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Remating opportunities and low costs underlie maternal desertion

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Abstract

Parental care can enhance offspring survival but may impose significant costs to parents. The costs and benefits of care are key to understanding patterns of parental care, where parents can benefit by having their partner increase investment in care, while reducing their own effort. However, investigating the costs and benefits of parental care in wild populations is challenging. Here we use highly detailed behavioral observations in families of a small shorebird, where one parent frequently deserts its offspring, to explore the potential costs and benefits of desertion in a wild population. We first show that females desert their broods more frequently than males. Second, we investigate the benefits of this frequent female desertion in terms of additional mating opportunities, and the costs of desertion to females in terms of the growth and survival of deserted offspring. Our results indicate that female desertion is favored by a combination of remating benefits and a lack of costs to brood growth and survival, as abandoned male parents continue to provide care after desertion. Our results shed light on the costs and benefits underlying natural desertion strategies and suggest that female desertion is a fine-tuned behavior that responds to seasonally changing benefits of desertion.

Keywords: desertion, parental care, reproductive strategies, sexual conflict

Introduction

Across the animal kingdom parental care encompasses a diverse array of physiological and behavioral adaptations (Clutton-Brock, 1991; Royle et al., 2012; Wilson, 1975). However, the balance of care between parents varies widely: in some species both parents care, while in others, males or females desert their family and leave their partner to care alone (Alger et al., 2020; Cockburn, 2006; Furness & Capellini, 2019; Liker et al., 2013; Székely et al., 1996; Ward et al., 2009). Understanding the evolutionary diversity of biparental, male-only, and female-only care hinges on explaining patterns of desertion in nature with implications for our understanding of patterns of evolutionary sex roles and sexual selection (Clutton-Brock & Parker, 1992; Fromhage & Jennions, 2016), sexual conflict (Lessells, 2012; McNamara & Wolf, 2015; Székely, 2014), social evolution and cooperation (Barta et al., 2014; Socias-Martínez & Kappeler, 2019) and population dynamics (Dudeck et al., 2018; Holman & Kokko, 2013).

A substantial theoretical literature has addressed the evolution and maintenance of parental care, and has pinpointed the costs and benefits of care and desertion as the key to understanding parental strategies (Alonso-Alvarez & Velando, 2012; Houston & Davies, 1985; Houston et al., 2005; Klug et al., 2012; McNamara & Leimar, 2020; McNamara et al., 2000; McNamara, 2022). The provision of care to offspring by parents can be favored by natural selection if it enhances the condition and survival of offspring (Alonso-Alvarez & Velando, 2012; Klug & Bonsall, 2014). However, caring can incur significant costs in terms of energy, time, and survival, that ultimately trade off with the future reproductive output of parents (Alonso-Alvarez & Velando, 2012; Balme et al., 2017; Drent & Daan, 1980; Santos & Nakagawa, 2012; Zink, 2003). For example, in the golden egg bug (*Phyllomorpha laciniata*) parents carrying eggs are predated at a higher rate compared to individuals without eggs (Reguera & Gomendio, 1999). Similarly, male European starlings (*Sturnus vulgaris*) with increased opportunities to attract female mates, decreased their share of incubation duties, suggesting a trade-off between mate acquisition and parental care (Smith, 1995). When such costs are sufficiently high, they may outweigh the potential benefits of caring. In such cases parents may instead benefit by ceasing all care and deserting offspring, which may enable them to invest greater time and effort into future breeding attempts (Keenleyside, 1983; Korpimäki et al., 2011; McNamara et al., 2000; Owens, 2002; Székely et al., 1996, 1999). Crucially, the advantages of desertion also depend on the behavior of the abandoned

partner and the costs imposed on the deserted offspring (van Dijk et al., 2007; Houston et al., 2005), since if the remaining parent does not, or cannot, compensate for the absent parent, offspring growth and survival may suffer (Klug et al., 2012; Lehtonen et al., 2011; Pilakouta et al., 2018).

