





RESEARCH ARTICLE

Mate desertion affects offspring survival, development and physiology in a songbird with multiple parental strategies

Valentina Alaasam¹  | Alejandro Cantarero²  | Matteo Beccardi³ |
 Alejandro Corregidor-Castro^{4,5} | Manuel Fuertes-Recuero² | Matteo Schiavinato⁶ |
 Lia Zampa⁷ | Alessandro Grapputo^{4,5} | Matteo Griggio⁴ | Jenny Q. Ouyang⁸  |
 Andrea Pilastro^{4,5} | Davide Baldan⁸ 

¹Department of Biology, New York University, New York, New York, USA; ²Department of Physiology, Veterinary School, Complutense University of Madrid, Madrid, Spain; ³Institute of Avian Research, Wilhelmshaven, Germany; ⁴Department of Biology, University of Padova, Padova, Italy; ⁵National Biodiversity Future Center, Palermo, Italy; ⁶Wageningen University and Research, Wageningen, The Netherlands; ⁷Department of Behavioural Ecology, Adam Mickiewicz University, Poznań, Poland and ⁸Department of Biology, University of Nevada, Reno, Reno, USA

Correspondence

Valentina Alaasam

Email: valentina.alaasam@gmail.com**Funding information**

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Handling Editor: Jean-François Lemaître**Abstract**

1. Sexual conflict affects the amount and duration of offspring care each parent invests, resulting in multiple parental care strategies sometimes coexisting within a single population. Understanding the persistence of multiple parental care strategies requires a precise estimate of the benefits and costs associated with parental decisions. Even though the benefits of brood desertion are well known, the reproductive costs of desertion (*i.e.*, nestlings' physiological conditions and survival), are less explored.
2. We use rock sparrows, *Petronia petronia*, a species in which both uniparental and biparental care occur in the same population, to investigate the costs of brood desertion. Specifically, we continuously monitored breeding attempts to explore the behavioural mechanisms (desertion decision and compensatory responses) and the reproductive and physiological consequences (offspring corticosterone concentrations, oxidative stress, telomere attrition) of parental care strategies.
3. We show that male desertion was not related to the initial value of the brood (clutch size, brood size) but was associated with a reduction in the survival probability of the nestlings. Females caring alone increased their per capita feeding rate, partially compensating for the lack of male care. Nestlings deserted earlier also experienced higher oxidative stress and had higher corticosterone concentrations during the early stages of development, but these effects did not persist to fledging, and there were no differences in telomere attrition.
4. Our findings indicate combined reproductive and physiological costs associated with brood desertion. Considering these costs is essential to understand the evolution and persistence of polymorphic patterns of care.

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KEYWORDS

brood desertion, corticosterone, developmental stress, oxidative stress, parental strategies, sexual conflict, telomere attrition

1 | INTRODUCTION

Family life is a source of both cooperation and conflict. Parents benefit from joint investments in their shared offspring (Royle et al., 2012), but the cost of parental care is individually paid in terms of reduced survival and future reproductive opportunities (Alonso-Alvarez & Velando, 2012; Williams, 1966). Asymmetry between the costs and benefits of care produces sexual conflict, an evolutionary conflict of interests over how much each parent should invest in their offspring (Houston et al., 2005; Trivers, 1972). This tension between the two sexes has led to the evolution of a variety of parental care strategies, ranging from cooperative biparental care, uniparental care, and no care (Lessells, 2006; Székely, 2014; Webb et al., 1999). Parental care strategies are often fixed within species (Furness & Capellini, 2019; Remeš et al., 2015; Vági et al., 2024; West & Capellini, 2016), but sometimes intraspecific variation exists, with some individuals/pairs in a population performing biparental care and others defecting care (Balshine-Earn, 1997; Dijk et al., 2012; Griggio & Pilastro, 2007; Ward et al., 2009; Zheng et al., 2018). Understanding the mechanisms driving the presence and maintenance of these polymorphisms in parental care patterns is a prominent effort in behavioural ecology.

Existing work has shown that parental cooperation (*i.e.*, biparental care) sits on extremely fragile grounds. Brood desertion by one or both parents, usually followed by subsequent remating with a different partner, often occurs when the current brood value (Beissinger, 1990; Erikstad et al., 1997; Olsson, 1997; Székely & Cuthill, 2000) or condition of the deserted mate is low (Barta et al., 2002; Olsson, 1997). Concurrently, brood desertion is also more predominant in social and environmental conditions that facilitate the finding of a new mate (Pilastro et al., 2001; Székely et al., 1999) or decrease the cost of care (Brown et al., 2010; Eldegard & Sonerud, 2009; Moss & Moore, 2021; Vincze et al., 2013; Wisenden, 1994). Theory suggests that brood desertion by one parent (followed by uniparental care by the partner) is evolutionarily stable only if the expected reproductive benefits derived from subsequent broods outweigh the potential desertion costs in the first brood (*e.g.*, reduced offspring growth or survival (Maynard Smith, 1977; Webb et al., 1999).

While the benefits of desertion for the deserting parent are intuitive, that is initiation of a new brood shortly after (McDonald et al., 2022; Pilastro et al., 2001) or improved survival to future breeding seasons (Osorno, 1999; Tavecchia et al., 2002; Urano, 1992), the reproductive costs of desertion are less clear (Houston et al., 2005; Webb et al., 1999). Costs of desertion on reproductive success are typically estimated by measuring offspring growth and survival as proxies of offspring fitness. Several field studies on plovers (*Charadrius*), precocial species that exhibit flexible parental care strategies, have shown

no apparent costs associated with brood desertion (Kupán et al., 2021; McDonald et al., 2022). This is to be expected in precocial species, where nestlings are independent from an early age and capable of finding food to sustain their growth with relatively little parental assistance (Kupán et al., 2021; McDonald et al., 2022). Indeed, the consequences of mate desertion have been shown to depend on the contribution of the parent to offspring provisioning (Møller, 2000), which is typically greater when offspring are altricial. Still, across species (both altricial and precocial), experimental removals of one parent in naturally biparental care systems have found conflicting evidence for the costs of mate desertion on offspring growth and survival, with some reporting reductions while others report no effect (Harrison et al., 2009; Møller, 2000). If it is true that one parent can withdraw at no cost, leaving the other to fully compensate for its absence (Griggio et al., 2005; Harrison et al., 2009; Smiseth et al., 2005), biparental care would not be an evolutionary stable solution: desertion would consistently be the most profitable strategy and biparental care systems would rapidly evolve to uniparental care (Houston & Davies, 1985; Johnstone & Hinde, 2006; McNamara et al., 1999).

One explanation for this apparent paradox is that brood desertion can have consequences for offspring other than affecting growth and survival (Lynn & Kern, 2014; Oers et al., 2015; Pravosudov & Kitaysky, 2006; Schmidt et al., 2014). For example, a few previous studies have found that reduced nest attendance and parental provisioning behaviour can negatively affect offspring physiological phenotype by elevating baseline corticosterone levels (Rensel et al., 2010) and inducing oxidative damage (López-Arrabé et al., 2016), both of which are well-studied biomarkers of chronic physiological stress and can have long-term effects on fitness. Mate-removal studies on zebra finches (*Taeniopygia guttata*) have shown that divorce/parental deprivation increases offspring corticosterone stress response (Banerjee et al., 2012; Crino et al., 2017). Insufficient provisioning can also increase the rate of telomere attrition during the developmental period (Boonekamp et al., 2014; Nettle et al., 2015; Wood & Young, 2019), a molecular consequence of oxidative damage and a reliable predictor of survival and longevity (Angelier et al., 2013; Barrett et al., 2013; Bize et al., 2009). These signals of early developmental stress can have profound effects on offspring behaviour, physiology and fitness during adulthood (Barou-Dagues et al., 2025; Boogert et al., 2014; Brandl et al., 2019; Romero-Haro & Alonso-Alvarez, 2020; Schoech et al., 2011). Thus, parental decisions regarding 'if and when to desert' may have more subtle and important consequences for reproductive success, yet examples of these outcomes are currently limited.

