Current Zoology, 2026, 00, 1–14
https://doi.org/10.1093/cz/zoag055
Published: 10 August 2026
Original Article

Delayed plumage maturation is linked to body condition, ectoparasite load, and partner's parental effort in a Neotropical songbird

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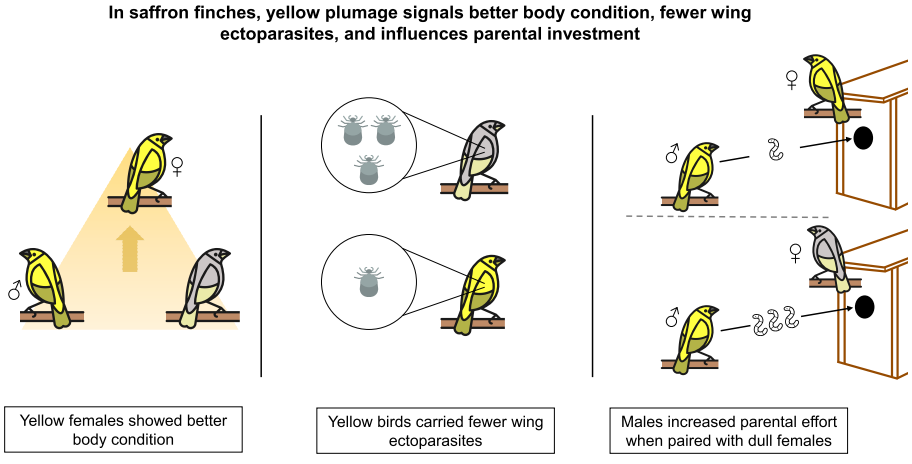
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Handling editor: Zu-Shi Huang

Abstract

In many bird species, plumage ornamentation plays a crucial role in mate choice by signaling individual quality. Plumage coloration may also signal reproductive success and parental effort, a key driver of offspring recruitment. In a wild population of saffron finches (*Sicalis flaveola*), a socially monogamous species with delayed plumage maturation in both sexes and biparental care, we captured, monitored, and video-recorded breeding pairs using nest boxes. We examined whether social class (based on age- and sex-dependent plumage coloration) signals body condition and wing ectoparasite load and whether plumage color (yellow or dull) is related to parental effort of paired females and males. We also assessed whether nesting success was associated with post-hatching parental effort and plumage color. Yellow females had better body condition than dull individuals, and yellow birds of both sexes had fewer wing ectoparasites. Males showed greater parental effort when paired with dull females, whereas females tended to invest more when paired with yellow males. Females contributed more to parental care than males, but nesting success was unrelated to plumage class or parental effort. These results suggest that yellow plumage in saffron finches signals female body condition and wing ectoparasite load in both sexes and may influence parental investment by mates.

Keywords carotenoid-based coloration, maternal effort, parental care, reproductive compensation, saffron finch

Graphical abstract



Received: March 19, 2025. **Accepted:** August 6, 2026
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In many bird species, ornamental traits such as plumage coloration vary substantially within populations (Dale 2006). These ornaments often function in mate choice and intraspecific competition and can act as honest signals of individual quality (Rohwer et al. 1980; Keyser and Hill 2000; Palmerio and Massoni 2009, 2011; Marques-Santos et al. 2018). Such variation has been explained by sexual and social selection favoring more elaborate traits (Zahavi 1975; Lyon and Montgomerie 2012). Brighter individuals are often older and more experienced (Préault et al. 2005; Bitton and Dawson 2008; Trigo and Mota 2016), which may result in improved performance in tasks such as nest building and territory acquisition and ultimately higher fitness through increased survival and reproductive success (Martin 1995; Wolfenbarger 1999; Roper 2005; Palmerio and Massoni 2024). Accordingly, several studies have reported positive relationships between plumage coloration and reproductive success (Siefferman and Hill 2003; Bitton et al. 2008; Crary and Rodewald 2012; Bulluck et al. 2017; Marques-Santos et al. 2018), although this pattern is not universal (Freeman-Gallant et al. 2014). Plumage coloration may signal parental ability, influence mate investment, or reflect genetic quality affecting offspring development (Møller 1994; Bulluck et al. 2017; Horn and Ritchison 2017).

In some species, sexually mature individuals develop a conspicuous definitive nuptial plumage, whereas in others the acquisition of definitive plumage is delayed until after the first potential reproductive period (delayed plumage maturation; Hill 1996). The adaptive function of this delay has been widely debated (Selander 1965; Rohwer et al. 1980; Lyon and Montgomerie 1986; Hawkins et al. 2012; Lyu et al. 2015), with no clear consensus (Bentz and Siefferman 2013). One hypothesis proposes that second-year individuals delay acquiring definitive plumage to reduce competition with older individuals that are more effective at defending resources (status signaling hypothesis; Lyon and Montgomerie 1986). Alternatively, delayed plumage may provide more cryptic coloration that reduces predation risk (cryptic hypothesis; Selander 1965) or allow young males to resemble females, thereby reducing aggression from older males and increasing opportunities for sneaky copulations (female mimicry hypothesis; Rohwer et al. 1980).

Plumage coloration may result from pigments such as melanin and carotenoids or from feather microstructures (McGraw 2006). In species with structural and melanin-based coloration, plumage color has been associated with body size, condition, and parental effort (Keyser and Hill 2000; Siefferman and Hill 2003; Magalhães et al. 2014). Carotenoids are obtained from the diet and can be metabolized but not synthesized by vertebrates (Goodwin 1992; Hill et al. 2023), meaning that carotenoid-based coloration may signal individual quality (Goodwin 1984; Powers and Hill 2021), in part through variation in the acquisition of high-quality food resources (Silva et al. 2026), particularly in species with red, orange, or yellow plumage (Brush 1990), such as the saffron finch (*Sicalis flaveola*). Carotenoid coloration has also been linked to physiological condition, including antioxidant capacity and immune function (Simons et al. 2012; Trigo and Mota 2016). According to the parasite-mediated sexual selection hypothesis, only individuals in good condition can afford the physiological costs of ornamentation, including potential trade-offs between immune competence and plumage coloration expression (Zahavi 1975; Hamilton and Zuk 1982; Dawson and Bortolotti 2006; Dougherty et al. 2023). When the development of carotenoid plumage is delayed, it may indicate parasite resistance if older or healthier individuals are more capable of producing carotenoid-based ornaments (Inouye et al. 2001; Roulin et al. 2007), potentially reflecting immune maturation or improved carotenoid acquisition with age (Wolfenbarger 1999; McGraw 2006; Silva et al. 2024).