To understand the costs of desertion and patterns of parental compensation, studies in multiple species have manipulated partner effort by artificially removing one partner (i.e., experimentally enforced desertion; Harrison et al., 2009; Hunt & Simmons, 2002; Lavery & Reebs, 1994). A meta-analysis of such studies in birds indicates that artificially deserted parents typically partially compensate for the lack of care from their absent partner, that is, deserted parents increase their rates of care but overall rates of offspring care remain lower when compared to biparental families (Harrison et al., 2009). Fewer studies have investigated the reproductive costs in terms of deserted offspring growth and survival, however partial compensation in care rates may indicate a reduction in offspring survival. For example, in the biparental California mouse (*Peromyscus californicus*) the removal of male parents resulted in reduced offspring survival (Gubernick & Teferi, 2000). While such experimental manipulations provide key insights into the costs of desertion, their ability to shed light on the costs and benefits associated with natural desertion strategies in wild populations are limited. For example, costs measured after the experimental removal of parents in species without natural desertion strategies may not resemble those costs in species in which desertion strategies are biologically frequent, and parental behavior evolved under a risk of desertion (Clutton-Brock, 1991; Székely et al., 1996). Moreover, in species where desertion naturally occurs, the artificial enforcement of desertion upon families in which desertion may have never occurred, may overestimate costs by enforcing maladaptive desertions. Therefore, a full understanding of the evolution of desertion also necessitates studies of natural desertion patterns. However, despite strong theoretical underpinnings, estimating the costs and benefits associated with such natural desertion strategies in wild populations represents a significant challenge, requiring (a) the estimation of fitness implications of both caring and deserting in a natural setting, not only before and after desertion but also within biparental families in which no desertion occurs and (b) repeated observations of families both before and after desertion to understand the behavioral interactions between parents and offspring that underlie the costs of desertion.

Here we overcome these challenges and investigate the costs and benefits associated with female desertion using detailed repeated observations of individual Kentish plovers (*Charadrius alexandrinus*) and their families from a well-monitored wild population (Kosztolányi et al., 2006). Both male and female Kentish plover parents incubate their clutch of eggs (modal clutch size of three eggs) laid in shallow scrapes on the ground (Amat et al., 1999b; Székely et al., 1994). After hatching both males and females may care for their self-feeding offspring by leading them to feeding habitats, perform thermoregulation of young chicks by brooding, and guarding them from conspecifics and predators (Kosztolányi et al., 2006; Székely et al., 2006). Brooding is an essential part of care for young shorebird chicks that cannot effectively control their own body temperature (Visser & Ricklefs, 1993, 1994). Kentish plover chicks are commonly predated by avian and mammalian predators (e.g., terns, kestrels, and foxes) (Fraga & Amat, 1996) and can be killed by conspecific adult rivals

during territorial intrusions (Székely & Cuthill, 1999). Kentish plover parents thus frequently remain vigilant in close proximity to offspring and display a variety of behaviors that function to distract approaching predators away from chicks, and aggressively defend chicks from conspecifics and predators by mobbing and fighting (Fraga & Amat, 1996; Simmons, 1951; Székely & Cuthill, 1999). Crucially, however, these diverse brood care behaviors are not always performed by both parents, because after hatching of the chicks either the male or the female may abandon the family and leave their partner to care alone (Amat et al., 1999a; Lessells, 1984; Székely & Lessells, 1993; Székely et al., 2006). As a result, Kentish plovers provide an outstanding opportunity to explore the mechanisms underlying the evolution of desertion in nature by providing both uniparental families in which one parent has deserted and biparental families with no desertion (Figure 1A).

We first (a) characterized the frequency of male and female desertion strategies in our population, throughout brood development and across the breeding season. Second, we assessed the reproductive (b) benefits and (c) costs of desertion. Because male desertions were comparably rare in our population, we focused on the costs and benefits of desertion for females. We estimated the benefits of desertion to females by quantifying the frequency at which deserting females initiate additional subsequent breeding attempts compared to females that do not desert, and the costs of desertion via the survival and growth of deserted broods. Finally, we (d) investigated patterns of care behaviors and chick feeding rates across brood development for families before female desertion, after female desertion, and in families that remained biparental to understand the behavioral mechanisms that may mediate the costs of desertion.