Systems with natural variation in parental strategies within populations are key to understanding the costs of desertion and the evolutionary stability of alternative strategies. To date, most of what is known about the costs of desertion comes from parent-removal experiments on species in which mate desertion is not a naturally

occurring parental strategy (Møller, 2000). Observational field studies examining mate desertion have focused mostly on precocial species, for which the consequences of desertion may be less severe compared to altricial species, whose nestlings rely completely on their parents for provisioning (Kupán et al., 2021; McDonald et al., 2022; Szekely, 2014). Moreover, few studies have considered physiological consequences for offspring that may be important predictors of offspring quality and contribute to the costs of nest desertion.

In this study, we investigated the reproductive costs of brood desertion by quantifying effects on offspring growth, physiology and survival in a wild population of rock sparrows (*Petronia petronia*). The rock sparrow is an altricial avian species characterized by a pronounced polymorphism in parental care strategies. In some pairs, both parents care for offspring until they fledge (biparental care), while in others one parent interrupts its care contribution during the offspring provisioning period (Baldan & Griggio, 2019; Griggio et al., 2005). We continuously monitored a total of 41 nests, quantifying parental care decisions (if and when desertion occurs) and provisioning rates, following the fate of offspring from hatching to fledging. This allowed us to dynamically assess the nest condition when parental decisions were made and the consequences of such decisions on offspring growth and survival. We also integrated physiological markers of developmental stress (corticosterone levels, oxidative stress, and telomere length) at two stages of offspring development to evaluate the extent to which mate desertion affects offspring physiological phenotype. These biomarkers are not independent and may represent different components of a cascading physiological response to stress (Angelier et al., 2018; Haussmann & Marchetto, 2010). We predicted that (1) mate desertion would lead to reduced offspring provisioning, resulting in decreased growth and survival of offspring and (2) mate desertion would increase baseline corticosterone concentrations, oxidative stress and telomere attrition in offspring. We also hypothesized that the costs of desertion may depend on the timing of desertion and predicted that negative consequences for offspring would be greater in nests that were deserted earlier in the nesting period. Lastly, we considered an alternative hypothesis: if the remaining parent could fully (or partially) compensate for the deserting mate by increasing provisioning rates, the negative consequences on offspring growth, physiology and survival might be fully (or partially) buffered.

2 | METHODS

2.1 | Ethics statement

Permissions for handling birds were provided by Consejería de Medio Ambiente de Castilla y León (protocol numbers sG_2020_0241 and AUES/SG/09/2022). The work was approved by Consejería de Medio Ambiente de la Comunidad de Madrid (approval ref. PROEX 088.7/22).

2.2 | Study species

The rock sparrow is a small passerine bird with a wide geographic distribution, ranging from the Mediterranean basin to the Middle East and Central Asia (Perrins, 1978). Rock sparrows typically breed from May to the end of July (Griggio et al., 2005; Griggio & Pilastro, 2007; Mingozi et al., 2021). Females lay clutches of an average size of 5–6 eggs, and upon hatching, nestlings are usually fed at the nest for an average period of 16–18 days until fledging (Griggio & Pilastro, 2007). The rock sparrow parental care system is highly variable (Baldan & Griggio, 2019; Griggio & Pilastro, 2007). Some nests are biparental, with both parents provisioning equally until offspring fledge (65% of first brood). In others, one sex deserts the brood at some point during the offspring provisioning period, leaving the remaining parent to care alone (25% of first broods are female-only care, 10% of first broods are male-only care). However, the frequencies of each parental care strategy are extremely variable across populations. In the Spanish population where this study was conducted, female desertion is extremely rare (2.7% of nests) and uniparental nests with male desertion are more frequent (32.7%; A. Cantarero, unpublished data).

2.3 | Experimental design

We conducted our study from May to July in 2021 and 2022 on a wild rock sparrow population breeding in nest boxes on the grassland slopes of Valsain (Segovia, central Spain, 40°53'74" N, 4°01' W, 1200 m a.s.l.). This population has been monitored since 2013 (Cantarero et al., 2019; Corregidor-Castro et al., 2022). We routinely checked nest boxes for clutch initiation and determined the onset of egg laying, incubation and hatching.

After hatching, we recorded videos of all nests to quantify provisioning and desertion behaviour on days 3, 6, 8, 11 and 14. All recordings were 1.5 h in duration and took place in the morning between 7:30 AM and 12:30 PM (Figure S1). Digital video cameras (Sony Handcam CX405) were placed approximately 20 m away from the nest boxes such that they would capture a ~2 m radius surrounding the nest box. To minimize observer bias, one researcher (M.F.R.) scored all the video recordings and was unaware of the research aims. During each filming session, we recorded provisioning rates (visits to the nest per hour) by the male and female, individually. We considered provisioning visits any event in which parents were observed bringing food (visible) for the nestling into the nest box (Baldan et al., 2019). Total per capita feeding rate was calculated as the number of total visits by both parents, divided by the number of nestlings present. Per capita feeding rates were also calculated for each parent individually, as the number of visits by each parent divided by the number of nestlings. The frequencies of provisioning visits before desertion observed in this study (male visit rate: 7.03 ± 3.91 ; female visit rate: 8.71 ± 3.75 ; mean \pm SD) were very similar to those obtained in previous studies (Baldan & Griggio, 2019; Cantarero et al., 2019). If a female was observed to be provisioning

alone, with no male present, we considered the brood uniparental during that observation. We determined a brood to be deserted by the male when the male was not present during the entire duration of the video (Griggio et al., 2005) and did not reappear in any subsequent videos throughout the development period. The time of desertion was estimated as the midpoint between the two consecutive recordings in which a male was present and then not present (Griggio et al., 2005). During the 2 years of study, only male desertion was observed (no occurrences of female desertion). All deserted broods in the present study, therefore, represent female-only care.

After each recording, we measured tarsus (nearest mm) and mass (nearest 0.1 g) of all offspring. On day three, we marked offspring with non-toxic nail polish on their nails for individual identification and then metal banded them on day six. On days eight and 14 blood was collected from the nestling's brachial vein (<150 µL) with capillary tubes within 3 min of approaching the nest box and immediately stored on ice (for less than 4 h) until transport to the laboratory, where plasma was separated from red blood cells and stored at -80°C. Blood sampling was carried out by a team of five researchers each year to ensure blood collection from all the nestlings was within 3-min. On day seven, adults were captured in the nest box during daytime using a conventional nest box trap set at the entrance, measured (mass and tarsus) and colour banded for individual identification. Because this population has been monitored long-term, many of the adults were recaptures that had already been banded (57%), and so, we were able to estimate adult age and confirm sex based on our records. We recorded the minimum possible age of adults based on the year of first capture. We were unable to capture males at many of the nests, especially those that were deserted earlier in the nesting season. So, we only include female parent age in our main analyses.