Carotenoid-based plumage coloration may also signal parental performance, including nestling feeding rates (Senar et al. 2002; Bulluck et al. 2017), or influence the parental care provided by a mate (Horn and Ritchison 2017). Because parental investment requires time and energy and may reduce parental survival and future reproductive opportunities (Trivers 1972; Clutton-Brock 1991), plumage conspicuousness may be associated with variation in parental effort. This relationship may be positive if more ornamented individuals invest more in offspring (good parent hypothesis; Hoelzer 1989) or negative if more ornamented males allocate more effort to seeking or attracting extra-pair mates at the expense of parental care (trade-off hypothesis; Magrath and Komdeur 2003). In the latter case, females paired with highly conspicuous males may increase their own investment, potentially compensating for reduced male care (differential allocation hypothesis; Burley 1986).

Contrary to expectations, Palmerio and Massoni (2011) found no association between male carotenoid-based plumage coloration and nestling feeding rates by either sex in saffron finches (*S. f. pelzelni*), where females remain dull and only males acquire yellow plumage with age. In contrast, when delayed plumage maturation occurs in both sexes, additional mate-choice scenarios may arise, allowing the role of female ornamentation to be explored (Amundsen et al. 1997; Bulluck et al. 2017). The subspecies studied here (*S. f. brasiliensis*) shows delayed plumage maturation in both sexes (Marques-Santos et al. 2018): males develop yellow plumage with brownish-olive tones on the back and wings and an orange forehead (Ridgely et al. 2015), whereas females become entirely yellow but slightly duller (Sick 1997). In this subspecies, female yellow plumage has been associated with larger clutch sizes and shorter incubation periods (Marques-Santos et al. 2018).

In this study, we investigated whether social class (based on age- and sex-dependent plumage coloration) signals individual body condition, wing ectoparasite load, and parental investment (in eggs and nestlings) in a thraupid bird, the saffron finch (*S. f. brasiliensis*). We also evaluated whether parental investment is related to the plumage color (yellow or dull) of the breeding partner and whether nesting success (the probability that at least one nestling fledges) can be predicted by post-hatch parental care and parental plumage color. Maternal investment was assessed through clutch size and egg volume, and during the nestling stage by the number of nest visits, the percentage of time spent in the nest, and fecal sac removal. Paternal investment was measured during the nestling stage through the number of nest visits, the percentage of time spent in the nest, and fecal sac removal. We tested the following predictions: 1) yellow individuals have better body condition and fewer ectoparasites in their wing feathers than dull individuals; 2) yellow individuals invest either more in offspring (good parent hypothesis) or less in offspring (trade-off hypothesis) than dull individuals; 3) individuals paired with yellow partners invest more in offspring than those paired with dull partners (differential allocation

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Figure 1 Saffron finches (*Sicalis flaveola brasiliensis*; Aves: Thraupidae) representing the social classes considered in this study: yellow male (a), yellow female (b), and dull individual (c). Photos: Leonardo Casadei (a), Antonio Lemos Maia (b), and Marcos Cesar Campis (c). Photos a) and b) reproduced with permission; photo **c** licensed under the Creative Commons Attribution-ShareAlike 3.0 license.

hypothesis); and 4) nesting success is higher in nests with yellow parents and in those receiving greater parental care.

Materials and methods

Study area

The study was carried out at the Vila Velha University Experimental Eco Farm (20.5916°S, 40.4572°W) and neighboring sites in Guarapari, southern Espírito Santo state, Brazil, during 2 breeding seasons (2018–2019 and 2019–2020). The study area covers 69,000 m^2, of which 23,000 m^2 consist of preserved forest classified as Dense Ombrophilous Forest within the Atlantic Forest biome, while the remaining area consists mainly of buildings and pastures. The site is used for experimental activities by students from Vila Velha University. The regional climate is tropical monsoon (Am), according to the Köppen–Geiger climate classification, with a mean annual temperature between 22 and 24 °C and mean annual rainfall between 1,200 and 1,300 mm (Alvares et al. 2014).

Study species and plumage color classification

The saffron finch (*S. f. brasiliensis*) is a Neotropical passerine in the family Thraupidae. It feeds mainly on grains and seeds and has golden-yellow plumage likely derived from carotenoid pigments (McGraw 2006). In the study area, food is abundant due to feed offered to domestic animals, which is also consumed by saffron finches. The species is a secondary cavity nester (Marques-Santos et al. 2016), using only pre-existing cavities for nesting (e.g., openings in tree trunks and human constructions, and old nests of the Rufous Hornero *Furnarius rufus*). Individuals form socially monogamous pairs and exhibit biparental care: egg incubation is performed only by females, whereas both sexes participate in nestling feeding and nest cleaning (i.e., removal of fecal sacs; Palmerio and Massoni 2009; Espinosa et al. 2017). Breeding in this population occurs mostly from late October to mid-March (Alvarenga 2017), during which saffron finches may perform 2 to 3 nesting attempts within a single breeding season (Marques-Santos et al. 2016). In the same population studied here, reproductive success averaged 58.8% (Alvarenga 2017).

Saffron finches (*S. f. brasiliensis*) exhibit delayed plumage maturation in both sexes (Marques-Santos et al. 2018). Individuals were visually classified according to plumage color class (yellow or dull). We also assigned individuals to social classes based on age- and sex-dependent plumage coloration, following Marques-Santos et al. (2018). Social classes included yellow female, yellow male, and dull individual, with additional subdivision of dull individuals when sex could be determined. Previous studies validated this visual classification method, showing that it is equivalent to classifications based on color metrics extracted from photographs (Marques-Santos et al. 2018) and spectrophotometric analyses of yellow breast feathers in saffron finches (*S. f. brasiliensis*) (Araújo-Silva et al. 2023; Cruz-Bernate et al. 2023). Yellow individuals (after-second-calendar-year individuals) have a completely yellow body, with intrasexual and intersexual variation in tonality. Males have brighter yellow plumage with an orange forehead (Fig. 1a), whereas females have slightly darker yellow plumage (Fig. 1b). Dull individuals (second-calendar-year individuals of both sexes) show grayish-white plumage with dark streaks over most of the body and yellow coloration on the collar and lower wing regions (Fig. 1c).

Capture and banding of adults

We captured individuals using a mist net during the following periods: July–November 2018, February–June 2019, August–November 2019, and January–March 2020. One mist net was installed at the same location in the study area during the morning (8 AM–12 PM) and/or afternoon (2 PM–5 PM), totaling approximately 216 h of capture effort. This location was selected because of the high abundance of saffron finches observed, likely associated with nearby feeders. Each bird received a unique combination of colored plastic bands and a metal band provided by the Centro Nacional de Pesquisa e Conservação de Aves Silvestres (CEMAVE).