Methods

Fieldwork and behavioral observations

We studied a population of Kentish plover between 1996 and 1999 in an area surrounding Tuzla lake in southern Turkey (36° 43′ N, 35° 03′ E) composed of a continuous saltmarsh habitat that was approximately 100–500 m wide and 7 km long (Székely and Cuthill, 1999, 2000; Székely et al., 1999). Previous studies of this population found ecological differences within the study area associated with proximity to Tuzla village, and we follow those studies by defining two sites within our study area; site A closer to Tuzla village and site B more distant from the village (Székely & Cuthill, 1999). Our study included 121 closely monitored Kentish plover families, a subset of which have been previously studied (Kosztolányi et al., 2007; Székely & Cuthill, 1999, 2000; Székely et al., 1999). As our aim was to study natural variation in brood care, our data set included only families in which neither parents nor brood size were manipulated. This included 49 non-experimental families, 31 families from unmanipulated control groups in previous experiments (Székely & Cuthill, 1999, 2000; Székely et al., 1999) and 41 families that were manipulated at the nesting stage by cross-fostering eggs between families while holding brood size constant.

A total of 81 families were identified at the nesting stage and their hatching date was determined by repeat visits to the nest every 1–2 days over the last days of incubation (Székely & Cuthill, 1999). The remaining 40 families were identified after hatching, and the brood's age was estimated from tarsus length measurements via previously defined linear growth
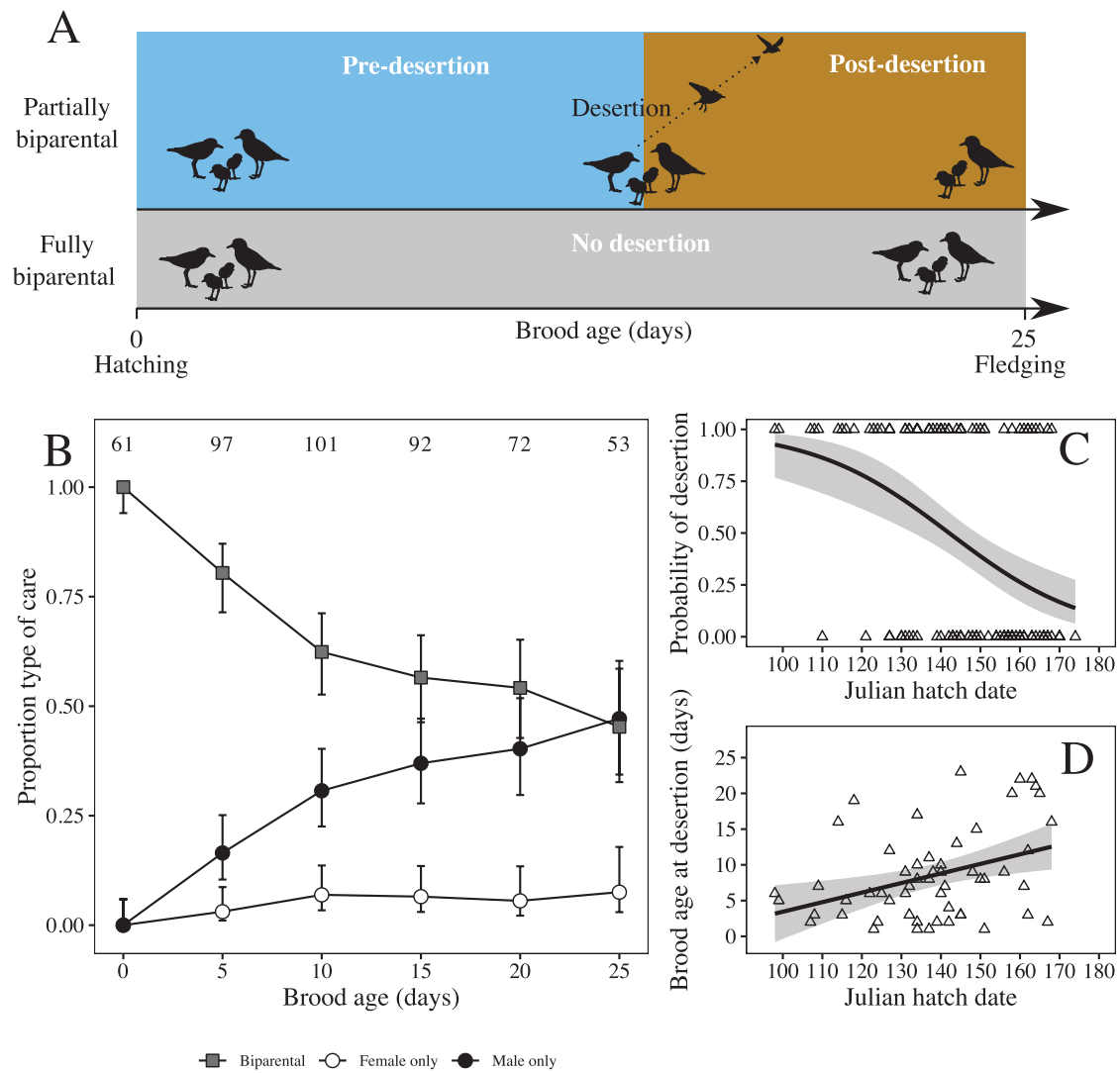
Figure 1. Patterns of parental care in Kentish plover (*Charadrius alexandrinus*). (A) Diagram outlines variation in brood care and desertion in Kentish plover families, where the male, the female or neither parent may abandon the family, resulting in biparental families and uniparental families. (B) The proportion of families with male-only (black circles), female-only (white circles), and biparental care (gray squares) (± 95% CI). The number of families used to calculate proportions is given. (C, D) Univariate relationships (± 95% CI) between brood hatch date and the probability broods were deserted by a parent (C) and the age of broods at the time of desertion (D).