2.4 | Corticosterone

We measured offspring plasma corticosterone level using enzyme-linked immunosorbent assays (Enzo Life Sciences; Farmingdale, NY, USA) following manufacturer instructions and read optical density on a plate reader at 405 nm. We first validated this assay for rock sparrows by using serial dilutions of plasma with two different concentrations of steroid displacement reagent (SDR; 0.5% and 1% of plasma volume) and a standard curve. From this, we determined an optimal plasma dilution of 1:10 with 0.5% concentrated SDR for subsequent assays. Samples' order was randomized across plates. Intra- and inter-plate CV, calculated from plasma run in triplicates, were 17.6% and 16.8%, respectively.

2.5 | Oxidative stress

To measure reactive oxygen metabolites (dROMs) we used a kit for detecting hydroperoxides (MC003, Diacron, Grosseto, Italy), which signal both protein and lipid oxidative damage (Costantini

& Dell'Omo, 2006). Briefly, we diluted 2 µL of blood plasma in the provided acidic buffered solution (1:50) and followed the end-point mode protocol from the manufacturer (with modifications for use on a 96-well microplate) and read optical density on a plate reader at 546 nm. Samples were run in duplicate, and intra- and inter-assay variation was 4.8% and 15.9%, respectively. To measure antioxidant capacity (oxy), we used an OXY-adsorbent test (MC 435; Diacron, Grosseto, Italy), which measures blood antioxidant barrier by quantifying the oxidant action of hypochlorous acid (HClO; Vassalle et al., 2008). Briefly, we diluted 2 µL of blood plasma in distilled water (1:100) and followed the manufacturer protocol (with modifications for use on a 96-well microplate). We then mixed a 5 µL subsample of diluted plasma with 195 µL of proved HClO solution. All samples were run in triplicate, with calibrators distributed vertically and horizontally across the plate. Intra- and inter-assay variation was 8.1% and 5.3%, respectively.

A biologically relevant assessment of oxidative stress includes both the levels of circulating dROMs and the absorbance capacity of the blood (Oxy) within individuals. So, we used an integrative index of oxidative stress to combine these measures (Vassalle et al., 2008). We standardized dROM and oxy using the function 'scale' and then calculated the difference between scaled values for each individual, such that higher values of the oxidative stress index correspond to a greater differential between dROM and oxy.

2.6 | Telomeres

Genomic DNA was extracted from erythrocytes using the Qiagen DNeasy Blood and Tissue Kit, following the manufacturer's protocol with a modification: the wash with buffer 2 was repeated twice. Sample elution from the column was also performed twice with 30 µL of AE buffer provided in the kit. DNA quality of each elution was assessed using a Nanodrop ND-2000 C spectrophotometer (Thermo Scientific, USA), with 260/280 and 260/230 ratios greater than 1.8 considered acceptable. DNA quantification was performed using Qubit (Invitrogen) with the AccuGreen Broad Range dsDNA quantification kit (Biotium). Samples were diluted to a concentration of 3 ng/µL.

Relative telomere length (RTL) was measured using quantitative real-time PCR (qPCR) (Cawthon, 2002), calculating the ratio between telomeric DNA and the single-copy reference gene Glyceraldehyde-3-phosphate dehydrogenase (GAPDH). Telomeric primers Tel1b and Tel2b, and GAPDH primers GAPDH-F and R were employed (Crisuolo et al., 2009). Amplifications were performed on a BioRad CFX384 Touch Real-Time PCR System.

Each reaction was conducted in a 10 µL volume, containing 2 µL of 5× HOT FIREPol® EvaGreen® qPCR Mix Plus (without ROX) (Solis BioDyne), 6 ng of genomic DNA, and 200 nM of each forward and reverse primer. The qPCR profile consisted of an initial step at 95°C for 12 min, followed by 40 cycles of 95°C for 20 s, 58°C for 18 s and 72°C for 1 min. Upon completion of each run, a melt curve (65°C–95°C, with 0.5°C increments for 5 s) was generated to confirm qPCR specificity.

Each plate contained samples collected from nestlings at 8 and 14 days after hatching, two interpolate calibrators and a negative control for both telomere and GAPDH, all run in triplicate. Baseline and cycle quantification (Cq) values were corrected using LinRegPCR software ver. 2017.1 (Ruijter et al., 2009). Between-run variation was removed using Factor qPCR (Ruijter et al., 2015). Relative telomere length was calculated following the equation proposed by Pfaffl (2001), as reported in Morbiato et al. (2023) and in Monteforte et al. (2020). An acceptance threshold for amplification efficiency was set at $100 \pm 20\%$. Inter-assay coefficients of variation (CV) were 3.7% for telomere and 1.3% for GAPDH, while intra-assay CVs were 1.3% for telomere and 1.4% for GAPDH.

2.7 | Statistical analyses

2.7.1 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Individual	Nest	41
Individual	Offspring	189

For all analyses (unless otherwise specified), we ran Bayesian regression models in R version 4.3.2 (R Development Core Team, 2017) using STAN through the package brms (Bürkner, 2017), with specified distributions and link functions, and z-transformed all continuous response variables using the function 'scale'. Trace plots were assessed visually to check for model convergence, pp_check was used to assess model fit, and Rhat was close to 1 in all models (Bürkner, 2017). The timing of brood desertion (day of desertion) was classified as an integer between 1.5 and 14. We estimated the minimum day of desertion to be 1.5 if the male was not observed at the nest on our first day of behavioural observation (day 3), indicating desertion took place sometime between hatching and day 3. Day 14 indicates that the male was continuously observed provisioning at the nest through fledging (no desertion). Laying and hatching dates of nests were highly correlated (correlation coefficient=0.74); therefore, we only chose one to include in our models (laying date in models of hatching success and hatching date in models of fledging success). Year was included as a fixed effect in all initial models to account for data collection in two different years (2021 and 2022) but was removed to avoid overfitting models and because there was no difference in the response variables between years. Hatching success was computed as the proportion of eggs that hatched and fledging success as the proportion of hatched chicks that successfully fledged.

Our first set of analyses examined the relationship between brood desertion and reproductive success at the nest level. In these models, female ID was included as a random effect to account for any females whose nests were monitored in both years. First, we tested whether male desertion was related to clutch size and brood size, using a log link and Poisson distribution, with parental strategy, female age and laying date (Julian day) as covariates. Next, we tested whether male

desertion was related to hatching success. We used an aggregated binomial logistic regression model (link=logit), with the number of nestlings hatched as a proportion of the clutch size. Day of desertion, hatching date (Julian day), female age, and clutch size were included as fixed effects. Third, we tested whether male desertion was associated with fledging success. Again, we used aggregated binomial logistic regression models (link=logit), with the number of nestlings fledged as a proportion of the number of nestlings hatched. We assumed offspring fledged successfully if they were observed alive in the nest on the last day of observation (day 14). Day of desertion, hatching date, female age and brood size were included as fixed effects.

Our second set of analyses examined observation-level data with repeated measures of feeding rate at each nest across the nesting period and repeated measures of individual offspring characteristics (mass and physiology) across development. We tested for associations between brood desertion and nestling corticosterone, oxidative stress and telomere attrition with brood size, hatching date, female age and nestling mass included as fixed effects and nest ID and nestling ID as nested random effects. We included the interaction of brood desertion and nestling age as a fixed effect in models for corticosterone and oxidative stress because physiological measurements were taken on days 8 and 14 of development and effects of brood desertion may differ at different developmental stages. Telomere attrition represented the difference in telomere length in individuals at age 8 and 14 and was only possible to measure in nestlings that survived until age 14. Estimated marginal means of interacting predictors and HPDs were calculated using the package emmeans (Lenth, 2024).

