Original Article

Offspring desertion with care? Chick mortality and plastic female desertion in Snowy Plovers

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Offspring desertion is often a plastic behavioral strategy that requires precise timing as the termination of parental care may have profound consequences for the fitness of parents and offspring. However, the decision process involved with termination of care is still poorly understood. Snowy Plovers *Charadrius nivosus* show highly flexible brood care with some females deserting the brood early and re-mate, whereas others provide extended care until the young are independent. Using a dynamic modeling framework, we investigated the effect of multiple factors on the decision-making process of female brood care in Ceuta, Mexico over a 7-year period. Females were more likely to stay with larger broods, while their probability of care was lower at the beginning of the season, when re-mating opportunities are higher than later in the season. Offspring condition at hatching did not influence the length of female care. Chick death and offspring desertion frequently coincided, suggesting that deteriorating offspring condition may trigger female desertion. Females deserted broods with high survival prospects when their absence did not impact negatively chick survival. Conversely, females deserted broods with low survival prospects when chick mortality despite female care reduced the value of the brood and re-mating was still possible. This suggests that female Snowy Plovers are sensitive to the needs and the value of their broods and adjust their parental care strategy accordingly. Taken together, we conclude that offspring desertion is a highly plastic behavior that allows females to maximize their reproductive success in a stochastic environment.

Key words: behavioral plasticity, offspring desertion, parental care strategies, polyandry, reproductive success, trade-off

INTRODUCTION

Parental care increases parental fitness by improving offspring growth, condition, and ultimately survival (Klug and Bonsall 2014). At the same time, parental care adds major costs to reproduction that may compromise adult survival and/or future fecundity of the parent (Gross and Sargent 1985; Smith and Wootton 1995; Zink 2003; Buzatto et al. 2007; Royle et al. 2012). In particular, multiple breeders of long-lived species face a trade-off between improving the prospects of the current brood through care and the reduction of their own future reproductive success and/or survival through extended care (Williams 1966; Trivers 1972; Westneat and Sargent

1996; Webb et al. 1999; Ackerman et al. 2003; Magrath and Komdeur 2003).

One possible way of escaping the strains of parental duty is premature care termination through offspring desertion. Originally considered as maladaptive or "abnormal behavior" (Fujioka 1989; Hrdy 1999), theoretical and experimental studies have shown that offspring desertion is often beneficial for the parents. When survival of the current brood is not compromised, desertion followed by re-mating can lead to increased lifetime reproductive success for the deserter (Trivers 1972; Maynard Smith 1977; Smith and Wootton 1995; Székely et al. 1996; Webb et al. 1999; Ward et al. 2009; Royle et al. 2012). In order to make an adaptive decision over desertion, parents should consider the following five key parameters: 1) the needs of the current offspring, 2) the value and

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prospects of the current brood, 3) re-mating opportunities, 4) their own condition, and 5) behavior of the other parent in biparental systems (Kelly and Kennedy 1993; Székely 1996; Webb et al. 2002; Houston et al. 2005).

First, the needs of the current brood may depend on the environment in which the offspring will grow up. For example, in a harsh environment one parent may not be able to raise the young alone, whereas in a benign environment the offspring may fare as well with one parent as with both, leaving one parent free to desert (Beissinger and Snyder 1987; Székely et al. 1996; Blanken and Nol 1998; Amat et al. 1999a; Magrath and Komdeur 2003; Eldegard and Sonerud 2009; Kosztolányi et al. 2009).

Second, the value and prospects of the current brood are primarily determined by brood size and offspring condition. Brood size is the most obvious predictor of desertion with parents usually caring longer for larger than for smaller broods (e.g., Beissinger and Snyder 1987; Fujioka 1989; Steinhart et al. 2008; Ward et al. 2009). Brood condition and prospects may chiefly depend on environmental conditions, thus, parents need to assess offspring survival with or without their contribution in the current environment (Steinhart et al. 2008).

Third, the deserting partner must assess its re-mating opportunities. Re-mating opportunities determine who gains more from deserting the family and who gains more from care (Keenleyside 1985; Fujioka 1989; Balshine-Earn and Earn 1998; Pilastro et al. 2001; Roulin 2002; Eldegard and Sonerud 2009; Thomson et al. 2014). Recent studies have shown that reproductive behavior is often tied to sex ratios of the adult population (Kokko and Jennions 2008; Liker et al. 2013; Grant and Grant 2019) with biased sex ratios altering potential for sequential polygamy in each sex. In that case, the rarer sex has a higher opportunity for polygamy and is more likely to desert the brood (Eberhart-Phillips et al. 2018).

Fourth, the parent should consider its future reproductive prospects. Parents need to assess their own condition and survival prospect in this process. When parental care depletes energy reserves or increases the risk of predation, desertion may improve the prospect of adult survival and enable them to reproduce again (Osorno 1999; Currie et al. 2001; Jamieson 2012).

Fifth, a deserting parent will leave dependent offspring behind. The deserter needs to consider the ability and behavior of the remaining parent, who will be left with the young alone. When the remaining parent is able to fully compensate for the lack of the second carer, continued care by both parents is not necessary (Fujioka 1989; Székely et al. 1996; Roulin 2002; Osorno and Székely 2004; Harrison et al. 2009; Ward et al. 2009).

Importantly, all of these factors change through the brood care period. Furthermore, they are often intertwined and not independent from each other. It is essential to understand the relationship between these factors in order to establish the motive behind, and the adaptivity of early termination of care. For example, the brood size might decrease over the brood care period apparently decreasing the value of the current brood. However, the value for the parents often also depends on the re-mating opportunities; if brood size decreases in early broods when re-mating opportunities are still high, parents may be better off prioritizing future reproduction over their current offspring. By contrast, if late broods decrease in size, re-mating opportunities are often low and, consequently, parents may be better off to continue caring. Similarly, brood age may be related to the length of care. Older chicks usually have better survival opportunities than young chicks. Therefore, parents of older broods may decide to complete care even if mortality

occurs. When desertion happens during an early stage of care, the young are still vulnerable and the remaining parent might not be able to fully compensate. In this case, early termination of care will only be adaptive if the gains from additional matings are higher than the losses incurred in the deserted brood (Ezaki 1988; Eldegard and Sonerud 2009; van Dijk 2009).