rates of chicks (Székely & Cuthill, 1999). We aimed to capture and uniquely color ring all parents, and to recapture chicks every 4 days to measure tarsus length (mm) and body mass (g) to the nearest one decimal place.

We aimed to monitor families to record the parental status and number of chicks present (hereafter brood records) for up to at least 25 days after hatching (i.e., the approximate age at which chicks fledge, Dos Remedios et al., 2015; Székely & Lessells, 1993, Figure 1A). Briefly, identified families were searched for every 2–3 days and observed to record the care type (uniparental male, uniparental female, or biparental) and the number of chicks present (for detailed accounts on monitoring protocols see Székely et al., 1999; Székely & Cuthill, 1999, 2000; Székely & Kosztolányi, 2006). The final data included 1,072 brood records of parents with chicks with an average of 8.86 records per family and a gap of 2.40 ± 1.92 (mean ± 1 SD) days between brood records for each family.

For a subset of families (*N* = 66), we also collected detailed behavioral observations. We aimed to observe each of these families for one hour once every 2 days. During each 1-hour observation we scan sampled the behavior of all present parents and chicks every 30 seconds (totaling 120 scans) and estimated distance in meters between the parent(s) and each chick every 5 min (for a detailed account see Kosztolányi et al., 2006; Székely et al., 1999; Székely & Cuthill, 1999, 2000). Only one behavior was recorded per individual per scan and parent-chick distances were subsequently rounded upwards to the nearest 5 m. Here, we focus throughout on three key behaviors (a) brooding, (b) average parent-chick distances, and (c) substrate pecking. Brooding is important in maintaining chick body temperatures but costly for the parents by imposing thermoregulatory costs and limiting other activities (e.g., feeding) (Beintema & Visser, 1989b; Tjørve et al., 2009). Parents lead chicks to food resources and defend them from attacks from predators and conspecifics, therefore,

the distance between parents and chicks provides a proxy via which chicks may be "exposed" to such threats (Amat et al., 1999a; Kosztolányi et al., 2006). Substrate pecking provides an indicator of feeding rates and is expected to be beneficial for chicks (Székely & Cuthill, 1999). We calculated the proportion brooding and pecking as the proportion of scan samples in which chicks were observed performing the behavior, where each observed chick was included in both the numerator and denominator. For average parent-chick distances, we calculated the mean distance between the present parent and each chick at every 5-minute sample and then calculated the grand mean across all distance values within an observational period. When both parents were present, for each chick we used the distance to the nearest parent regardless of sex. Average distances from the chicks' perspective thus equal the mean distance to the nearest parent regardless of sex.

