00589.x>
- Miño, C. I., and V. Massoni. 2017. Sexual differences in the effect of previous breeding performance on nest-box reuse and mate retention in White-rumped Swallows (*Tachycineta leucorrhoa*). *Emu - Austral Ornithology* 117(2):130-140. <https://doi.org/10.1080/01584197.2017.1282827>
- Palmerio, A. G., and V. Massoni. 2009. Reproductive biology of female Saffron Finches does not differ by the plumage of the mate. *Condor* 111(4):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>
- Pärt, T. 1994. Male philopatry confers a mating advantage in the migratory Collared Flycatcher *Ficedula albicollis*. *Animal Behaviour* 48:401-409. <https://doi.org/10.1006/anbe.1994.1254>
- Pizarro Muñoz, A., M. Kéry, P. V. Martins, and G. Ferraz. 2018. Age effects on survival of Amazon forest birds and the latitudinal gradient in bird survival. *Auk* 135(2):299-313. <https://doi.org/10.1642/AUK-17-91.1>
- R Core Team. 2021. R Statistical environment (v4.1.2).
- Rappole, J. H., and P. Jones. 2002. Evolution of old and new world migration systems. *Ardea* 90:525-537.
- Ridgely, R. S., and G. Tudor. 1989. *The birds of South America*. Vol. 1. Oxford University Press, Oxford, UK.
- Sæther, B. E. 1989. Survival rates in relation to body weight in European birds. *Ornis Scandinavica* 20(1):13-21. <https://doi.org/10.2307/3676702>
- Salewski, V., W. M. Hochachka, and W. Fiedler. 2013. Multiple weather factors affect apparent survival of European passerine birds. *PLoS ONE* 8(4):e59110. <https://doi.org/10.1371/journal.pone.0059110>
- Santos, E. S. A., and S. Nakagawa. 2012. The costs of parental care: a meta-analysis of the trade-off between parental effort and survival in birds. *Journal of Evolutionary Biology* 25:1911-1917. <https://doi.org/10.1111/j.1420-9101.2012.02569.x>
- Sanz-Aguilar, A., A. Cortés-Avizanda, D. Serrano, G. Blanco, O. Ceballos, J. M. Grande, J. L. Tella, and J. A. Donazar. 2017. Sex- and age-dependent patterns of survival and breeding success in a long-lived endangered avian scavenger. *Scientific Reports* 7:40204. <https://doi.org/10.1038/srep40204>
- Scholer, M. N., P. Arcese, M. L. Puterman, G. A. Londoño, and J. E. Jankowski. 2019. Survival is negatively related to basal metabolic rate in tropical Andean birds. *Functional Ecology* 33(8):1436-1445. <https://doi.org/10.1111/1365-2435.13375>
- Scholer, M. N., M. Strimas-Mackey, and J. E. Jankowski. 2020. A meta-analysis of global avian survival across species and latitude. *Ecology Letters* 23:1537-1549. <https://doi.org/10.1111/ele.13573>
- 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>
- Shutler, D., and R. G. Clark. 2003. Causes and consequences of Tree Swallow (*Tachycineta bicolor*) dispersal in Saskatchewan. *Auk* 120(3):619-631. <https://doi.org/10.1093/auk/120.3.619>
- Soares, L., K. L. Cockle, E. Ruelas Inzunza, J. T. Ibarra, C. I. Miño, S. Zuluaga, E. Bonaccorso, J. C. Ríos-Orjuela, F. A. Montaña-Centellas, J. F. Freile, et al. 2023. Neotropical ornithology: reckoning with historical assumptions, removing systemic barriers, and reimagining the future. *Ornithological Applications* 125:duac046. <https://doi.org/10.1093/ornithapp/duac046>
- Stamps, J. A. and R. R. Swaisgood. 2007. Someplace like home: experience, habitat selection and conservation biology. *Applied Animal Behaviour Science* 102(3-4):392-409. <https://doi.org/10.1016/j.applanim.2006.05.038>

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK. <https://doi.org/10.1093/oso/9780198577416.001.0001>

Stenhouse, I. J. and G. J. Robertson. 2005. Philopatry, site tenacity, mate fidelity, and adult survival in Sabine's Gulls. *Condor* 107:416-423. <https://doi.org/10.1093/condor/107.2.416>

Switzer, P. V. 1993. Site fidelity in predictable and unpredictable habitat. *Evolutionary Ecology* 7:533-555. <https://doi.org/10.1007/BF01237820>

Tavares-Damasceno, J. P., J. L. Gomes de Souza Silveira, T. Câmara, P. de Castro Stedile, P. Macario, G. S. Toledo-Lima, and M. Pichorim. 2017. Effect of drought on demography of Pileated Finch (*Coryphospingus pileatus*: Thraupidae) in northeastern Brazil. *Journal of Arid Environments* 147:63-70. <https://doi.org/10.1016/j.jaridenv.2017.09.006>

Tinoco, B. A., L. Graham, P. X. Astudillo, A. Nieto, J. M. Aguilar, S. C. Latta, and C. H. Graham. 2019. Survival estimates of bird species across altered habitats in the tropical Andes. *Journal of Field Ornithology* 90(2):105-116. <https://doi.org/10.1111/jof.12293>

Trivers, R. L. 1972. Parental investment and sexual selection. Chapter 7 in B. Campbell, editor. *Sexual selection and the descent of man*. Routledge, Chicago, New York, New York, USA. <https://doi.org/10.4324/9781315129266-7>

Weatherhead, P. J., and M. R. L. Forbes. 1994. Natal philopatry in passerine birds: genetic or ecological influences? *Behavioral Ecology* 5:426-433. <https://doi.org/10.1093/beheco/5.4.426>

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120-139. <https://doi.org/10.1080/00063659909477239>

Wojczulanis-Jakubas, K., M. Jiménez-Muñoz, D. Jakubas, D. Kidawa, N. Karnovsky, D. Cole, and E. Matechou. 2020. Duration of female parental care and their survival in the little auk *Alle alle* - are these two traits linked. *Behavioral Ecology and Sociobiology* 74:82. <https://doi.org/10.1007/s00265-020-02862-9>