It is often not clear whether low survival prospects of the offspring are cause or consequence of desertion. In the former case, the deserting parent may essentially abandon a sinking ship as continued care will not improve the offspring survival prospects. The deserter then chooses to make the best of a bad job by starting a fresh mating attempt to offset its initial low reproductive success (Székely et al. 1996; Ackerman et al. 2003; Klug and Bonsall 2007). In the latter case, the deserter already takes into account lower future survival of the deserted offspring but expects to obtain an overall higher reproductive success through desertion and re-mating than when remaining with the first brood (Osorno 1999).

Plovers (Charadriinae) are small shorebirds with high variation and flexibility in parental care (e.g., Vincze et al. 2017; Eberhart-Phillips et al. 2018). They typically lay small clutches with two to four eggs, which implies that reproductive success can only increase through producing multiple clutches (or double brooding, Blomqvist et al. 2001). Precociality of the offspring has facilitated the evolution of plastic brood care systems that may feature bi- or uniparental brood care (Székely and Reynolds 1995; Houston et al. 2005; Thomas and Székely 2005; Eberhart-Phillips 2019). The frequency of desertion varies not only between species but also between and within populations (Eberhart-Phillips et al. 2018). Several predictors of the length of biparental care have been identified previously including initial brood size (also referred to "current brood size," Székely and Cuthill 2000; Ward et al. 2009), biotic environment (such as population density and/or predation pressure, Amat et al. 1999a; Kosztolányi et al. 2006), and abiotic environment (e.g., temperature, AlRashidi et al. 2010). Desertion is strongly linked to re-mating opportunities that are influenced by adult sex ratios (Székely et al. 1999; Amat et al. 1999a; Stenzel et al. 2011; Parra et al. 2014; Carmona-Isunza et al. 2017; Eberhart-Phillips et al. 2017; Eberhart-Phillips et al. 2018; Eberhart-Phillips 2019).

In many plover populations, desertion appears positively related to chick mortality (Székely and Williams 1995; Székely et al. 1996; Székely and Cuthill 1999; Amat et al. 1999b; Cruz-López et al. 2017). It was previously reported that the majority of deserted Snowy Plover *Charadrius nivosus* families were characterized by low chick survival, which might imply that brood desertion is maladaptive (Cruz-López et al. 2017). However, whether desertion is cause or consequence of reduced chick survival remained unclear. Following up on these results, we investigated the phenology and fitness consequences of brood care in Snowy Plovers breeding at Bahía de Ceuta, Mexico (hereafter "Ceuta"). We focused on female care as this parental behavior has the highest plasticity in this population (Cruz-López et al. 2017). The male-biased sex ratio that in the population emerges during the juvenile stage (Eberhart-Phillips et al. 2017) presumably provides better re-mating opportunities to females. Consequently, brood desertion by males is extremely rare, whereas brood desertion by females is frequently observed (Cruz-López et al. 2017). Using the fates of 262 families collected over seven breeding seasons we assessed the adaptive value and the dynamics of female brood care and offspring desertion. We used a dynamic modeling method (Schmidt et al. 2010) to identify both static and dynamic predictors of female desertion. We considered present brood size, that is, the brood size on a specific day, and brood age as

dynamic variables that represent changing values and needs of the brood. We used hatching date, male, female and brood condition as static predictors. Specifically, we 1) described the pattern of female brood care strategies in this population, 2) compared reproductive success of the different female strategies, 3) tested which of the dynamic and static social and environmental variables predict the length of female care and, 4) examined the temporal association of chick mortality and termination of female care. With this we explored whether and how chick mortality influences the decision of the females to continue or terminate care.

METHODS

Field work and data collection

We studied breeding Snowy Plovers at Ceuta, a coastal wetland in Northwest Mexico between April and July from 2006 to 2012. During the study period, about 50–100 Snowy Plover pairs nested annually on tidal salt flats of an abandoned salt extraction site surrounded by mangrove forests and agricultural fields (Cruz-López et al. 2017; Eberhart-Phillips et al. 2017; Plaschke et al. 2019). We monitored Snowy Plover families daily using the methodology described in Székely et al. (2008).

We searched for nests and families by scanning the salt flats for incubating plovers with binoculars and scopes from a mobile hide or a car. When a nest was found, we recorded the location and established laying and hatching dates based on the floating technique assuming a 25-day incubation period (Plaschke et al. 2019). We caught incubating parents on the nests with a funnel trap and marked them with a unique color-metal-ring combination consisting of three color rings and a numbered metal ring. We revisited the nests approximately every 2–4 days until we heard the chicks calling or pecking inside the eggs and afterwards daily to capture, measure and mark chicks before they leave the nest scrape (Cruz-López et al. 2017; dos Remedios et al. 2015). We marked the chicks with a metal and a single color ring. This allowed us to follow the individual fates of most chicks. We took body measurements and a blood sample of adults and chicks for molecular sex identification. We re-sighted families if possible at least once every 2 days until the brood had reached an age of 5 days and approximately every 3 days until the brood age reached 25 days at which brood age Snowy Plovers become independent (Cruz-López et al. 2017). At each sighting, we observed broods for at least 15 minutes or until each previously attending parent had been seen to identify all family members present (Székely and Cuthill 1999). If a bird was not seen during this period, we recorded it as "missing" for that day.

Data processing and statistical analysis

We collected brood attendance data for a total of 367 broods. These broods are part of the CeutaOPEN core data set by Eberhart-Phillips et al. (2020). From these, 12 (3.3%) did not have hatching date information, 38 (10.4%) had two or fewer observations, in 7 (2%) broods the male deserted or disappeared and in a further 48 (13.1%) broods the female deserted in a period between two brood observations that were longer than 3 days apart. After removing these broods, we included 262 broods for further analyses. The number of broods varied annually, paralleling a strong population decline throughout the study period (Cruz-López et al. 2017).

In case broods disappeared or failed before fledging age, we noted the day the brood was last seen. We assumed that both parents were present with the clutch until hatching as incubation in Snowy Plovers is biparental (Vincze et al. 2013; Vincze et al. 2017). We calculated the duration of female and male care for each brood in days from the hatching of the first chick. In 2007–2009 and 2011, we performed brood manipulations such as cross-fostering of freshly hatched chicks and eggs ($N = 112$). The manipulations either increased brood size (up to five chicks, $N = 11$), left brood size unchanged with either eggs or chicks swapped between broods ($N = 65$), or reduced brood size ($N = 36$). We repeated our main model i) using only data from unmanipulated broods and ii) with an additional "manipulation" predictor with manipulation types as factorial levels to test whether manipulation effected female care behavior. The results of these additional models were qualitatively similar (data and results are available on GitHub, see Data availability statement).