We measured body mass using a dynamometer-type balance (50 g capacity; precision: 0.5 g) and measured right tarsus length

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with a digital caliper (precision: 0.01 mm). Because sex could not be determined from plumage alone in dull individuals captured in the mist net, social classes included yellow female, yellow male, and dull individual. We visually inspected the remiges on the ventral side of both extended wings for ectoparasites under ambient light (similar to Galván et al. 2012). We then summed the estimated number of ectoparasites observed on both wings of each individual ($n = 34$ yellow females, 104 dull individuals, and 32 yellow males). Although ectoparasites were not identified in this study, feather mites (Acari: Astigmata) are commonly found on Neotropical passerines. Previous studies have reported feather mites, including the genera *Trouessartia* and *Pterodectes*, on saffron finches and other closely related Neotropical passerines (Roda and Farias 1999; Lyra-Neves et al. 2003; Kanegae et al. 2008; Hernandes 2014). We estimated body condition using the ratio between the natural logarithm of body mass and the natural logarithm of tarsus length (body condition index; Peig and Green 2009; $n = 40$ yellow females, 129 dull individuals, and 39 yellow males).

Nest boxes, nest monitoring, and parent identification

Nest boxes have been installed periodically in the study area since 2013 along forest edges and primarily in open areas. In total, 118 artificial nests were installed on wooden posts, concrete posts, and trees. The nest boxes measured $28 \times 15.5 \times 15$ cm (height × width × depth) and had a 4-cm-diameter entrance. Before the start of the 2019–2020 breeding season, the height of the nest boxes was reduced from 2.57 ± 0.02 m (mean ± SE; range = 1.71–3.02 m; $n = 110$) to 2.06 ± 0.03 m (range = 1.51–2.95 m; $n = 114$) to facilitate monitoring and reduce the need for ladders during nest inspections. Despite this change, nest occupancy was similar between seasons: 93 nests were found during the 2018–2019 breeding season and 121 during the 2019–2020 season (including nests later discarded; see details below). A map of the study area was created, and each nest was numbered and its location recorded.

We monitored nests at 3–4-day intervals during the 2 breeding seasons (October to March in 2018–2019 and September to March in 2019–2020), with shorter intervals of 2–3 days during the peak activity period (December and January). During each inspection, we recorded the date and time of each visit, nest status ("Active" when evidence of an ongoing breeding attempt was present, including nest materials, eggs, or nestlings, and "Inactive" when the nest box was empty), number of eggs, number of nestlings, and approximate nestling age. Nest contents were inspected through the lateral access door of each nest box using a small hand mirror, and routine inspections generally lasted less than 1 min per box, except during egg measurements or nestling banding procedures. Adults were assigned to specific nest boxes based on repeated observations of individuals entering and exiting the same nest box throughout the breeding cycle. Additional details regarding egg measurements, clutch size, nestling age estimation, and parental care observations are provided in the corresponding subsections below.

We monitored 180 saffron finch nests across 2 breeding seasons (84 in 2018–2019 and 96 in 2019–2020). Among these nests, 55% ($n = 99$) had at least one parent captured and banded during the mist-netting sessions (female only: $n = 31$; both parents: $n = 28$; male only: $n = 40$). For nest-monitoring analyses, sex was determined for all dull individuals based on pair composition and behavioral observations, including female-only incubation. A total of 108 females and 103 males occupied nest boxes, with the distributions of plumage coloration and banding status provided in Table 1. Some individuals had more than one breeding attempt across seasons (females: $n = 44$; males: $n = 48$).

Table 1 Sex, plumage coloration, and banding status of saffron finches (*Sicalis flaveola brasiliensis*) occupying nest boxes.

Plumage	Female		Male	
	n (individuals)	Banded	*n* (individuals)	Banded
Yellow	59	17	89	24
Dull	49	8	14	3
Total	*108*	*25*	*103*	*27*

Most nesting pairs consisted of 2 yellow individuals (60%; $n = 109$), whereas 30% ($n = 54$) consisted of a yellow male paired with a dull female and 9% ($n = 16$) of 2 dull individuals. Only one pair (~1%) consisted of a yellow female paired with a dull male. The maximum number of breeding attempts recorded for the same pair within a single breeding season was 4 ($n = 1$; considering only banded individuals), which is higher than the maximum of 3 attempts reported by Marques-Santos et al. (2016) for saffron finches in a single season.

We assumed that a non-banded pair represented the same individuals across breeding attempts in the same nest box within a season, except in the following cases: 1) when an individual previously classified as yellow was later observed as dull, given that plumage color reversal has not been reported for this species (Palmerio and Massoni 2009, 2011; Marques-Santos et al. 2018); 2) when an individual previously classified as dull was later observed as yellow, considering the short time interval between breeding attempts within the same season; or 3) when an individual was banded in one attempt but the individual of the same sex was observed not banded in the subsequent attempt. In the opposite situation of case (3), we considered the same individual only when banding occurred between the 2 breeding attempts and the plumage color remained the same.

We excluded from all analyses: 1) nests without information on parental plumage color and banding status ($n = 33$), 2) nests with plumage color information for only one parent ($n = 7$), and 3) nests found during June and July ($n = 5$), which were monitored less frequently. Nests lacking banding information for one or both parents but with information on parental plumage color were retained ($n = 16$).

Eggs and clutch size

We measured egg length and breadth with a digital caliper (precision: 0.01 mm) and estimated egg volume using Hoyt's formula (Hoyt 1979):

$$V = 0.51 \times L \times B^2$$

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where V is egg volume (mm^3), L is egg length (mm), and B is maximum egg breadth (mm). This equation estimates egg volume within approximately 2% of the actual volume.

For clutch size analyses, we excluded nests that were predated during the egg stage before clutch completion or that were first found during the nestling stage ($n = 13$). The date of first egg laying was estimated according to nest condition. For nests with a complete clutch, we used the midpoint (rounded up) of the interval between the day the nest was found without eggs and the estimated laying date of the first egg. The latter was calculated as the day after eggs were first detected minus the number of eggs present, assuming that saffron finches lay one egg per day (Marques-Santos et al. 2016; Espinosa et al. 2017, for *S. f. flaveola*). For nests found during incomplete laying that was later completed, the first egg date was estimated as 1 day before detection for clutches of 2 eggs and 2 days before detection for clutches of 3 eggs. For nests found with one egg, the observation day was considered the laying date unless one egg was still present at the following monitoring visit. Nests with nestlings ($n = 5$), nests that were abandoned or predated after being found ($n = 4$), and nests with monitoring errors ($n = 1$) were excluded from analyses of clutch size and egg volume in relation to parental plumage color.