Finally, we conducted survival analyses by fitting a Cox proportional hazards model, using the package coxme() with nest ID as a random effect, to test whether the probability of survival for nestlings was related to brood desertion, feeding rate, or nestling physiology (Therneau, 2024). We created a survival object with time-to-event defined as the maximum age of the nestling recorded (time-to), and whether the nestling survived to fledging age (event). We used model selection to disentangle the effects of brood desertion, per capita feeding rate and nestling physiology on nestling survival. All models also included hatching date, brood size and starting nestling mass (day 3) as fixed effects and nest ID as a random effect to account for repeated measures. Desertion was modelled as a time-dependent covariate so that, within a nest, the status can change over time. In other words, the nestling environment could switch from biparental to uniparental after the male had deserted. In this way, we could infer whether nestling survival is a predictor of or dependent on male desertion. Feeding rate was calculated as the total number of observed parental visits to the nest, divided by the brood size, to obtain per capita rate.

3 | RESULTS

We monitored a total of 41 nests and 189 nestlings across the two studied years (21 nests in 2021, 20 nests in 2022). Laying date (first egg) ranged between the 22nd of May and the 15th of June. Clutch

sizes ranged between three and seven (mean no. of eggs 5.5 ± 0.8), and the number of fledged nestlings (observed alive on day 14 and confirmed later on during nest cleaning) ranged between zero and six (mean 3.7 ± 1.7). Of the nests monitored, 58% were biparental, cared for by both parents until fledging (no desertion), and 42% of nests were deserted partway through the provisioning period (between days 0 and 14). Lay date ($\beta = -0.02$, $pd = 95.0\%$), and brood size ($\beta = -0.14$, $pd = 95.0\%$) were negatively associated with the female age. There was no association between laying date and the timing of male desertion ($\beta = -0.01$, $pd = 53.6\%$). There was no association between clutch size or brood size and the timing of male desertion (Table S1; Figure S2A,B).

3.1 | Hatching success

There was a moderate, positive correlation between the day of desertion and hatching success ($\beta = 0.08$, $pd = 0.94\%$; Table S2; Figure S2C). There was also a positive correlation between the day of desertion and total mass of broods at hatching ($\beta = 0.23$; $pd = 91.0\%$). Nests with lower hatching success and total brood mass were deserted earlier in the development period.

3.2 | Provisioning and nestling growth

As expected, per capita provisioning rate increased with nestling age and decreased with brood size in all models (Table 1; Figure 1). Per capita provisioning rate had a strong association with male

desertion, with 42% lower provisioning rates in nests that were deserted (Table 1, top; Figure 1a; Figure S2D). Females partially compensated for males deserting by increasing the frequency of their feeding visits; female per capita provisioning rates were higher when females were the sole care provider, compared to when they had help from a male (Table 1, bottom; Figure S2E). There was also a significant interaction between desertion status and nestling age, where females increased their provisioning rate more with nestling age when they were the sole care provider (Table 1, bottom; Figure S3). The timing of desertion also played a role: females that were deserted by their partner earlier increased their provisioning rates enough to ultimately match the per capita provisioning rates of biparental nests by day 14, while females that were deserted later did not (Figure 1b). Thus, while offspring in deserted nests received less provisioning overall (Figure 1a), females partially compensated for the absence of their partner (Figure 1b) and did so more successfully if experiencing desertion earlier in the nesting period.

Since desertion was associated with lower per capita feeding rates and feeding rates were positively correlated with nestling mass (Table S3), we tested whether there was an effect of desertion on nestling growth. Nestlings that were deserted earlier weighed 28% ($pd = 99\%$) and 20% ($pd = 99\%$) less on day 3 compared to those that were deserted later or not at all, respectively. However, growth rates across development were highest in nests deserted early (trend = 1.99, HPD = 1.85–2.13) compared to those deserted later (trend = 1.78, HPD = 1.69–1.87) and not at all (trend = 1.91, HPD = 1.86–1.97), resulting in all nestlings weighing the same at fledging (Figure 1c). Brood size and initial nestling mass were also positively correlated with nestling growth across all groups (Table S3).

TABLE 1 Bayesian generalized linear models testing the relationship between per capita provisioning rate and male desertion.

	Estimate	Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS	pd
<i>Total provisioning rate ~ strategy + n_age + brood size + f_age + (1 NestID)</i>								
Intercept (Biparental)	3.39	0.12	3.14	3.63	1.00	564	1026	1.00
Uniparental	-1.43	0.13	-1.67	-1.17	1.00	2119	2896	1.00
Nestling age	0.70	0.04	0.63	0.77	1.00	3390	3171	1.00
Brood size	-0.50	0.07	-0.64	-0.35	1.00	1219	1838	1.00
Female age	0.02	0.11	-0.18	0.24	1.00	645	1218	0.59
<i>Female provisioning rate ~ strategy × n_age + brood size + f_age + (1 NestID)</i>								
Intercept (Biparental)	1.91	0.10	1.73	2.12	1.00	549	860	1.00
Uniparental	0.20	0.11	0.00	0.39	1.00	1702	2110	0.97
Nestling age	0.36	0.03	0.31	0.42	1.00	2437	2585	1.00
Brood size	-0.34	0.06	-0.46	-0.22	1.00	987	1395	1.00
Female age	-0.01	0.09	-0.18	0.17	1.00	629	1312	0.52
Strategy × nestling age	0.32	0.07	0.19	0.46	1.00	2095	2731	1.00

Note: Nest ID was included as a random effect to account for repeated measures of each nest across time. Non-significant interaction terms were removed in favour of a simpler model. Overall provisioning rates were lower in nests that were deserted (i.e. uniparental; top), but females provisioned at higher rates when they were sole providers (bottom). 95% CIs indicated in bold, >80% CIs not overlapping indicated in bold and parentheses. Estimates are the median of the posterior distribution.

Abbreviations: ESS, effective samples sizes; l-95% CI, lower 95% credible interval; pd, probability of direction; Rhat, Markov chain Monte Carlo convergence diagnostic; u-95% CI, upper 95% credible interval.

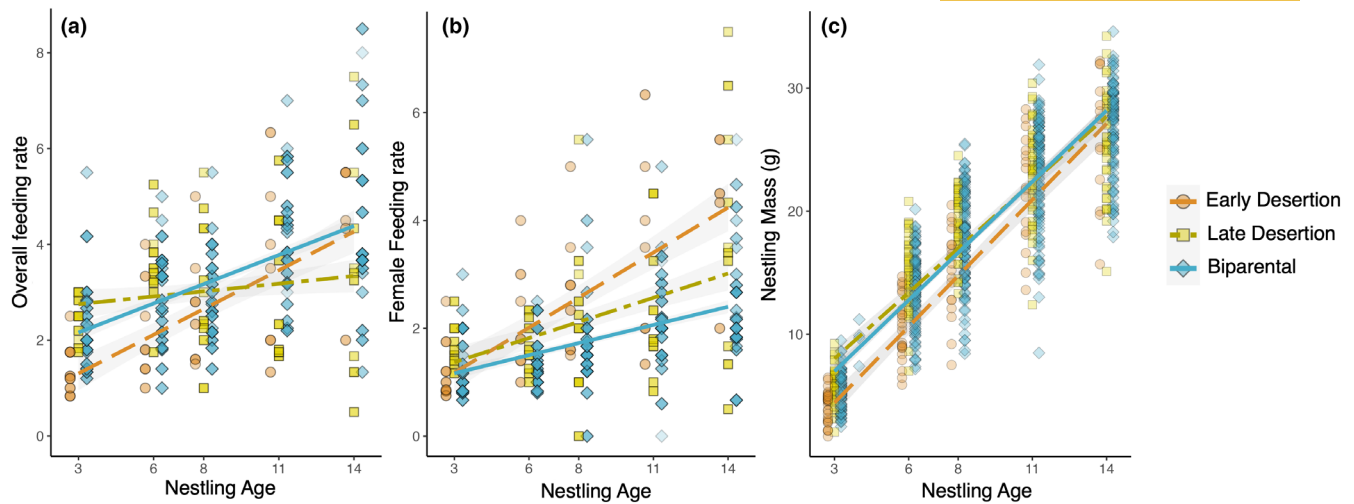


FIGURE 1 (a) Total per capita provisioning rate, (b) female per capita provisioning rate and (c) nestling growth across development. Coloured points represent raw data and lines represent model predictions and 95% credible intervals. Broods deserted earlier had overall lower provisioning rates (a), though females compensated by increasing their provisioning rates when they were the sole provider (b). Nestlings deserted early weighed less on day 3, but all nestlings had similar mass at fledging (c).