For each family member (parent or chick), we defined the last day of presence as the mid-point between the day the bird was last observed with the family and the first day the focal bird was either observed permanently without the family, or the family was observed permanently without it. For parents, permanent absence meant that they deserted the broods. We considered temporarily absent family members, that is, those that were subsequently re-sighted with the family, as "present." The maximum duration of care was 26 days (from day 0, when the first chick hatched in the brood, until day 25, the fledging age). To test whether our estimation of the desertion date would somehow impact our results, we created a stricter data set where we only included broods for which the exact day of female desertion was known ($N = 114$). Again, in this analysis, we obtained similar results (data and results are available on GitHub, see Data availability statement).

Female brood care

We considered four scenarios to describe the termination of female care. 1) Desertion: the female left the brood while at least one chick was still attended by the male. 2) Brood failure: either both parents were observed without the chicks, or the male was seen alone within 3 days of the last observation of the brood attended by both parents. 3) Full term care: the female stayed until at least one chick fledged. 4) Unfinished observations: unfledged broods with unknown fate that were attended by the female at the last observation.

Reproductive success and breeding time

To assess the fitness consequences of female brood care strategies, we compared the seasonal reproductive success and breeding time (i.e., the total number of days a female spent with breeding related activities) of females that for the first clutch either provided full term care or deserted and then re-mated locally (Figure 1). We calculated reproductive success as the total number of fledglings for a certain female parental care strategy within a season. Many females disperse to different breeding sites between breeding attempts (Stenzel et al. 1994). Here, we compared the local breeding time of females that stayed for at least two breeding attempts or provided full term care in Ceuta. The breeding time represents the cumulative number of days of egg formation and incubation (3 + 25 days) and the days from hatching of the first chick to the end of care of the last brood. It also includes the time that the female spent on finding a new mate after desertion (Figure 1). In the full-term care group, all females had only one breeding attempt, whereas in the deserting group, all females had two breeding

A Full care providing females
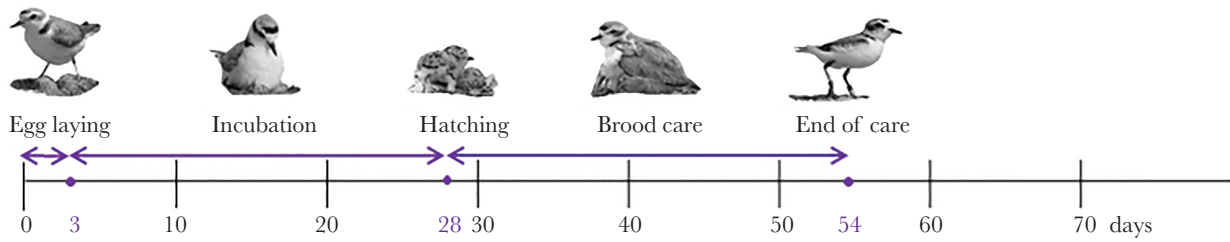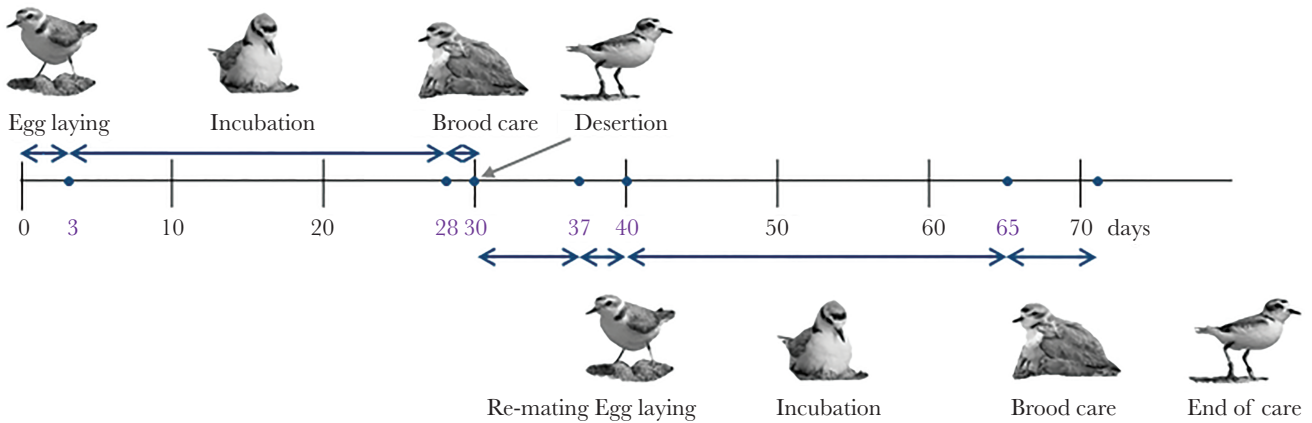

B Deserting and re-mating females

Figure 1
Schematics for calculating breeding time (length of care in days) in full-term care providing ($N = 5$) (a), and deserting and locally re-mating ($N = 9$) females (b).

attempts with hatchlings with different males. We compared breeding time (in days) of the two groups using a Linear Model with "type of care" as predictor. We compared reproductive success (total number of fledglings) between the two groups using a Generalized Linear Model (GLM) with Poisson error distribution.

Predictors of the length of female brood care
As a dynamic measure for the length of female care we calculated a novel response variable: probability of care. Probability of care was derived in a similar manner as the commonly used daily nest survival, an established unbiased measure in ecology to understand fundamental mechanisms of population dynamics (Schmidt et al. 2010; Converse et al. 2013). Probability of care refers to the probability that a female will care on a certain day given the probability of care on the previous day. We adopt this measure to assess the drivers for termination of parental care as it allows us to assess not only static but also dynamic predictors that are changing over the care period. We analyzed the effects of seven biologically meaningful predictor variables on the probability of care. Five of these were static predictors: hatching date, male tarsus length, male condition, female condition, and chick hatching condition.

Hatching date provides a measure for the progress of the breeding season and we predicted that females would be more likely to stay and care for the chicks later in the season as re-mating opportunities diminish (Székely and Cuthill 2000). We used relative hatching date, which is the z-transformation of the Julian hatching dates for each year. We calculated relative hatching date by using all broods with available hatching date information.