Parental care

We video-recorded parental activity using GoPro HD HERO2 and Kodak Zx1 cameras positioned approximately 1 m from the nest boxes and attached to wooden supports fixed to the boxes. Recordings were made in the morning (7 AM–12 PM) or afternoon (2 PM–5 PM), with a preference for the morning period due to the higher nest activity observed in the field. Videos had an average duration of 2.29 ± 0.05 h (range = 0.33–3.24 h; $n = 184$), with recording length limited by battery life. The mean number of recordings per nest was 1.59 ± 0.07 (range = 1–3; $n = 122$ recordings from 77 nests). During each recording, we noted the number of nestlings and their estimated age. Nests were filmed at different stages of nestling development to maximize sample size despite nest predation. The hatching date was estimated as the midpoint between the last monitoring visit in which eggs were present and the first visit in which nestlings were observed, following a procedure similar to Colombo et al. (2021). Nestling age was then calculated relative to this estimated hatching date. When nestlings were observed among broken eggshells and/or without down feathers and alongside eggs that had not yet hatched, they were assumed to have hatched that day (age = 0 days). Videos were excluded from parental care analyses in 3 situations: 1) when neither parent visited the nest ($n = 23$), 2) when only one parent visited ($n = 29$ for males; $n = 17$ for females), and 3) when females spent less than 1% of the recording time in the nest ($n = 8$). These exclusions were intended to remove potential cases of camera-induced behavioral inhibition. Using the CowLog 3.0.2 software (Hänninen and Pastell 2009), we recorded for each parent the number of nest visits (entries), the number of visits involving fecal sac removal, and the total time spent in (within) the nest (in seconds).

Nesting success

We considered nests successful when they were found empty after the average nestling period (14–15 days; Alvarenga 2017) and showed no signs of predation (e.g., structural damage to the nest, feathers, or blood; Dutra et al. 2021). Nests were excluded from post-hatch nesting success analyses under the following conditions: 1) irregular monitoring resulting in intervals longer than the standard 3–4-day monitoring interval since the previous check ($n = 8$), 2) nests with eggs damaged during monitoring ($n = 2$), and 3) nests lacking information on their final status ($n = 9$).

Statistical analysis

All analyses were conducted in R 4.3.2 (R Core Team 2023).

Body condition and ectoparasitism

Body condition and ectoparasite counts can vary seasonally (Cox et al. 2011; Fecchio et al. 2020). To evaluate whether these variables could be compared across social classes, we first tested for seasonal bias in capture dates among classes using a generalized additive mixed model (mgcv package; Wood 2011). Julian day as the response variable, social class and year as fixed effects, and bird identity as a random intercept. Capture date did not differ significantly among classes ($F = 2.61$, $P = 0.08$; $n = 146$ dull individuals, 40 yellow females, and 44 yellow males). We therefore considered body condition and wing ectoparasite counts broadly comparable among social classes, as differences are unlikely to reflect seasonal sampling bias or variation in reproductive stage.

We compared body condition among social classes ($n = 129$ dull individuals, 40 yellow females, and 39 yellow males) using a Kruskal–Wallis test followed by Dunn's post hoc test with false discovery rate correction (FSA package; Ogle et al. 2023) (Table 2). To compare wing ectoparasite counts among social classes ($n = 104$ dull individuals, 34 yellow females, and 32 yellow males), we fitted a zero-inflated negative binomial generalized linear model (GLM, glmmTMB package; Brooks et al. 2017) (Tables 2; Supplementary Table S1), selected after detecting overdispersion in a Poisson model and zero-inflation in a negative binomial model (performance package; Lüdecke et al. 2021). We assessed the significance of social class using Type II Wald χ^2 tests (car package; Fox and Weisberg 2019) and performed pairwise contrasts using the emmeans package (Lenth 2024).

Parental investment

We used generalized linear mixed models (GLMMs) to examine parental investment in relation to plumage color, analyzing maternal (5 models) and paternal (3 models) behaviors separately (Table 2; Supplementary Table S2). The response variables were: clutch size (egg stage; up to 3 eggs or above 3 eggs; binomial error distribution), egg volume (gamma family), visitation rate (number of visits per hour, Gamma distribution), fecal sac removal rate (number of departures from the nest with a fecal sac per hour, tweedie distribution), and total time spent in the nest (proportion of total video recording duration; beta distribution). All models included the plumage color of the focal individual and its partner (yellow or dull), as well as breeding season (2018–2019 or 2019–2020), as fixed effects. For pre-hatching care, we included date within the season (days since the first nest was found) to account for seasonal variation in egg investment (Decker et al. 2012). For post-hatching care, we included nest

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Table 2 Summary of response variables and predictors used in the statistical analyses to evaluate variation in individual quality (body condition index and wing ectoparasite load), parental investment, and nesting success in relation to social class (based on age- and sex-dependent plumage coloration) in saffron finches (*Sicalis flaveola brasiliensis*).

Category	Response variable	Predictors
Individual quality	Body condition index	Social class
	Wing ectoparasite load	Social class
Pre-hatching maternal investment	Clutch size	Female color class + Male color class + Breeding season + Date in season
	Egg volume	Female color class + Male color class + Breeding season + Date in season
Post-hatching parental investment (analyzed separately by sex)	Nest visits per hour	Female color class + Male color class + Breeding season + Nest age + Clutch size + Time of day
	Percentage of time in the nest	Female color class + Male color class + Breeding season + Nest age + Clutch size + Time of day
	Fecal sacs removal per hour	Female color class + Male color class + Breeding season + Nest age + Clutch size + Time of day
Sex-differences in parental investment	Nest visits per hour	Sex + breeding season + Nest age + Clutch Size + Time of day
	Percentage of time in the nest	Sex + breeding season + Nest age + Clutch Size + Time of day
	Fecal sac removals per hour	Sex + breeding season + Nest age + Clutch Size + Time of day
Nesting success	Probability of fledging ≥1 chick	Female color class + Male color class + Residual female nest visit rate + Residual male nest visit rate
		Female color class + Male color class + Residual female time in nest + Residual male time in nest

age (age on the day of filming relative to the hatching date of the first egg), clutch size (nestling stage; number of nestlings at the time of filming), and time of day (time of video recording). All models included nest identity nested within parental identity as a random intercept, except for the clutch size model, which included only female identity. One outlier was removed from the male time-in-nest model.