3.3 | Physiology

Nestlings from nests deserted earlier had higher corticosterone concentrations (Table 2, top). There was also an interaction between the timing of desertion and nestling age. In nests deserted early, nestling corticosterone levels stayed the same from age 8 to 14 (trend = -0.001 , HPD = -0.23 – 0.24), whereas corticosterone increased in nestlings deserted later (trend = 0.20 , HPD = 0.03 – 0.36) or not at all (trend = 0.20 , HPD = 0.07 – 0.33 ; Figure 2a). Correspondingly, nestlings deserted early had higher corticosterone on day 8, but there was no difference in corticosterone between groups on day 14 (Table S4). There was no difference in corticosterone levels of nestlings on day 8 between those that died and those that survived across all nests ($p = 0.43$; Figure S4), suggesting that corticosterone levels on day 8 did not independently predict the probability of a nestling's survival.

Similar to results for corticosterone levels, there was a significant association between desertion and nestling oxidative stress, as well as an interaction between the timing of desertion and nestling age (Table 2, middle; Figure 2b). Nestlings that were deserted earlier had a higher oxidative stress on day 8 (Table S5), and this trend was driven by an increase in dROMs: nestlings from nests deserted earlier had higher dROM levels on day 8 compared to those deserted later (contrast = 2.3 , $pd = 95.2\%$) or not at all (contrast = 2.4 , $pd = 98.1\%$), which did not differ from each other. In contrast, nestlings deserted earlier had lower oxidative stress on day 14 (Figure 2b; Table S5), and this was driven by increased oxy absorbance: nestlings from nests deserted earlier had higher oxy absorbance on day 14 compared to those deserted later (contrast = 52.36 , $pd = 97.9\%$) or not at all (contrast = 56.35 , $pd = 99.1\%$), which did not differ from each other. Younger nestlings (age 8) also had higher levels of oxidative stress overall (Table 2, middle) due to lower oxy absorbance ($\beta = 52.95$, $pd = 97.6\%$). There was no relationship between oxidative

stress levels and corticosterone levels (Table 2, middle). There was no effect of desertion, corticosterone levels or oxidative stress levels on telomere attrition (Table 2, bottom; Figure 2c).

3.4 | Fledging success and survival

Fledging success was positively associated with the day of male desertion (Table 3; Figure 3; Figure S2F), with a 23% increase in the odds of fledging success associated with each later day of desertion. Therefore, there was also a positive correlation between the timing of male desertion and the total mass of broods at fledging ($\beta = 3.89$, $pd = 99.4\%$). Even though the mass of individual nestlings was similar on day 14, the total mass of broods deserted early was 34.46% lower than broods deserted late, and 44.71% lower than those that were not deserted.

Cox proportional hazard models (Figure 3b) indicate that the effects of male desertion on nestling fledging success were partially mediated by effects on feeding rate and corticosterone. In these models, positive coefficients represent an association with nestlings *not* reaching fledging age, and negative coefficients represent an association with survival. In the simplest model (Table S6, top), the day of desertion had a negative effect on survival (coef = -0.68 , $p = 0.01$), where earlier desertion decreased the nestling probability of survival to fledging. More importantly, we found evidence that male desertion was the predictor, and not the consequence, of nestling mortality because most offspring deaths occurred after male desertion. Specifically, of the 78 nestlings that were deserted at some point during the nesting period, 88.5% of the mortality events occurred after the male deserted.

The effect of desertion on survival was reduced when feeding rate was added to the model (coef = -0.52 , $p = 0.05$), although AIC scores were similar ($\Delta AIC < 0.1$). The best model (Table S6, bottom)

TABLE 2 Bayesian generalized linear model testing the relationship between male desertion and nestling corticosterone levels (top), oxidative stress (middle) and telomere attrition (bottom).

	Estimate	Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS	pd
<i>Log(Cort) ~ Day deserted * n_age + n_mass + brood size + f_age + (1 NestID/NestlingID)</i>								
Intercept	5.87	1.35	3.31	8.49	1.00	3144	2852	1.00
Day deserted	-0.18	0.10	-0.38	0.01	1.00	3299	3011	0.97
Nestling age	0.03	0.12	-0.21	0.26	1.00	3155	3009	0.60
Nestling mass	-0.13	0.18	-0.47	0.22	1.00	5992	2823	0.76
Brood size	0.29	0.13	0.03	0.54	1.00	5806	2939	0.99
Female age	-0.16	0.12	-0.39	0.09	1.00	5728	2739	0.90
Day deserted x age	0.01	0.01	0.00	0.03	1.00	3219	2753	0.95
<i>OxStress ~ Day deserted * n_age + log(cort) + n_mass + brood size + f_age + (1 NestID/NestlingID)</i>								
Intercept	4.63	1.69	1.29	7.98	1.00	1994	1941	1.00
Day deserted	-0.33	0.13	-0.57	-0.08	1.00	2009	1906	0.99
Nestling age	-0.93	0.33	-1.56	-0.28	1.00	1996	1957	1.00
Log(cort)	0.09	0.10	-0.11	0.29	1.00	5334	3080	0.81
Nestling mass	0.04	0.15	-0.25	0.33	1.00	4070	3293	0.61
Brood size	-0.11	0.13	-0.36	0.13	1.00	3832	2893	0.81
Female age	-0.16	0.11	-0.39	0.06	1.00	3301	2706	0.93
Day deserted x age	0.06	0.02	0.02	0.11	1.00	1948	1912	1.00
<i>Telomere attrition (deltaRTL) ~ Day deserted + n_mass + brood size + f_age + log(cort) + OxStress</i>								
Intercept (Desertion)	-0.09	0.47	-1.02	0.84	1.00	5241	5451	0.57
Day deserted	0.00	0.04	-0.08	0.08	1.00	4841	5008	0.51
Nestling mass	0.08	0.21	-0.36	0.48	1.00	4708	4955	0.66
Brood size	0.03	0.15	-0.26	0.33	1.00	7717	5877	0.58
Log(cort)	0.20	0.21	-0.21	0.61	1.00	6952	5449	0.83
Oxidative stress	0.01	0.16	-0.30	0.32	1.00	7142	5868	0.52
Female age	-0.09	0.47	-1.02	0.84	1.00	5241	5451	0.57

Note: Plasma corticosterone concentrations (ng/ μ L) were log-transformed. Measures of oxy absorbance (μ mol HClO/mL) and reactive oxygen metabolites (mg H₂O₂/dL) were collected from each blood sample simultaneously. Values were then scaled and differenced to create an index of oxidative stress. In corticosterone and oxidative stress models, nestling ID and nest ID were included as nested random effects to account for repeated measures of nestlings over time and multiple nestlings measured within each nest. Corticosterone was measured in 154 nestlings across 39 nests, oxidative stress was measured in 165 nestlings across 40 nests, and telomeres were measured in 54 nestlings across 28 nests. Telomeres were only measured in nestlings that survived to age 14. All 95% CIs indicated in bold and >80% CIs not overlapping indicated in bold and parentheses. Estimates are the median of the posterior distribution.