For ringed male and female parents, we recorded all evidence that parents initiated subsequent additional breeding attempts (rebreeding) in the same breeding season following the focal brood. Evidence for subsequent additional breeding attempts was collected daily throughout the study period and included all instances of reproductive behavior including nest scraping, copulation, and incubation of a new nest. Out of the 121 broods included in the analyses, four individuals had two focal broods each: two males had two focal broods (both in different years and with different females) and two females also had two focal broods (both in different years, one female with a differently ringed mate and the second female with an unringed male). A total of 23 out of 33 uniquely ringed deserting female parents (78.8%) were either resighted at least 1 week after their presumed desertion day or were observed initiating a subsequent breeding attempt after desertion, indicating that desertion rather than mortality is the driver of female absence from broods. Male desertions were rare ($N = 8$) and a total of 2 out of 6 ringed deserting males (33.33%) were resighted at least one week after their presumed desertion day.

All research was carried out in accordance with research visas issued by the Turkish authorities, and with the approval of the local environment authorities in Adana, Turkey, and the University of Bristol Animal Welfare Ethical Review Body.

Data analysis

We scored families as either fully biparental or partially biparental based on the sequence of brood records. Partially biparental families were those families where one parent deserted the brood before 25 days of brood care (i.e., the age which chicks typically fledge, Dos Remedios et al., 2015). Desertion was determined by at least two consecutive uniparental care recordings (i.e., two male-only or female-only care recordings in a row) with no further observation providing evidence for care by the other parent. For desertion to occur before 25 days, the first of the two consecutive uniparental observations must occur prior to day 25 of brood care. The day of desertion was determined as the midpoint between the last biparental and first uniparental record, rounded upwards to the nearest day. If only uniparental care was observed for a given family, the midpoint between the hatch date (day 0) and the first uniparental record was assumed to be the desertion day. Fully biparental families were those families in which no desertion was recorded before 25 days of brood care. All studied families had a minimum of two brood records and at least one record prior to

25 days. Across all 1,072 repeated brood records collected from all 121 families, in only 13 cases were two consecutive uniparental observations followed by confirmation of biparental care, indicating that two consecutive observations is reasonable proxy for desertion. In these 13 cases, the given uniparental observations were imputed to be biparental care.

All analyses were conducted using R statistical software version 3.6.3 (R Core Team, 2019). We use generalized linear models (GLMs) and test significance of individual predictors using likelihood ratio tests (LRTs) or F tests by removing the variable of interest. For models that utilize repeat observations of individuals from the same family across brood care, we use linear or generalized linear mixed-effects models ((G)LMMs) in "lme4" with a random effect for family identity to account for repeated measures (Bates et al., 2015). For (G)LMMs we utilize a model comparison approach using Akaike Information Criterion corrected for small sample sizes (AICc) to identify the most parsimonious models (Grueber et al., 2011). The most parsimonious models are those with a ΔAICc (difference between given model and the model with the lowest AICc) of < 2. The best minimal model is the model from the parsimonious model set that contains the fewest parameters. Throughout we treat the inclusion of a given predictor in the best minimal model as strong evidence of a relationship between predictor and response. Male desertion was rare: we had only eight families with male desertion (see above), of which only three had detailed behavioral observations. Therefore, we do not include these male-deserted families in the current study beyond reporting overall patterns of parental care; we focus on female desertion.