To test whether post-hatching parental investment differed between sexes, we fitted 3 additional GLMMs (Table 2; Supplementary Table S3), each with one of the following response variables: visitation rate (tweedie distribution), fecal sac removal rate (tweedie distribution), or time spent in the nest (beta distribution). Predictor variables included sex (female or male), breeding season, date within the season, nest age, clutch size (nestling stage), and time of day. Nest identity nested within parental identity was included as a random intercept.

Nesting success

To assess whether nesting success was related to social class or to the parental investment of the focal individual or its reproductive partner, we used data from 66 nests, encompassing 45 females and 41 males for whom this information was available. Here, only 2 categories of parental care for each sex were considered: nest visit rate and time spent in the nest. First, we built 4 linear models with each combination of parental care and sex (nest visit rate by males, nest visit rate by females, time spent in the nest by males, and time spent in the nest by females) as the response variable. These models followed a structure similar to that described above for the analysis of parental investment as a function of plumage color. As predictor variables, we included breeding season, nest age, clutch size, and time of day. These variables were important predictors in one or more models of parental investment as a function of plumage color (Supplementary Tables S5–S15). All models included nest identity nested within parental identity as a random intercept.

Subsequently, the residuals of these models were averaged within each nest and parent identities and used as predictor variables of parental care in 2 additional nesting success models (success or failure; binary response variable) (Table 2; Supplementary Table S4). A nest was considered successful when at least one chick fledged. These two models were GLMMs (binomial family, cloglog link function). The first model included the following predictor variables: female plumage color (yellow or dull), male plumage color (yellow or dull), residual female nest visit rate, and residual male nest visit rate. The second model had the same structure, except that residual nest visit rate was replaced by residual time spent in the nest. We included nest visit rate and time spent in the nest in separate models to avoid collinearity. Parental identities were included as random intercepts in all models.

Model performance and validation

We used the glmmTMB package (Brooks et al. 2017) to fit the models, DHARMa (Hartig 2026) to evaluate residual diagnostics and overdispersion, and parameters (Lüdecke et al. 2020) to extract standardized coefficients (standardization: "refit") and *P*-values. Error distributions were adjusted when necessary based on residual diagnostics. Statistical significance was set at $P \leq 0.05$.

Results

Body condition and ectoparasitism

Body condition varied among social classes (Kruskal–Wallis $\chi^2 = 9.81$, $P = 0.007$; Fig. 2a). Dull individuals had lower body

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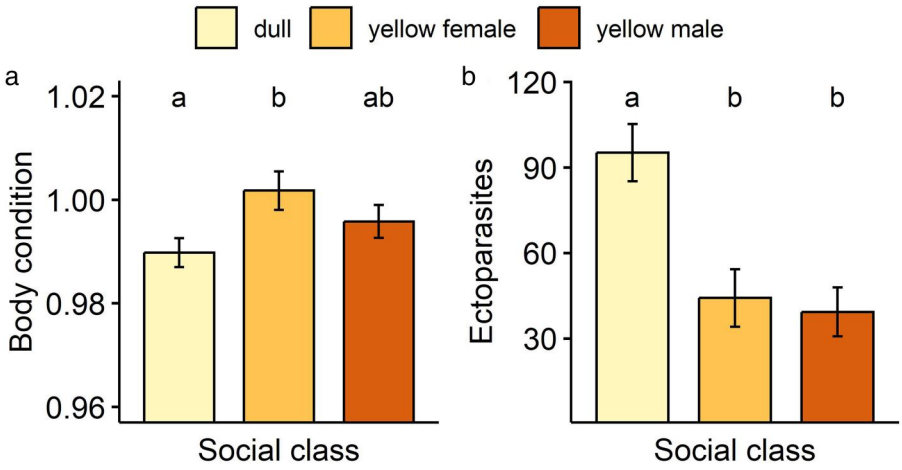


Figure 2 Body condition index (a) and number of ectoparasites in the remiges (b) as a function of social class (based on age- and sex-dependent plumage coloration) in saffron finches (*Sicalis flaveola brasiliensis*). Dull individuals were not classified by sex. Values are means ± SE. Different letters above the bars indicate statistically significant differences based on the results of Kruskal–Wallis and Dunn tests (a) and a GLM (b). Sample sizes were: a) 129 dull individuals, 40 yellow females, and 39 yellow males; b) 104 dull individuals, 34 yellow females, and 32 yellow males.

conditions than yellow females (Dunn's test, $Z = -2.89$, $P = 0.011$). Body condition did not differ between yellow males and yellow females (Dunn's test, $Z = -0.83$, $P = 0.40$) or between yellow males and dull individuals (Dunn's test, $Z = 1.84$, $P = 0.10$). Wing ectoparasite load varied among social classes (Type II Wald $\chi^2 = 12.84$, $P = 0.001$; Fig. 2b). Dull individuals had higher wing ectoparasite loads than yellow females ($\beta = -0.71 \pm 0.24$, post-hoc contrast, $P = 0.01$) and yellow males ($\beta = -0.64 \pm 0.24$, post-hoc contrast, $P = 0.01$). Wing ectoparasite counts did not differ between yellow males and females ($\beta = -0.07 \pm 0.30$, post-hoc contrast, $P = 0.81$).

Parental investment

Clutch size and egg volume were not related to female or partner plumage color (Table 3, Supplementary Tables S5 and S6). Nest visit rate was not related to the plumage color of the focal parent (Fig. 3a; Table 3; Supplementary Tables S7 and S8) or of the respective partner (Fig. 3b; Table 3; Supplementary Tables S7 and S8). Time spent in the nest was not related to the plumage color of the focal parent (Fig. 3c; Table 3; Supplementary Tables S9 and S10). However, females paired with yellow males tended to spend more time in the nest, on average, than females paired with dull males ($P = 0.066$; Fig. 3d; Table 3; Supplementary Table S9). Time spent in the nest by males also varied according to the plumage color of their partner. In contrast to females, males paired with dull females spent more time in the nest than males paired with yellow females (Fig. 3d; Table 3; Supplementary Table S10). Fecal sac removal rate was not related to the plumage color of the focal parent (Table 3; Supplementary Tables S11 and S12) or, in females, to the plumage color of their partner (Table 3; Supplementary Table S11). Males paired with dull females tended to remove fewer fecal sacs than males paired with yellow females (Table 3; Supplementary Table S12).

When parental care was compared between the sexes, females invested significantly more than males in caring for nestlings (Table 4). Females visited nests more frequently (Fig. 3a; Supplementary Table S13), spent more time in the nest (Fig. 3c; Supplementary Table S14), and removed more fecal sacs than males (Table 3; Supplementary Table S15). Although nests received more visits from both females ($\beta = 0.19$, 95% CI: 0.12 to 0.26, $P < 0.001$; Supplementary Table S7) and males ($\beta = 0.11$, 95% CI: 0.04 to 0.19, $P = 0.004$; Supplementary Table S8) at later nestling stages, the proportion of time spent in the nest decreased as nestlings developed for both females ($\beta = -0.40$, 95% CI: −0.51 to −0.25, $P < 0.001$; Supplementary Table S9) and males ($\beta = -0.08$, 95% CI: −0.17 to 0.01, $P = 0.076$; Supplementary Table S10), likely reflecting reduced brooding effort.