Abbreviations: ESS, effective samples sizes; l-95% CI, lower 95% credible interval; pd, probability of direction; Rhat, Markov chain Monte Carlo convergence diagnostic; u-95% CI, upper 95% credible interval.

included a fixed effect of corticosterone on day 8 and shows that higher corticosterone on day 8 was associated with lower survival (Δ AIC=219.9). Because corticosterone was not measured earlier than day 8, this model excludes nestlings that died between days 3 and 8. A post-hoc analysis of marginal effects suggests a link between nestling corticosterone levels on day 8 and subsequent survival probability only among nests that experienced male desertion (Figure S5), but this effect was non-significant ($p=0.2$). Nestlings that weighed less on day 3 were also less likely to survive to fledging age (day 14) in all models ($p<0.001$). Overall, these models indicate that nestling fate is affected by a combination of parental decisions (male desertion and partial compensation by the female) and offspring state (mass and physiology).

4 | DISCUSSION

We present insights into the consequences of mate desertion, leveraging an avian system in which biparental and uniparental (male desertion) strategies co-exist within a population. Our study indicates that male desertion can occur at any point during the offspring provisioning phase, with varying consequences. Brood desertion by the male was not associated with any measurable characteristics of the clutch before desertion, but it did negatively affect subsequent nestling condition and survival: offspring from male-deserted nests suffered from higher corticosterone and oxidative stress levels and a reduced probability of survival. The timing of desertion also affected the severity of consequences for offspring, with higher physiological

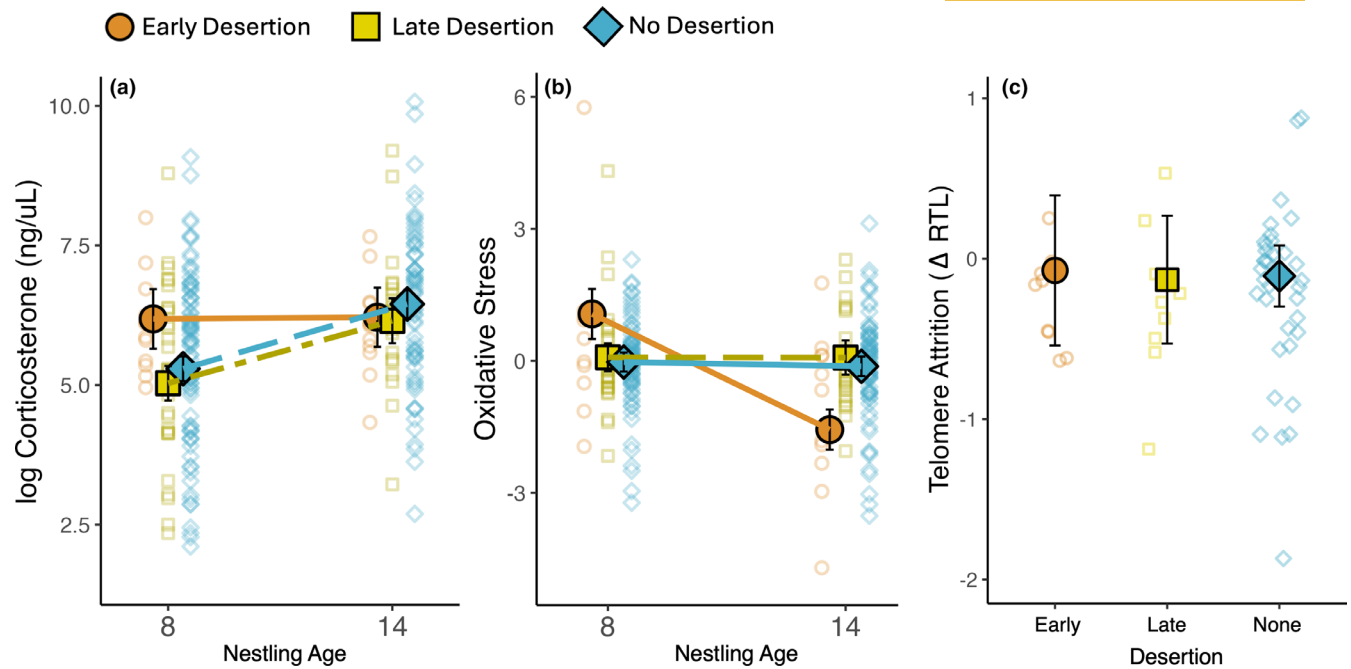


FIGURE 2 Nestling corticosterone concentrations (a), oxidative stress (b) and telomere attrition (c) across parental care strategies. Open circles represent raw data, filled circles represent model predictions and standard errors. Oxidative stress index values represent the individual difference between scaled oxy absorbance ($\mu\text{mol HClO}/\text{mL}$) and reactive oxygen metabolites ($\text{mg H}_2\text{O}_2/\text{dL}$) levels within individuals.

stress and reduced survival associated with earlier male desertion. As predicted, these consequences of male desertion on offspring seem to result from a reduced per capita provisioning rate, where females did not fully compensate for the loss of paternal care. Our data provide a unique look into the reproductive costs of parental decisions and how the consequences of desertion are mediated by a combination of behavioural and physiological responses in parents and offspring, respectively.

Mate desertion is a complex behavioural decision that is determined by a wide array of environmental and brood-related factors. Among the latter, lower brood value (low clutch or brood size) and lower offspring condition have been seen to promote interruption of care by one parent (Beissinger, 1990; Fujioka, 1989; Kupán et al., 2021; Ward et al., 2009). This idea of 'abandoning a sinking ship' is based on the concept that when further investments have marginal prospective benefits (*i.e.* Concorde Fallacy; Dawkins & Carlisle, 1976; Winkler, 1991), the best decision is to interrupt care instead of continuing to invest. Indeed, a previous correlative study on plovers found that female desertion co-occurred with events of offspring mortality, indicating that abandonment was the consequence of a progressive loss in brood value (Kupán et al., 2021). In our study, instead, we do not find support that the initial size of nests before or after hatching (*i.e.* clutch size, brood size) was the cause of desertion decisions. We did find that hatching success predicted the timing of male desertion, suggesting that mortality at hatching may contribute to a male's decision to desert earlier in the nesting season, but it did not predict the decision to desert immediately. Additionally, we report that offspring mortality mostly occurred

after a male deserted the nest. This outcome suggests that offspring mortality is the consequence, and not the cause, of male desertion in our population.

Still, we cannot exclude the possibility that there are cues associated with the reproductive value of a brood beyond those we considered in our study, which males use to dynamically adjust their parenting decisions. For example, we found that nestlings that were deserted earlier had lower mass on day 3 and that nestlings with lower mass on day 3 were less likely to survive to fledging. It is possible that males might respond to nestling mass or the initial mass of the entire brood by pre-emptively deserting the nest before mortality starts. Further studies with experimental manipulation of brood value or offspring state (*e.g.*, brood size manipulation, food supplementation (Baldan et al., 2019; Eldegard & Sonnerud, 2009; Ward et al., 2009)) could confirm these hypotheses about the decision-making process of male desertion in this system.