As a measure of male size, we used male tarsus length, the mean length of left and right tarsus of the male parent. As males are the main care providers, larger males may be better at protecting their chicks in conflicts with other families or better at thermoregulation. We predicted that females would be more likely to care longer to support smaller mates than larger ones. As another set of quality measures we calculated "male/female/chick condition" using the scaled mass index method by Peig and Green (2009). This method fits a linear regression between tarsus and weight data points and for each individual calculates a relative weight value according to the mean tarsus length of the population using the slope value of the regression estimates. Positive values refer to individuals with better than population average condition and negative values refer to individuals with worse than average condition. Chick condition was calculated using the hatching mass and size values of the chick in best condition in a brood within 1 day after hatching. This variable highly correlated with the mean condition value of the brood ($R = 0.93$). Similarly, to male tarsus length we predicted that females would stay longer with males in lower condition. We predicted that females would desert chicks with better condition faster as they have higher survival prospects than chicks with worse condition that might require more care. Alternatively, females might stay and care longer for chicks in better condition as their survival prospects (and hence their reproductive value) are higher.

Present brood size and brood age are two dynamic variables whose values were determined every day over the brood care period. Present brood size, the brood size on a given day, allowed us to test whether females would take into account the present number of their chicks when deciding whether to desert or

continue to care. We predicted that females would be more likely to continue to care for bigger than for smaller broods. Finally, for brood age we predicted that older broods are more likely to be deserted as chicks are more independent (Gratto-Trevor 1991; Currie et al. 2001). However, this relationship may be modified by seasonality. Because of reducing re-mating opportunities through the season, some females especially at the end may stay longer and care until fledging. Therefore, we also included the second polynomial of brood age (brood age²). Present brood size, the brood size on a certain day, may provide a more precise estimate on the effect of brood size on care than initial brood size. Importantly, present brood size differs from the commonly used current brood size (Székely and Cuthill 2000; Ward et al. 2009), which refers to the initial brood size of the current breeding attempt and is fixed for a given breeding attempt. By contrast, present brood size may change during the care period, that is, it decreases with chick mortality. Basing our models on present rather than initial brood sizes allowed us to investigate the female decision to continue or terminate care without assuming the "Concorde fallacy" (Dawkins and Carlisle 1976), that is, that past investment instead of future prospect has the strongest impact on the parental care decision (Ackerman et al. 2003).

We set up a binomial generalized linear mixed model to estimate the effect of the predictors on probability of care using a Markov-chain Monte Carlo (MCMC) algorithm in a Bayesian framework (Korner-Nievergelt et al. 2015). We used STAN (Stan Development Team 2018) through the R packages rstan, rstanarm (Stan Development Team 2018) and arm (Gelman and Hill 2007). We fitted two random intercepts: year and female ID since females can have multiple breeding events within and between years. We modeled probability of care of each female with Bernoulli errors.

The likelihood to continue care for a given day was formulated as

$$y_{care}\,[i,t] \sim bernoulli\,(y_{care}\,[i,t-1]\,,\ S_i,t)\,;$$

$$\text{logit}\,(S_i,t) = \beta_0 + \beta_1\ \text{present brood size}_{i,t} + \beta_2\ \text{hatching date}_i$$

$$+\ \beta_3\ \text{chick condition}_i + \beta_4\ \text{male tarsus length}_i$$

$$+\ \beta_5\ \text{female condition}_i + \beta_6\ \text{male condition}_i + \beta_7\ \text{brood age}_{i,t}$$

$$+\ \beta_8\ \text{brood age2}_{i,t} + \sigma\ \text{year} * u\ \text{year}_i + \sigma\ \text{female ID} * w\ \text{female ID}_i;$$

where y_{care} represents female care for each day as binary variable ("1" for care and "0" for no care) with dimensions i as the number of broods ($N = 262$) and t as the length of the brood care period (0–25 days). S is the daily care continuation probability, which relates to brood and day specific predictors of the model. All fixed variables were z-transformed with mean = 0 and standard deviation (SD) = 1. We used normal priors with mean = 0 and SD = 5 on fixed effects, normal priors (mean = 0, SD = 1) on random effects and Cauchy (0,5) priors on the sigma parameters (year, female ID).

Since STAN currently does not accept missing values for the estimations, we substituted missing values with the population average for male tarsus length and condition variables ($N_{females} = 25$, $N_{males} = 23$, $N_{chicks} = 8$). Importantly, the model can distinguish between different end of care events. The last value the model considered for a certain brood was always the last observation day, that is, the first day the female did not provide care anymore in deserted and failed broods, therefore had the value of 0. Alternatively, for broods with unknown fate or full term biparental care the value was 1

and referred to the last day the female still provided care (Korner-Nievergelt et al. 2015). We obtained samples of the posterior distribution of the model parameters from five independent Markov chains with 4000 iterations each. We discarded the first 2000 values of the burn-in period of each chain and then calculated posterior parameter estimates from the remaining iterations. For analytics and visual inspection to determine convergence of the model we used *shinystan* package (Stan Development Team 2018). All models had fully converged with the $\hat{R}$ values = 1 (Gelman et al. 2004). For visualization of the results, we used the *bayesplot* (Gabry and Mahr 2017) and *MCMCvis* packages in R (Youngflesh 2018).

Termination of care and chick mortality

In this analysis, we examined the relationship between female termination of care and chick mortality. First, we tested whether females were more likely to terminate care on days when one or all chicks died than when the brood size did not change. We included all broods belonging to the desertion, brood failure and full term care categories, excluding unfinished broods. Second, we examined whether females were more likely to desert on days when chick mortality happened. For this, we only considered deserted broods where at least one chick died and tested whether desertion occurred randomly or coincided with chick loss. We included all broods for which the last pre- and first postdesertion observations were no more than 3 days apart. Deteriorating chick condition, because of starvation, injury or disease, may precede chick loss by 1 or 2 days. Females may be able to anticipate chick death and leave such broods before the actual reduction of brood size as we often observed chicks moving sluggishly and lagging behind the family shortly before they disappeared (C.K., M.C.L., personal observations).

We used co-occurrence models (conditional logistic regression) to test whether female desertion and chick mortality co-occurred more frequently than expected by chance. We coded both desertion (i.e., the change in probability of care) and chick mortality as "1," and continued female care and no chick loss as "0." We added Nest ID as a grouping variable for the model. We used the "clogit" function of the *survival* R package for the analysis (Therneau and Lumley 2015). For all statistical analyses, we used R version 3.5.3. (R Development Core Team 2010).