Nesting success

Of the 66 nests monitored, 54 (82%) fledged at least one chick, whereas the remaining 12 (18%) failed due to predation (7 cases) or nestling death (5 cases). The probability of fledging at least one chick was not related to either parental plumage color or parental investment (Supplementary Tables S16 and S17). The first model (including residual nest visit rate as a predictor variable) showed that nesting success was not related to female plumage color ($\beta = -0.14$, 95% CI: −0.87 to 0.59, $P = 0.71$), male plumage color ($\beta = 0.26$, 95% CI: −0.95 to 1.48, $P = 0.67$), nest visit rate by the female ($\beta = -0.05$, 95% CI: −0.39 to 0.29, $P = 0.79$), or nest visit rate by the male ($\beta = 0.23$, 95% CI: −0.11 to 0.57, $P = 0.18$).

Similarly, the second model (including residual percentage of time spent in the nest as a predictor variable) showed that nesting success was not related to female plumage color ($\beta = -0.41$, 95% CI: −1.21 to 0.39, $P = 0.31$), male plumage color ($\beta = -0.02$, 95% CI: −1.31 to 1.32, $P = 0.98$), time spent in the nest by the female ($\beta = 0.15$, 95% CI: −0.19 to 0.49, $P = 0.38$), or time spent in the nest by the male ($\beta = -0.13$, 95% CI: −0.43 to 0.16, $P = 0.37$). However, it is important to note that only one dull-plumaged male and 3 dull-plumaged females experienced nesting failure (i.e., did not produce a fledgling).

Discussion

We tested whether the plumage coloration of saffron finches (*S. f. brasiliensis*) signals body condition, wing ectoparasite

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Table 3 Mean values, sample sizes (*n*), coefficients (β), and 95% confidence intervals (CI) from generalized linear mixed models examining the relationship between individual and partner plumage color and parental investment in the saffron finch (*Sicalis flaveola brasiliensis*).

Model no./variables	Individual social class				Partner social class			
	Mean (*n*)		β (95% CI)	*P*	Mean (*n*)		β (95% CI)	*P*
	Dull	Yellow			Dull	Yellow		
Female								
1. Clutch size	3.61 (62)	3.68 (103)	0.50 (−0.59; 1.59)	0.37	3.40 (15)	3.68 (150)	0.93 (−0.75; 2.61)	0.28
2. Egg volume	2,079.55 (108)	2,121.07 (162)	0.01 (−0.03; 0.13)	0.60	2,015.94 (28)	2,114.70 (242)	0.06 (−0.01; 0.13)	0.10
3. Nest visits per hour	1.65 (39)	1.85 (83)	0.09 (−0.11; 0.29)	0.39	1.53 (8)	1.80 (114)	0.19 (−0.16; 0.53)	0.30
4. Percentage of time in the nest	6.67 (39)	8.72 (83)	0.24 (−0.09; 0.57)	0.16	3.04 (8)	8.42 (114)	0.63 (−0.04; 1.31)	0.066*
5. Fecal sac removals per hour	0.86 (39)	0.93 (83)	0.06 (−0.36; 0.48)	0.78	1.15 (8)	0.89 (114)	−0.28 (−0.95; 0.40)	0.42
Male								
6. Nest visits per hour	1.15 (8)	1.38 (114)	0.20 (−0.16; 0.55)	0.28	1.36 (39)	1.37 (83)	−0.07 (−0.27; 0.13)	0.47
7. Percentage of time in the nest	2.98 (7)	2.29 (114)	−0.18 (−0.66; 0.30)	0.46	3.05 (38)	2.00 (83)	−0.37 (−0.63; −0.11)	**0.006**
8. Fecal sac removals per hour	0.60 (8)	0.62 (114)	−0.09 (−0.79; 0.62)	0.81	0.46 (39)	0.69 (83)	0.36 (−0.04; 0.77)	0.08*

An asterisk indicates a result close to statistical significance ($0.10 > P > 0.05$), and bold values indicate statistically significant results ($P \leq 0.05$). Sample sizes correspond to the following: number of nests (clutch size), number of eggs (egg volume), and number of video recordings (nest visits per hour, percentage of time in the nest, and fecal sac removals per hour).
Model 1 used a binomial distribution (logit link), Models 2, 3, and 6 used gamma distributions (log link), Models 5 and 8 used tweedie distributions, and Models 4 and 6 used beta distributions. Models 1 and 2 included the following fixed effects: individual social class (dull or yellow), partner social class (dull or yellow), breeding season (2018–2019 or 2019–2020), and date within the season (days relative to the date the first nest was found). Models 4–8 included the following fixed effects: individual social class, partner social class, breeding season, nest age (age on the day of video recording relative to the hatching date of the first egg), clutch size (nestling stage; number of chicks at the time of video recording), and time of day (at the start of the video recording). All models included parental identity as a random intercept; all except Model 1 also included nest identity nested within female identity. An outlier was removed from the male "percentage of time in the nest" model (Model 7).

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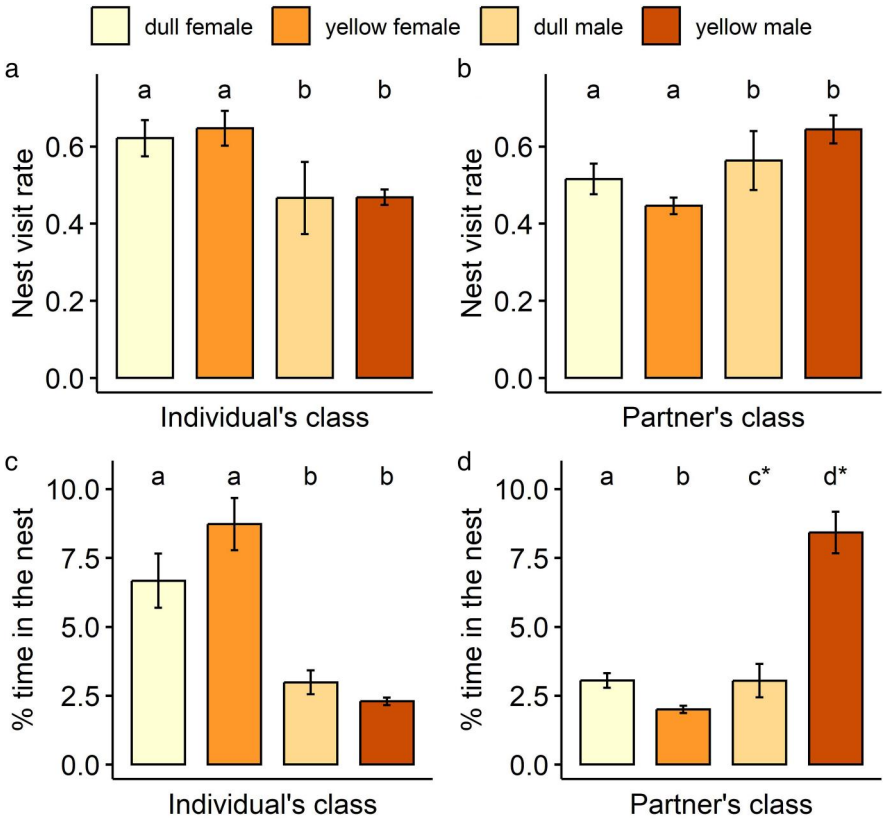