Patterns of care

We first characterized overall patterns of male and female desertion among those families in which one parent deserted, using a GLM with a binomial error structure and a binary response variable indicating whether the female (1) or male (0) parent deserted. Explanatory variables included linear and quadratic terms for the Julian date in which the brood hatched as well as a 4-level factor indicating the year and a 2-level factor indicating the site of brood care. To explore whether the probability of desertion may be affected by the 41 broods where eggs were cross-fostered at the nesting stage, we fitted an additional binomial GLM with desertion as a response as above and 2-level factor indicating whether the brood was manipulated at the nesting stage or not (see online supplementary material for details).

We next assessed whether the probability that a brood would be deserted by a parent (male or female) varied over the season across all fully and partially biparental families. We used a GLM with a binomial error structure and a binary response variable indicating whether the brood was deserted. Explanatory variables included linear and quadratic terms for the Julian date in which the brood hatched as well as a 4-level factor indicating the year and a 2-level factor indicating the site of brood care.

Finally, we explored variation in the age at which broods were deserted (i.e., the timing of desertion). We used a linear model with a Gaussian error structure with the age of broods in days when desertion occurred square-root transformed as a response variable. Explanatory variables included the sex of the deserting parent (male or female), linear and quadratic terms for the Julian date in which the brood hatched as well

as a 4-level factor indicating the year and a 2-level factor indicating the site of brood care.

Benefits of desertion

Desertion may be favored if it frees time and resources for deserting parents to initiate additional breeding attempts compared to parents that continue to care. We use GLMs with a binomial error structure to compare the probability that females were observed initiating subsequent additional breeding attempts within a season (rebreeding) between deserting females from partially biparental families and non-deserting females from fully biparental families (*N* = 90 ringed female parents in total). Females who were not re-sighted were scored as not rebreeding. Models included a binary response variable indicating whether females were observed rebreeding or not. Explanatory variables were a 2-level factor indicating whether the female deserted or not, a 4-level factor indicating year, and a 2-level factor indicating the site of brood care. In principle, females that breed earlier in the season may have a higher chance of being observed rebreeding than females who breed later in the season for two reasons; (a) later-breeding females are less likely to rebreed due to seasonal time constraints or differences in behavior, and (b) even if later breeding females are equally likely to rebreed, there are fewer sampling days in the field to observe rebreeding if it did occur. Given female Kentish plovers typically remate within approximately 2 days (Székely et al., 1999, 2006) it is unlikely that (b) could drive differences between deserting females and non-deserting females in their probability of rebreeding. Regardless, we also included the Julian date on which the focal brood hatched as a covariate to statistically control for the possibility that the seasonal timing of the focal breeding attempt may drive variation in the probability rebreeding was observed across deserting and non-deserting females. In addition, we repeated rebreeding comparisons between deserting and non-deserting females focusing on broods that hatched at least four weeks before last sampling day of the season in each year (i.e., excluding nests that may have fledged after the sampling period in each season). For completeness we also report the proportion of deserting males that were observed rebreeding (*N* = 6 ringed male parents), as well as the proportion of males observed rebreeding from partially biparental families in which females deserted and from fully biparental families (*N* = 94 ringed male parents).

Costs of desertion

Despite the potential benefits of remating, if desertion imposes strong costs on the viability of abandoned offspring, the net fitness pay-offs may not favor desertion. To assess the potential costs of female desertion we first compared the total number of fledglings produced between partially biparental families where females deserted and fully biparental families (i.e., the number of chicks alive at brood age of 25 days). For broods not observed on day 25 but with records after day 25, the number of chicks on the nearest day up to day 28 was used. Families with observations only before fledging (i.e., before day 25) were not included. GLMs with Gaussian error structures included a 2-level factor indicating fully or partially biparental care type, as well as Julian hatch date and factors indicating year (4 levels) and site (2 levels) of brood care. To explore whether the total number of fledglings produced may be affected by the 41 nests that included cross-fostered

eggs, we fitted additional GLM with the number of fledglings produced as a response variable and 2-level factor indicating whether the brood was manipulated at the nesting stage or not (see online supplementary material for details).