RESULTS

Female brood care

Among the 262 Snowy Plover broods examined, desertion was the most frequent terminal event of female care with 185 (71%) of all broods deserted. Desertion typically happened during early brood care, that is, in 93% of the deserted broods, the female left within 10 days after hatching. The peak of desertion occurred 2 days after hatching. In stark contrast, only a minority of five (2%) females cared for the brood until fledging. Fifteen (5%) broods failed before the female deserted. Finally, for 57 (22%) broods the terminal fate was not known and these females were still seen with the brood at the last observation.

Reproductive success and breeding time

Deserting females that re-mated locally at our breeding site and successfully hatched chicks from both attempts ($N = 9$) did not

have higher reproductive success than full time caring females (N = 5) (LM: Estimate: −0.17 ± 0.35, confidence interval [CI]: −0.87 to 0.52, P = 0.677, Figure 2a). Both groups fledged on average 2.5 chicks. However, deserting females showed a higher variance in reproductive success than caring females with the most successful female having up to five fledglings.

The breeding time of deserting females was, however, substantially longer than that of caring females (Figure 2b). Deserting females spent on average two and a half weeks (33%) longer at reproduction than females that cared for their chicks until fledging (GLM: Estimate: −17.1 ± 2.9, CI: −23.3 to −10.8, P < 0.001).

Predictors of the length of female brood care

Hatching date, present brood size, and brood age^2 were all associated with female "probability of care" (Figure 3a). Early in the season, females terminated care quickly to desert the brood. By the end of the season, females continued to care longer and probability of care increased from 0.45 (95% CrI: 0.23–0.67) to 0.97 (95% CrI: 0.94–0.99) over the season (Figure 3b). The probability of care for females caring for large broods were higher than those for females caring for small broods (Figure 3c). Mean probability of care for the broods with one chick was 0.7 (95% CrI: 0.5–0.83) and increased by approximately 0.03 for every additional chick to 0.83 (95% CrI: 0.7–0.9) for a five chick brood, the largest brood size in our sample. Brood age^2 also showed some association with length of female care. Rates of probability of care decreased from 0.8 (95% CrI: 0.76–0.88) at hatching to 0.75 (95% CrI: 0.62–0.84) at a brood age of 8 days and then increased to 0.95 (95% CrI: 0.76–0.99) for females that stayed until the age of 25 days (Figure 3d).

Neither male tarsus size nor any of the condition variables were statistically clearly related to the probability of care as CrIs overlapped with zero (Figure 3a). Similarly, brood manipulations had no clear effect on female probability of care. The analysis without the manipulated broods did not change the results qualitatively (data and results are available on GitHub, see Data availability statement).

Termination of care and chick mortality

In 55 (26.7%) broods, the female terminated care on the day a chick died (Figures 4 and 5). The conditional logistic regression model showed a clear association between chick mortality and female termination of care (P < 0.001). Co-occurrence of desertion and chick mortality was influenced by the present brood size at termination of care. When a brood had one chick nearly all females deserted before that chick died or fledged (co-occurrence for broods with one chick: 14.3%, P = 0.49) meaning that there were few co-occurrences of chick death and termination of care. However, co-occurrence became statistically clear in broods with more than one chick at the time of termination of care (two chicks: 29%, P < 0.001; three chicks: 32.7%, P < 0.001; more than three chicks: 40%, no P value as model did not converge since all chick death events coincided with (or after) female desertion, Figure 6). Restricting the analysis to include only those broods that were deserted (i.e., excluding one chick broods where desertion and mortality cannot co-occur by definition) resulted similar co-occurrence between female care termination and chick mortality (26.6%, P < 0.001).

DISCUSSION

How do parents decide whether to continue care or desert their offspring? Our analysis of female brood care in Snowy Plovers suggests that females constantly assess the needs, value, and survival prospects of their offspring while they provide care. This ability is a precondition for an adaptive decision about whether or not to continue care. Deserting and re-mating Snowy Plovers attempt to
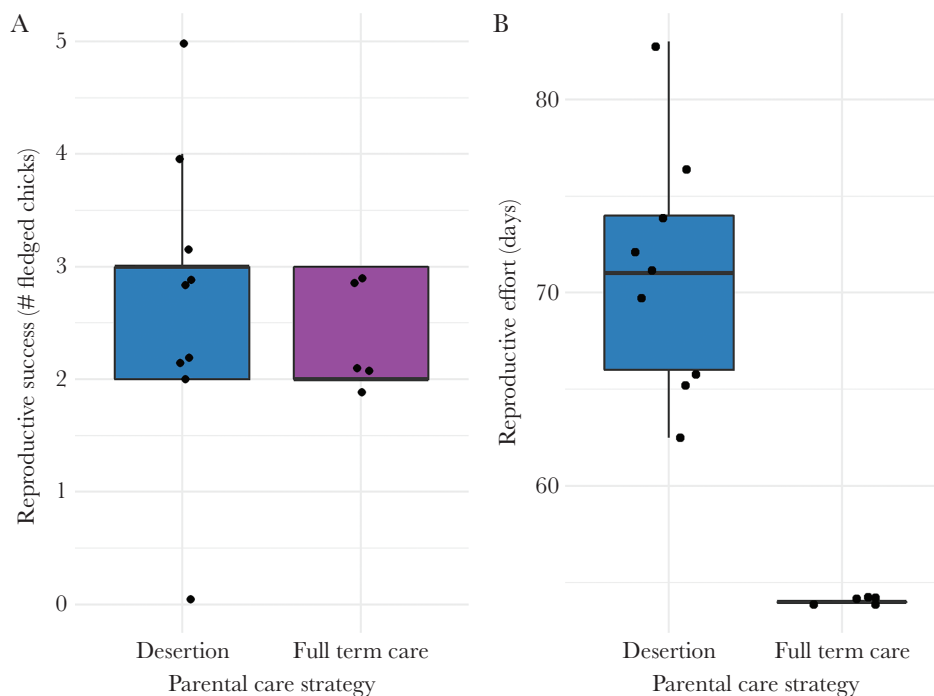