Figure 3 Nest visit rate (number of visits per hour divided by clutch size; a) and b) and percentage of time spent in the nest (c, d) by female and male saffron finches (*Sicalis flaveola brasiliensis*), according to the plumage color of the focal individual (a, c) and that of its reproductive partner (b, d). Values are means ± SE. Statistically significant differences are indicated based on GLMM results; the comparison between c* × d* in panel D was marginally non-significant ($P = 0.066$). Sample sizes (video recordings): 38 dull females, 83 yellow females, 8 dull males, and 114 yellow males.

Table 4 Means, coefficients (β), and 95% confidence intervals (CI) from generalized linear mixed models testing sex differences in parental investment in saffron finches (*Sicalis flaveola brasiliensis*).

Model no./variables	Mean ± SD		β (95% CI)	*P*
	Female	Male		
1. Nest visits per hour	1.79 ± 0.89	1.37 ± 0.68	−0.25 (−0.38, −0.12)	**<0.001**
2. Percentage of time in the nest	8.07 ± 7.95	2.33 ± 1.44	−1.05 (−1.28, −0.82)	**<0.001**
3. Fecal sacs removal per hour	0.91 ± 0.92	0.62 ± 0.65	−0.36 (−0.62, −0.09)	**0.008**

Statistically significant results ($P \leq 0.05$) are shown in bold.
Models 1 and 3 used tweedie error distributions, and Model 2 used a beta distribution. The parental care models for the nestling stage included the following covariates: sex (reference level: female), breeding season, date within the season, nest age, clutch size (nestling stage), and time of day. All models included nest identity nested within parental identity as a random intercept. An outlier was removed from the male "percentage of time in the nest" model. Sample sizes were 122 recordings, 76 nests, 53 females, and 48 males (Models 1 and 3); and 121 recordings, 75 nests, 53 females, and 48 males for time spent in the nest (Model 2).

load, parental investment, and fitness. Females with yellow plumage had better body condition, and individuals of both sexes with yellow plumage had fewer ectoparasites in their wing feathers than dull-colored individuals. Males spent more time in the nest when paired with dull females, whereas females tended to spend more time in the nest when paired with yellow males. No relationship was found between nesting success during the nestling stage and plumage coloration or parental investment. These results suggest that yellow plumage may honestly signal age-dependent body condition in females and wing ectoparasite load in both sexes and may influence parental investment by reproductive partners.

Body condition and ectoparasitism

We found a greater amount of ectoparasites on the wings of individuals with dull plumage, indicating that plumage color predicts wing ectoparasite load in the species. There was no difference in wing ectoparasite load between yellow males and

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females. Previous studies have also reported a negative relationship between plumage coloration and the number of ectoparasites in the remiges of other granivorous songbirds (Magalhães et al. 2014; Trigo and Mota 2016). A higher wing ectoparasite load in dull-plumaged individuals may be explained by their younger age (Senar 2006; Trigo and Mota 2016), which could increase the probability of ectoparasite transmission from parents in the nest (Johnson and Clayton 2003). Alternatively, the lower wing ectoparasite load observed in yellow individuals supports the parasite-mediated sexual selection hypothesis, which predicts that only individuals in good health can bear the metabolic costs of producing carotenoid-based ornamental plumage (Zahavi 1975; Hamilton and Zuk 1982; Dawson and Bortolotti 2006; Dougherty et al. 2023). The high frequency of breeding pairs with the same plumage coloration (69% of nest boxes were occupied by pairs with the same plumage coloration; $n = 125$; unpublished data) suggests assortative pairing in the species (i.e., a mating pattern in which individuals choose partners with similar phenotypic characteristics), a pattern previously reported for the same subspecies, *S. f. brasiliensis* (Marques-Santos et al. 2018). Therefore, both sexes may preferentially select yellow partners, which have lower wing ectoparasite loads and may thus indicate better health.

Yellow females showed better body condition than dull individuals. Similar relationships between plumage coloration, body condition, and sometimes age have been reported in other songbirds (e.g., Blue-black Grassquit *Volatinia jacarina*, Eastern Bluebird *Sialia sialis*; Harper 1999; Siefferman et al. 2005; Magalhães et al. 2014). In another population of saffron finches (*S. f. brasiliensis*), yellow males are heavier and yellow females have more subcutaneous fat than dull individuals in intrasexual comparisons (Marques-Santos et al. 2018). Body condition, development, and the conspicuousness of carotenoid-based plumage can be strongly influenced by food availability and quality (Hill and Montgomerie 1994; Hill 2000; Brown and Sherry 2006; Mahoney et al. 2022). Given the unintentional and indirect food supplementation in our study area, yellow females may either outcompete dull individuals for access to these resources or be physiologically more efficient at maintaining body mass (Carrascal et al. 1998). Supporting this idea, food supplementation experiments showed that yellow females were more socially dominant than other social classes in securing access to these resources (Araújo-Silva et al. 2023), suggesting that social dominance may contribute to their better body condition relative to dull individuals. In contrast, the absence of a similar pattern in males suggests that sex-specific physiological mechanisms may mediate the relationship between body condition and plumage coloration.

Because body condition and ectoparasite loads can vary seasonally (Cox et al. 2011; Fecchio et al. 2020), further studies are needed to determine whether the observed differences and similarities among social classes are consistent across breeding and non-breeding seasons and among different breeding stages.