Second, we compared chick survival between fully biparental families, and partially biparental families before and after female desertion. We, therefore, had three categories of parental care ("care type"); partially biparental families pre-desertion, partially biparental families post-desertion, and fully biparental families (Figure 1A). As we were focused on chick survival until fledging, models included families with at least two observations up to and including day 25 of brood care. For a subset of families with no records on day 25 but with information on chick survival up to 3 days after (i.e., day 28), we included those final observations. We ensured chick numbers were always decreasing, such that if chicks previously determined missing were later observed, all previous observations were imputed to include the observed chicks. As we had two levels of non-independence in our data including repeated measures of individual chicks across time, as well as measures of multiple chicks from the same family—and each family and chick within each family may have their own baseline—we used a mixed-effects Cox regression model using package "coxme" (Therneau, 2020) that included random intercepts for both family identity and chick identity (nested within family). Models included a 3-level factor indicating care type (fully biparental, partially biparental pre- or post-desertion), as well as Julian hatch date and factors indicating year (4 levels) and site of brood care (2 levels). We used confidence intervals of hazard ratios (HRs) to interpret post-hoc comparisons between factor levels using package "multcomp" (Hothorn et al., 2008).

The above analyses include a subset of families (*N* = 8) where observations indicated all chicks were absent, and hence all chicks died. While unlikely, some of these observations may represent outcomes other than brood failure, for example, if the lone parent deserted surviving chicks and/ or chicks fledged before 25 days. Nevertheless, to assess the sensitivity of our analyses to these complete brood failure records we repeated both (a) the number of fledgling and (b) survival analyses, excluding these records.

Finally, as costs of desertion may arise via reduced quality of fledglings, we explored the potential costs of desertion in terms of chick growth, by comparing the body mass and tarsus length of chicks from fully biparental families, partially biparental families before and after female desertion. Families where chicks were captured on at least two days between hatching and fledging (days 0–25) were included. Families identified after hatching were excluded to avoid circularity as the age of chicks in these families was estimated via tarsus length (see above). As the identity and number of chicks recaptured can vary for a given family, we calculated mean body mass and tarsus length of all chicks captured for a brood on a given day. Visual inspection of body mass and tarsus length indicated that growth at 25 days had not begun to asymptote and continues beyond fledging. Due to the non-independence in our data (i.e., repeated measures of chicks from the same family over brood care), and each family may have their own mean baseline body mass and tarsus length, we used LMMs that included random intercepts for family identity. LMMs included natural log-transformed body mass and tarsus length as response variables and Gaussian error structures. Explanatory variables included brood age, a 3-level factor

indicating care type, and their interaction to assess differences in growth rates between care types. Models also included Julian hatch date, factors indicating year (4 levels) and the site of brood care (2 levels) (see Tables S3–S4, online supplementary material for full model details). Finally, to explore whether the size and growth rates of chicks may be affected by the 41 broods in which eggs were cross-fostered, we fitted additional LMMs for both mean chick mass and tarsus length as above but including 2-level factor indicating whether the brood was manipulated at the nesting stage or not, and the interaction between brood age and the manipulation factor (see online supplementary material for details).

Behavioral dynamics of brood desertion

To investigate the potential behavioral drivers of cost and benefit profiles, we assessed how the behavioral dynamics of families varied as function of parental care strategies (i.e., fully biparental families where no parent deserted and partially biparental families where females deserted). Throughout we focus on data collected between brood ages 0 and 25 days (i.e., from hatching to fledging) and across three categories of parental care ("care type"); partially biparental families before female desertion (pre-desertion), partially biparental families after female desertion (post-desertion), and fully biparental families (Figure 1A).

For each behavior, we used (G)LMMs with a random effect for family identity to account for repeated observations of families across brood care. Models for proportion brooding and pecking used a binomial error structure. Parent-brood distances were log-transformed and used a Gaussian error structure. Models included age of broods in days, a factor indicating care type and the interaction between the age of broods and care type. The interaction between brood age and care type allows us to ask whether changes in behavior as chicks grow older varies among families with different care types. Models also included the current number of chicks in the brood, year (4-level factor), site (2-level factor), Julian date of observation, and the time of day of the observation in decimal hours (see Tables S5–S6, online supplementary material for full model details).