Figure 2
Reproductive success (a) and breeding time (b) of deserting and locally re-mating (N = 9) and full-term caring (N = 5) Snowy Plover females at Ceuta.
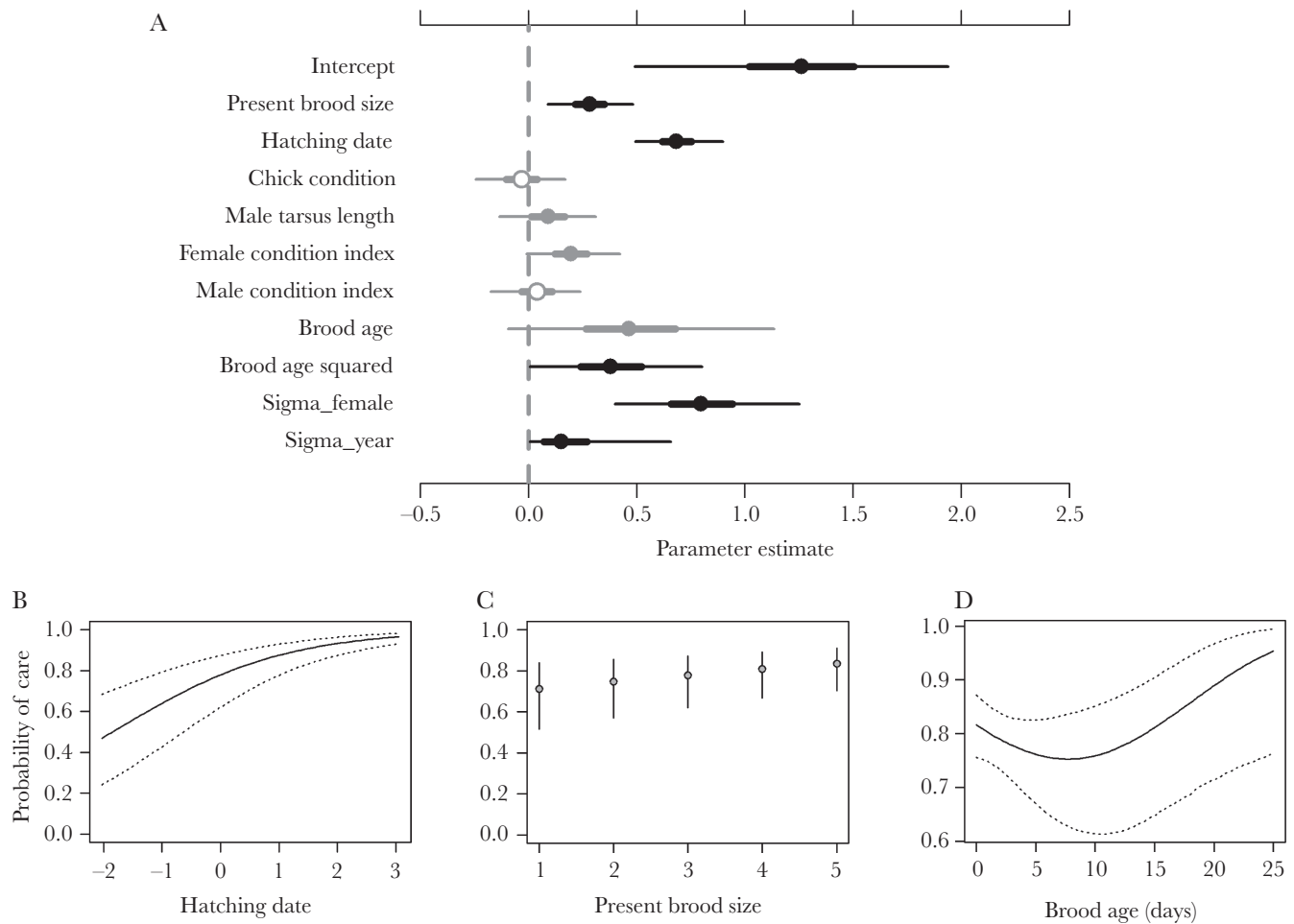
Figure 3

Predictors of the probability of female care in 262 Snowy Plover broods at Ceuta when all other predictors are kept at the mean. (a) Summary of all model predictors. *Sigma_female* and *Sigma_year* are random effects. Dots represent means, thick lines standard deviations and thin lines are the 95% credibility intervals (CrIs). Black symbols indicate no CrI overlap with zero, for grey symbols CrIs overlap with zero. (b,c,d) Details for fixed effects with a statistically clear impact on the probability of female care: hatching date (standardized to the annual mean) (b), present brood size (c), and brood age (d). Continuous lines refer to mean estimates and dotted lines represent the CrIs (b, d), circles represent the mean and continuous lines represent CrIs (c). For clarity, we plotted the predicted values for discrete observed present brood size categories whereas the statistical model was run on scaled values.

maximize their reproductive success by rapid divorce after hatching as divorced females produce a higher number of hatchlings than females that retain their mates (Halimubieke et al. 2019). Yet, we confirmed that desertion does not necessarily translate into producing more fledglings (Cruz-López et al. 2017). Our findings suggest that full term care providing females reach a similar reproductive success (measured as number of fledglings) as deserting and locally re-mating females but in significantly shorter time. Moreover, occasionally, caring females will still have enough time left to establish a new clutch and may hence increase their reproductive success further. The low number of locally re-mating females with successfully hatched chicks ($N = 9$) suggests that many deserting females disperse further to find new partners. However, it also shows that chick survival is generally low. Some of the dispersing females may reach higher reproductive success than locally re-mating females (Halimubieke et al. 2019). However, the breeding time of dispersers must be even higher than that of caring or locally re-mating females as some females disperse to great distances, therefore, breeding dispersal must take up further time (Stenzel et al. 1994). On the other hand, our results show that providing full

term care is not a common strategy of the females; we recorded only six females staying until fledging, whereas the large majority of females deserted before. In spite of the low numbers, our analysis shows the potentials of the two strategies and illustrates that re-mating does not necessarily provide advantages to females that chose this strategy.

When analyzing variables associated with the length of female care, we found both static and dynamic predictors that related to the probability that females will continue care. The dynamic modeling approach allowed us to analyze the consequences of changes in these predictors on individual decisions of females. Our study identified three either static or dynamic predictors for the length of female care. First, the hatching date of a brood was positively associated with the length of female brood care. In early broods, females cared for a shorter time and deserted the broods faster than in late broods. This is consistent with desertion for sequential polygamy and has also been observed in many other plover populations (Warriner et al. 1986; Székely and Williams 1994; Amat et al. 1999a; Székely and Cuthill 2000; Kosztolányi et al. 2009). Re-mating opportunities decrease with every day, so fast desertion

will maximize the reproductive potential of early breeding females whereas late breeding females may be better off providing care.