Parental investment

Our results show that differences in plumage coloration between individuals of the same sex in saffron finches (*S. f. brasiliensis*) do not lead to differences in the parental investment measures examined in this study (e.g., clutch size, egg volume, visitation rate, percentage of time spent in the nest, and fecal sac removal rate). These results reinforce the findings of Palmerio and Massoni (2011) for the subspecies *S. f. pelzelni*, in which no differences were found in visitation rate or fecal sac removal rate between dull and yellow males. In an intersexual context, however, partner plumage color predicted the time males spent in the nest, with males remaining longer in the nest when paired with dull females.

In females, we found no relationship between plumage coloration, either of the individual or of the mate, and the parental investment measures examined. These results therefore suggest that female plumage coloration in this species does not indicate parental ability, unlike the findings of Marques-Santos et al. (2018), in which yellow females produced larger clutches than dull females. The differences between the 2 studies may be explained by food availability in the study area of the present work. Dull females in our study might have benefited from the available food resources and produced clutch sizes similar to those of yellow females (Ruffino et al. 2014). Unlike previous studies (Préault et al. 2005; Mitchell et al. 2007; Bulluck et al. 2017), our results do not support the good parent or trade-off hypotheses, which relate conspicuous parental coloration to positive or negative correlations with parental investment, respectively (Hoelzer 1989; Magrath and Komdeur 2003).

Regarding investment in relation to partner plumage coloration, males showed the opposite pattern predicted by the differential allocation hypothesis (Burley 1986), investing more in offspring (in terms of time spent in the nest) when paired with dull females. This pattern supports the reproductive compensation hypothesis (Harris and Uller 2009), suggesting that males paired with dull females increase their parental effort to compensate for the presumed lower condition or parental investment of their mates. In females, we found a tendency toward greater investment (in terms of time spent in the nest) when paired with yellow males, although this effect was not statistically significant. Similarly, females of the subspecies *S. f. pelzelni* showed no significant differences in clutch size or egg volume when paired with yellow or dull males (Palmerio and Massoni 2009).

We also observed higher nestling care by females, which exceeded that of males in nest visit rate, time spent in the nest, and fecal sac removal. In a study conducted in Colombia on the subspecies *S. f. flaveola*, females also exhibited higher nest visit rates than males throughout nestling development (Espinosa et al. 2017). The lower parental effort by males may be related to uncertainty of paternity or reduced genetic relatedness to offspring (Whittingham et al. 1992). As predicted by parental investment theory, there is likely a trade-off between parental effort and the pursuit of additional reproductive opportunities (Trivers 1972; Maynard Smith 1977; Westneat 1988; Magrath and Komdeur 2003). Extra-pair paternity has been reported at relatively high frequency in the subspecies *pelzelni* (32%; Benítez-Saldívar et al. 2019). Although paternity was not assessed in the present study, these findings suggest that the relationship between paternity assurance and male parental effort remains to be investigated in our population.

Nesting success

The probability that at least one chick successfully fledged was not related to plumage coloration or parental investment (i.e., nest visit rate and time spent in the nest). Alternatively, plumage

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coloration, through the inheritance of viability, or parental investment may influence other measures of offspring development (e.g., mass, juvenile survival, longevity) and reproductive success (number of offspring produced) that were not investigated in this study (Møller 1994; Bjørnstad and Lifjeld 1996; Schwagmeyer and Mock 2008; López-Idiáquez et al. 2018). A similar result was reported in a Colombian population of saffron finches (*S. f. flaveola*), in which no relationship was found between parental investment and reproductive success, defined as the number of nestlings reaching 16 days of age (Burnham and Cruz-Bernate 2020). Although not investigated here, the age-dependent quality of an individual or its mate may influence long-term reproductive success (e.g., annual reproductive success). For example, female Japanese Tits (*Parus minor*) produce more clutches per season when paired with a high-quality, older male (Nomi et al. 2018). In another population of saffron finches (*S. f. brasiliensis*), female plumage coloration is linked to annual reproductive success, with yellow females producing 39% more nests per breeding season and resulting in twice as many fledglings as dull females (Marques-Santos et al. 2018).

Taken together, our findings suggest that plumage coloration signals age-dependent body condition in females and age-dependent wing ectoparasite load in both sexes in saffron finches (*S. f. brasiliensis*) and is related to the parental care provided to nestlings by the mate, but not by the focal individual. Future studies should examine whether sex-related differences in body condition and wing ectoparasite load exist among dull-colored individuals. Our results also suggest that, despite females investing heavily in offspring, neither age-dependent plumage coloration nor parental investment translates into greater nesting success, indicating that offspring recruitment in this species is likely influenced by other factors. Future studies should test the effects of environmental variables (e.g., resource availability, nest microclimate) and the type of food provided to nestlings on reproductive success. They could also examine alternative measures of reproductive success (e.g., nestling development or mass) or test whether age-dependent plumage coloration is positively related to other aspects of parental care, such as the amount of food delivered to nestlings per visit or post-fledging care.

Acknowledgments

We thank all the students who helped with field data collection, especially Bianca Lyrio, Adriano Souza, Amanda Portugal, and Maurício Roveré. We thank Professor Marco Pizo for helping us with the cameras. We thank Leonardo Casadei, Antonio Maia, and Marcos Campis for authorizing us to use their saffron finches' photos.

Authors' contributions

P.D. conceived the idea. C.D. and P.D. supervised the research. All authors collected the data. P.D. analyzed the data. M.B. wrote the manuscript, and P.D. and C.D. reviewed and edited it. All authors approved the final version for publication.

Supplementary material

Supplementary material can be found at https://academic.oup.com/cz.

Funding

This research was supported by Concessionária Rodovia do Sol S.A. (Rodosol) and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (CAPES). M.B. and B.A.S. were supported by CAPES Master's scholarships (Finance Code 001), while P.D. received CAPES postdoctoral fellowships (grant numbers 88882.317011/2019-01 and 88887.469218/2019-00). P.D. is currently funded by a postdoctoral fellowship from the São Paulo Research Foundation (FAPESP), Brazil (Process No. 2024/13237-3). M.B. is currently supported by a CAPES doctoral scholarship (Process No. 88887.712529/2022-00).

Conflict of interest statement

The authors have no conflict of interest to declare.

Ethics statement

This research was conducted according to the ethics committee of Universidade Vila Velha (Process No. 555–2019 CEUA–UVV).

Data availability

All data and R code supporting the analyses have been permanently deposited in Mendeley Data under the DOI https://doi.org/10.17632/m55t3nymt6.1.

Artificial intelligence–assisted technologies

Artificial intelligence (AI)–assisted technologies were used during the revision process for English language editing, grammar correction, and improvement of text clarity. AI was also used in the preparation of the graphical abstract.

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