Our results support the hypothesis that offspring mortality resulted from reduced provisioning rates in nests that were deserted, as females only partially compensated for the lack of male contribution. This result differs from a previous study of the same population, in which females showed no response to male desertion in a temporary mate-removal experiment (Cantarero et al., 2019). As has been pointed out by others (Baldan et al., 2023; Harrison et al., 2009), a temporary experimental manipulation of paternal care differs from long-term, permanent desertion and may not be sufficient to elicit the compensatory response we observed here. Our findings also contrast with another study on rock sparrows from a different population, in which females overcompensated for their partner's

TABLE 3 Aggregated binomial logistic regression model (link = logit) investigating the relationship between male desertion and fledging success across 41 nests.

	Estimate	Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS	pd
<i>fledglings trials(brood size) ~ day deserted + hatch date + brood size + f_age + (1 femaleID)</i>								
Intercept	-0.76	0.65	-2.10	0.47	1.00	1922	1911	0.89
Day deserted	0.23	0.06	0.12	0.37	1.00	1588	1700	1.00
Hatch date	-0.33	0.31	-0.97	0.24	1.00	1318	1551	0.85
Brood size	-0.39	0.35	-1.08	0.26	1.00	2087	2124	0.87
Female age	0.47	0.41	-0.31	1.30	1.00	1453	1514	0.88

Note: Fledging success was modelled as the number of nestlings fledged (*successes*) out of the number of nestlings in the brood (*trials*). Fledging success was positively associated with the day of male desertion. 95% CIs indicated in bold, 80% CIs not overlapping indicated in bold and parentheses. Estimates are the median of the posterior distribution.

Abbreviations: ESS = effective samples sizes; l-95% CI = lower 95% credible interval; pd = probability of direction; Rhat = Markov chain Monte Carlo convergence diagnostic; u-95% CI = upper 95% credible interval.

desertion by increasing per capita feeding rates beyond those of biparental nests (Griggio & Pilastro, 2007). These differences may depend on the cost of increasing feeding rate (associated, for example, with the availability of insects), which may differ between the two populations. In our population, there was much variability in how much females compensated for their partner's desertion, with some females notably increasing provisioning rates and others not at all (Figure S3), and this variation could reflect among-individual differences (Baldan et al., 2023), parental task specialization (Schiavinato et al., 2023) or spatial heterogeneity in territory quality and food availability (Moss & Moore, 2021).

Females that experienced desertion earlier increased their provisioning rates enough that their nestlings were ultimately getting fed at similar rates as those in biparental nests by day 14. On the contrary, females experiencing desertion later did not appear to adjust their behaviour sufficiently, and per capita feeding rates were lowest in these nests on day 14. Desertion later in the season may give females less time to either adjust their behaviour or broaden their foraging range to obtain high enough quality and quantity of food for their broods. However, we found that the total number of female provisioning visits per observational period did not differ between groups, only per capita rates. Therefore, the likeliest explanation is that because survival was lowest in nests deserted early, these females were experiencing brood size reductions that enabled them to increase per capita feeding rates without increasing overall effort. Still, the day of desertion affected female per capita feeding rates even after accounting for brood size.

Finding partial compensation by females aligns with theoretical predictions of mate desertion in species with flexible parental strategies (Houston et al., 2005; Johnstone & Hinde, 2006), and the significant reduction in nestling survival may explain why biparental care is the most frequent strategy in this species. Our finding also supports other work showing that the costs of desertion depend on the relative contribution of the deserting parent to offspring provisioning (Møller, 2000) and explains why costs are often small or absent for precocial species in which nestlings find food by themselves

with little to no parental assistance (McDonald et al., 2022; Székely et al., 1996, 1999).

Male desertion was not only associated with lower offspring survival, but also physiological stress for offspring in the early developmental period. This finding is concordant with a laboratory experiment on zebra finches, in which simulated mate desertion caused an increase in nestling stress (Crino et al., 2017). Furthermore, previous studies showed that developmental and environmental challenges can elevate corticosterone levels within the same developmental window of our study (Baldan et al., 2021; Mikkelsen et al., 2021; Ouyang et al., 2019). However, to our knowledge, we present the first demonstration that nest desertion can increase offspring physiological stress in a free-living and unmanipulated avian population. We also show that the timing of nest development played an important role: both corticosterone and oxidative stress levels were higher among nests that were deserted earlier in development. Therefore, physiological consequences for offspring may contribute to a dynamic decision of both if and when to desert.

Negative effects of desertion on offspring corticosterone and oxidative stress levels were detected only on day 8 and not on day 14. There are two non-mutually exclusive explanations for this observation. First, it could be that nestlings with high levels of stress exhibited higher mortality and did not survive to later stages, resulting in similar means between groups on day 14. We found partial support for this hypothesis: though corticosterone levels of nestlings on day 8 did not, alone, affect survival probability, Cox proportional hazard models revealed that the consequences of male desertion were partially mediated by corticosterone. A second possible explanation is that the effects of the rearing environment on oxidative stress and corticosterone are more prominent earlier than later in development and/or are not severe enough to induce physiological stress later in development. This suggests that rearing conditions could only have a temporary and limited effect on offspring physiology, contrary to what has been found in another study (Kraft et al., 2021). Indeed, although early effects on corticosterone and oxidative stress were significant, we did not

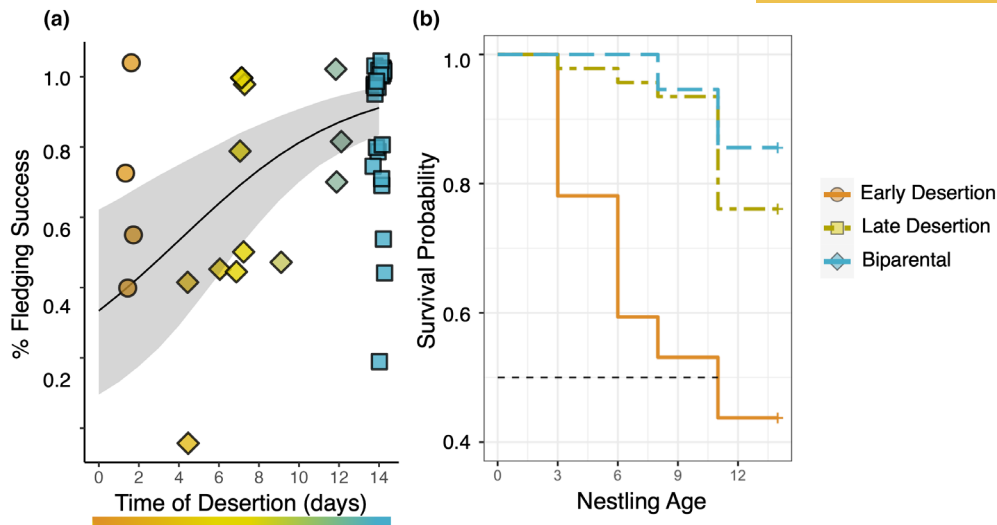


FIGURE 3 (a) Fledging success was positively related to the timing of male desertion. Coloured points represent raw data and error bars represent 95% credible intervals. Time of desertion was classified as an integer from 1.5 to 14, where 14 indicates no desertion. (b) Predicted nestling survivor function across parental strategies using Cox proportional hazards model (Therneau, 2024) and visualized using the package 'ggsurvfit'. Max age of nestlings recorded was considered time-to-death.

find differences in telomere attrition, which would have indicated a more severe developmental consequence. We also acknowledge that our intra and inter-plate variation was at the higher end of the typical accepted range for these types of assays (<15%), and thus our estimates of corticosterone values have higher uncertainty than some studies reporting smaller CVs. Nonetheless, our findings suggest that male desertion was associated with a moderate stress response in nestlings, but that this did not persist to fledging age. Future studies should explore other components of the glucocorticoid stress response (e.g., reaction norm, stress-induced corticosterone, receptor densities), participants in oxidative balance and metrics of physiological stress that could be affecting offspring long-term and were not measured here (Koch et al., 2021; Vágási et al., 2020; Zimmer et al., 2019). Taken together, our results show that while deserted broods experienced the highest nestling mortality, females compensated by increased provisioning enough to fledge nestlings that were of a comparable mass and physiological condition to those from biparental nests, albeit fewer of them.