Second, we found that the present brood size had an effect on the probability of female care. Females were less likely to stay when brood size decreased during the brood care period. This suggests that for females the value of the brood is not fixed and determined by initial brood size and/or the breeding season (Székely and Cuthill 2000) but rather is assessed regularly over the brood care period. Therefore, Snowy Plover females avoid the "Concorde fallacy" (Dawkins and Carlisle 1976; Armstrong and

Robertson 1988; Ackerman et al. 2003; Magalhães and Geoffrey White 2016). That survival prospects of the brood, particularly chick mortality, eminently affected the female's decision whether to continue or terminate care is shown by the close temporal association between chick mortality and desertion. The co-occurrence of chick mortality and desertion was much stronger than expected by chance. Chick death seemed to be an important trigger for females to terminate brood care albeit our data did not allow us to firmly determine whether the mortality necessarily preceded desertion. Instead some females may already desert the brood if
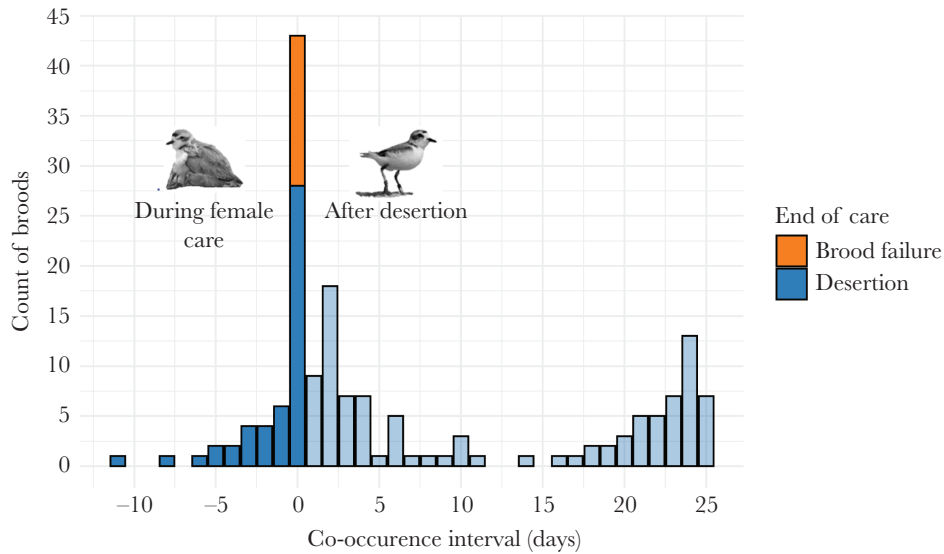

Figure 4

Co-occurrence of chick mortality and female care termination in 165 Snowy Plover broods with known dates of chick death or fledging. The diagram shows the interval between the most recent chick death and female termination of care within broods. Mortality and care termination coincide on the same day when the co-occurrence interval is zero. Negative values refer to mortality while the female still cared (dark blue). Positive values refer to cases when chick mortality happened after the female had deserted (light blue).
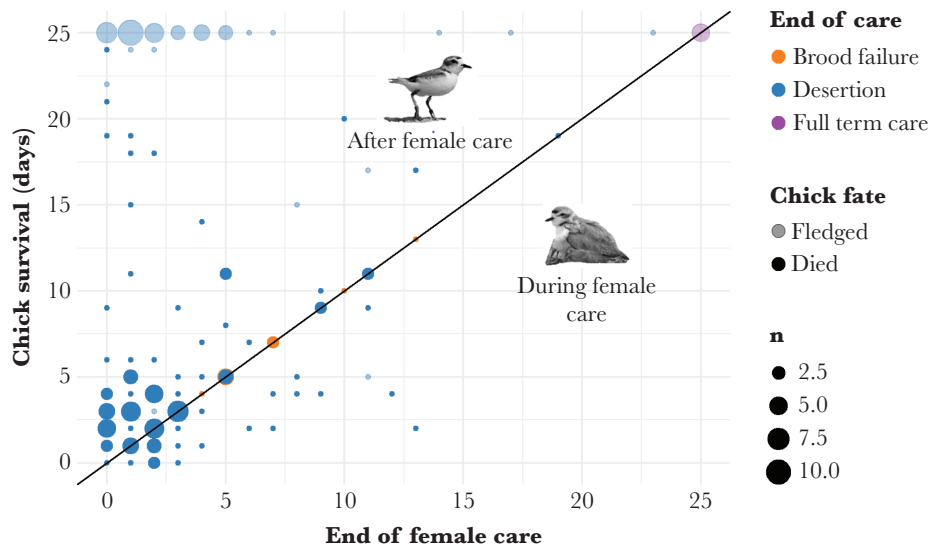

Figure 5

Chick survival from the first day of brood care in relation to length of female care for 170 Snowy Plover broods with known dates for chick death or fledging. Only one chick per brood, whose fate was most closely associated with the end of female care, is plotted. Dot sizes refer to number of broods. Coordinate (0,0) indicates the day of hatching and hence the start of female brood care. The diagonal line indicates co-occurrence of chick fate (died or fledged) and female care termination on the same day. Below the diagonal are broods in which the female continued to care after one chick had died, above the diagonal are broods where the female deserted before the first chick had died.
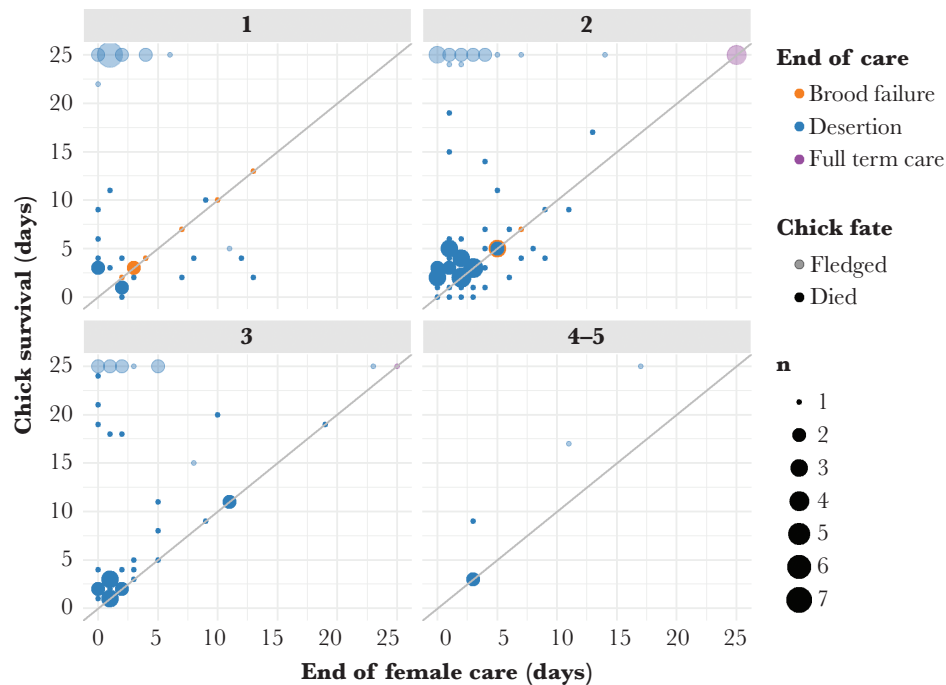
Figure 6

Chick survival from the first day of brood care and length of female care according to present brood size for 170 Snowy Plover broods, for which the date for mortality (or fledging) was exactly known. For each brood, only the chick whose fate was most closely associated with the end of female care is plotted. Dot sizes refer to number of broods. Coordinate (0,0) indicate the day of hatching and hence the start of female brood care. The diagonal line indicates co-occurrence of chick fate and female care termination on the same day. Below the diagonal are broods where the female continued to care after one chick had died, above the diagonal are broods where the female deserted before the first chick died. Present brood size refers to the number of chicks for the day the female ended care, which may differ from the initial brood size.

one chick is in bad condition due to sickness or starvation and, therefore, likely to die regardless of female care. We found that for broods with two or more chicks the co-occurrence of female care termination and chick mortality was particularly high. At the same time, nearly all broods with one chick were deserted by the female before the chick had died or fledged. This suggests that one-chick broods do not have enough reproductive value for the female to stay and care.

Third, we found that the probability of female care changed with brood age. Snowy Plover chicks are most vulnerable during the first 3 days of their lives (Colwell et al. 2007) and the peak of desertion fell into this period. We observed an initial decline in the probability to care until the age of 9 days. This is consistent with our expectations based on the needs of the brood. As chicks grow older, they improve their thermoregulation and require less brooding, one of the most time consuming care behaviors (Székely and Cuthill, 2000). Hence, the presence of the second carer becomes less important. Interestingly, after the age of 9 days, the relationship changed and the probability to continue to care increased until fledging. In precocial species such as the Snowy Plover, chick survival typically increases with age (Colwell et al. 2007; Cruz-López et al. 2017). For females that already cared for an extended period, care continuation may also be the best option as the value of the current brood is high, especially at the end of the season when the re-mating opportunities are low (Figure 3b, Székely and Cuthill 2000).

Similar to other studies, neither parent condition nor male size was clearly associated with the length of female care (Székely and Williams 1995; Amat et al. 1999b; Amat et al. 2000). As desertion rates declined with season, desertion does not seem to be a response

to energy depletion as in other species (Gratto-Trevor 1991; Osorno 1999; Currie et al. 2001). Chick condition at hatching had no clear effect on the length of female care either. Yet, the significant co-occurrence of desertion and chick mortality suggest that females are sensitive to changes in chick condition over the brood care period.

Parental brood care in plovers mainly consists of thermoregulation, warning chicks of predators and defending them from attacks of competitors (Carmona-Isunza et al. 2017). However, chick survival is also strongly dependent on the availability of high quality habitat with invertebrate food, which declines over the season (Kosztolányi et al. 2006; dos Remedios et al. 2015; Cruz-López et al. 2017). In a stochastic environment plastic care behavior that follows the changing value and needs of their brood can be highly advantageous. In Snail Kites *Rostrhamus sociabilis*, for example, one parent tends to desert the brood once a single parent can care for the chicks alone. In this system chick survival is generally low, therefore, parents do not compromise offspring survival by desertion. Rather desertion happens once the needs of the brood reached the "monoparental threshold" either due to brood size reduction or to advanced brood age (Beissinger 1986, 1990). In other studies the value of broods has been shown to be important for desertion. Female ducks tended to desert their clutches once the number of depredated eggs reached a certain proportion (Ackerman et al. 2003). Our results suggest that for many Snowy Plover females in this population desertion may have two different motives: 1) increase the reproductive success through sequential polygamy or 2) make the best of a bad job. Both scenarios are represented by distinct clusters in Figure 5. Early breeding females may utilize the good environmental conditions and desert to increase their reproductive success by producing a second clutch quickly without jeopardizing

the survival of the deserted brood (Osorno 1999). Similar to the "monoparental threshold" (Beissinger 1990), the value of the current brood is high while the needs for care are low. By contrast, to make the best of a bad job, females desert when their parental effort cannot prevent chick mortality. This is the main reason for desertion in our population where chick survival decreases with season (Cruz-López et al. 2017). Chick starvation and flooding, which are the main threats for offspring failure in the Ceuta population (Cruz-López et al. 2017; Plaschke et al. 2019), cannot be mitigated by the parents. After the death of one or more chicks the value of the brood will become too low for the female to continue care (similar to the "value threshold," Ackerman et al. 2003). Although the needs of the brood are still high, they cannot be fulfilled by the female. By contrast, continued care is only expected when both the needs and the value of the brood are high, that is, the resulting biparental care fulfils the offspring needs, for example, through protection.

In conclusion, the examination of high-resolution real-time data with a dynamic modeling approach revealed multiple hidden facets of the decision-making process of a species with a highly plastic parental care behavior. Our study demonstrates that for Snowy Plover females the decision over care or desertion is dynamically changing and responds to both the current needs and the value of the offspring, adjusted to the seasonally changing mating opportunities. Deserting females represent a heterogeneous group. They include some successful females that pursue polyandrous matings to multiply their reproductive success. Yet most deserting females use sequential polyandry as a plan B to compensate for low chick survival in their current brood. Our dynamic modeling approach allowed us to gain novel insight into the variety of plastic parental care strategies. The observed high behavioral plasticity may enable females to maximize their reproductive success in highly fluctuating environments through multiple adaptive reproductive strategies, which deserves further investigation.

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CONFLICT OF INTEREST:

The authors declare no conflict of interest.

Data availability: Analyses reported in this article can be reproduced using the data provided by Kupán et al. (2020). All data and R codes are available on GitHub repository: https://github.com/kupankrisztina/Snowy-Plover-Desertion.

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