If male desertion affects offspring physiology and reduces fledging success, why do some males desert? Theoretical models on alternative parental care strategies posit that mate desertion should evolve only if the benefits of desertion outweigh its costs (McNamara et al., 2000; Webb et al., 1999). Previous empirical studies have found that the benefits of nest desertion can include higher renesting probabilities within the same season (Dijk et al., 2012; McDonald et al., 2022; Pilastro et al., 2001) or a higher survival rate into the following years (Tavecchia et al., 2002; Urano, 1992). In our rock sparrow population, the breeding season is short and clutches are initiated nearly simultaneously (A. Cantarero, personal observations and unpublished data), so remating probability of a deserting male

is low, and the rate of male seasonal polygyny is also relatively low (Corregidor-Castro et al., 2022). Indeed, in the 2 years of the current study, only two males were found with a subsequent brood within the same season. Moreover, if the primary goal of desertion is to renest within a season, we would expect desertion to occur immediately after hatching or earlier in the season/developmental period (Pilastro et al., 2001), but this was not the case. In fact, it was far more common that males interrupted care partway through nestling development than before hatching. Therefore, we believe that the benefits of desertion in our system are more likely to be related to increasing the deserting parent's chance of surviving to the following year. Follow-up studies on male and female mortality rates and lifetime reproductive success between parental strategies (Santos & Nakagawa, 2012) are needed to elucidate the potential long-term costs and benefits of parental desertion (Dijk et al., 2012) and reach a comprehensive understanding of the maintenance of polymorphisms in care strategies.

Our results shed light on the mechanisms and reproductive consequences of multiple parental care strategies within populations. By closely monitoring nests and documenting the behavioural decisions of parents, we were able to quantify the reproductive costs of mate desertion and show that, in addition to offspring survival, offspring physiology may contribute to the costs associated with parental decisions of *if* and *when* to desert the nest. Only through this type of integration can we start to disentangle the behavioural and physiological mechanisms maintaining evolutionarily stable alternative parental care strategies.

AUTHOR CONTRIBUTIONS

Alejandro Cantarero, Matteo Griggio, Jenny Q Ouyang, Andrea Pilastro and Davide Baldan conceived the ideas and designed the

methodology; Alejandro Cantarero, Matteo Beccardi, Manuel Fuertes-Recuero, Matteo Schiavinato, Lia Zampa and Davide Baldan collected the data; Valentina Alaasam, Alejandro Corregidor-Castro and Alessandro Grapputo analysed the data; and Valentina Alaasam, Jenny Q Ouyang and Davide Baldan led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are made public on the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3n5tb2rtq> (Alaasam et al., 2025).

ETHICS STATEMENT

Permissions for handling birds were provided by Consejería de Medio Ambiente de Castilla y León (protocol numbers sG_2020_0241 and AUES/SG/09/2022). The work was approved by Consejería de Medio Ambiente de la Comunidad de Madrid (approval ref. PROEX 088.7/22).

ORCID

Valentina Alaasam  <https://orcid.org/0000-0003-1670-6780>
 Alejandro Cantarero  <https://orcid.org/0000-0002-5816-701X>
 Jenny Q. Ouyang  <https://orcid.org/0000-0002-5111-5145>
 Davide Baldan  <https://orcid.org/0000-0003-2049-4311>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Bayesian regression models of clutch size and brood size, using a Poisson distribution. Female ID was included as a random effect to account for the same females measured in subsequent

years. 95% CIs not overlapping 0 indicated in bold, 80% CIs not overlapping 0 indicated in bold and parentheses.

Table S2. Aggregated binomial logistic regression model (link = logit) investigating the relationship between male desertion and hatching success across 41 nests. Hatching success was modelled as the number of nestlings hatched (*successes*) out of the number of eggs in the clutch (*trials*). 95% CIs not overlapping 0 indicated in bold, 80% CIs not overlapping 0 indicated in bold and parentheses. Larger clutches had 59% greater hatching success, and older females had 38% reduced hatching success.

Table S3. Bayesian generalized linear model testing the relationship between nestling mass and total per capita provisioning rate (total visits from all parents, divided by number of offspring in nest). Per capita provisioning rates were positively associated with nestling mass. 95% CIs indicated in bold.

Table S4. Bayesian generalized linear model testing the relationship between plasma corticosterone levels (log-transformed) in nestlings on days 8 and 14, and the timing of nest desertion by the male. Nestlings deserted earlier had higher corticosterone on day 8, but there was no difference between groups on day 14. 95% CIs indicated in bold, >80% CIs not overlapping indicated in bold and parentheses.

Table S5. Bayesian generalized linear model testing the relationship between plasma oxidative stress levels in nestlings on days 8 and 14, and the timing of nest desertion by the male. Nestlings deserted earlier had higher oxidative stress on day 8, but lower oxidative stress on day 14. 95% CIs indicated in bold, >80% CIs not overlapping indicated in bold and parentheses.

Table S6. Cox proportional hazard models using the package *coxme()* with nest ID as random effect. Time-to-event was defined as the maximum age of the nestling recorded (time-to), and whether the nestling survived to fledging age (event). Positive coefficients represent an association with nestlings *not* reaching fledging age, and negative coefficients represent an association with survival. Top three models shown in order of increasing complexity with corresponding AICs reported.

Figure S1. Schematic of experimental design. Nest recordings (1.5 h) were conducted on days 3, 6, 8, 11 and 14, to quantify provisioning

and document parental care strategy. Chick mass and tarsus length was measured after each recording. Blood was collected from the brachial vein on days 8 and 14 to measure corticosterone, oxidative stress and telomere length.

Figure S2. Posterior distributions of Bayesian regressions, with 80% (thin line) and 95% (thick line) credible intervals shown in black. Response variables include (A) clutch size, (B) brood size, (C) hatching success, (D) per capita feeding rate, € female per capita feeding rate and (F) fledging success.

Figure S3. Females from partially deserted nests compensated for desertion by increasing per capita provisioning rates after mates deserted. Coloured points represent raw data and lines represent model predictions and 95% credible intervals. All points represent provisioning behaviour in nests categorized as partially deserted. Blue diamonds represent occasions in which both parents were present and orange circles represent occasions in which only the female was present.

Figure S4. Plasma corticosterone levels of nestlings measured at day 8 and 14. Corticosterone levels on day 8 was similar between nestlings that died and those that survived to fledging (day 14; Table S6).

Figure S5. Marginal effect of nestling corticosterone levels (Day 8) on the probability of their survival to fledging, across nests experiencing various levels of paternal desertion. Higher levels of corticosterone are associated with a lower probability of survival in nests where males deserted, though this effect is not statistically significant.

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