Finally, for families scored as fully biparental but not observed until 25 days of brood care, it is possible that one parent did desert before 25 days but this was not observed, or one parent would have deserted before 25 days but the brood died prior to this occurring (e.g., by predation). Designating families that may later be deserted as fully biparental, would be expected to reduce any observed differences in behavior between partially and fully biparental families (i.e., a conservative estimate). We, therefore, repeated our behavioral analyses excluding fully biparental families that were not observed until day 25 or more. These repeat analyses revealed qualitatively similar results (Figure S1, online supplementary material).

Results

Patterns of care

Forty-five percent of families (55 out of 121 families) were deserted by a parent before the chicks reached 25 days of age, and the majority of deserting parents were females (47 female vs. 8 male desertions; Figure 1B). The probability that a deserting parent was a female versus a male declined linearly over the breeding season ($N = 55$ broods, hatch date: β = -1.147, $SE = 0.545$, LRT $\chi_1^2 = 4.402$, $p = .036$, hatch date^2: LRT $\chi_1^2 = 0.549$, $p = .459$). The sex of the deserting parent did not vary across our two study sites ($N = 55$ broods, LRT $\chi_1^2 = 2.099$, $p = 0.147$) or between years (LRT $\chi_3^2 = 6.734$, $p = .081$).

Broods were deserted throughout the breeding season, however, the probability of desertion decreased toward the end of the breeding season ($N = 121$ broods, hatch date: LRT $\chi_1^2 = 20.764$, $p < .001$, hatch date^2: LRT $\chi_1^2 = 0.039$, $p = .844$, Figure 1C). The probability of desertion did not vary between years or sites (year: LRT $\chi_3^2 = 2.506$, $p = .474$, site: LRT $\chi_1^2 = 0.166$, $p = .684$). Broods that hatched later in the breeding season were deserted at an older age ($N = 55$ broods, hatch date: LRT $\chi_1^2 = 8.860$, $p = .002$, hatch date^2: LRT $\chi_1^2 = 2.116$, $p = .125$, Figure 1D). The age at which broods were deserted did not differ significantly between males and females, between years or across study sites (sex: LRT $\chi_1^2 = 2.746$, $p = .080$, year: LRT $\chi_3^2 = 6.539$, $p = .063$, site: LRT $\chi_1^2 = 2.489$, $p = .096$). We found no evidence that the probability of desertion was impacted by nest manipulations (see online supplementary material).

Benefits of desertion

Models assessing the probability that females were observed initiating a subsequent breeding attempt (re-breeding) within the same season revealed that deserting females were significantly more likely to initiate subsequent breeding attempts within the same breeding season compared to females that did not desert their broods (36% vs. 9%; $N = 90$ females, LRT $\chi_1^2 = 5.021$, $p = .025$, Figure 2A). Furthermore, rebreeding probabilities declined over the season (β = -0.082, $SE = 0.029$, LRT $\chi_1^2 = 10.607$, $p = .001$) (i.e., the probability a female would rebreed was lower for females from families that hatched later in the breeding season) but did not vary across years or sites (year: LRT $\chi_3^2 = 5.388$, $p = 0.146$, site: LRT $\chi_1^2 = 0.076$, $p = .783$). Proportion tests comparing the proportion of females rebreeding between deserting females (partially biparental families) and non-deserting females (fully biparental families) focusing only on broods that hatched at least four weeks before the last observed brood sighting in year (i.e., last sampling day of the season) ($N = 63$ females) provided qualitatively similar results, indicating a significantly higher probability of re-breeding for deserting females (proportion test: $\chi^2 = 5.059$, $p = 0.025$, Table S1, online supplementary material).

Males from fully biparental, and partially biparental families where their female partner deserted, were unlikely to rebreed (fully biparental = 2/57 males rebreeding, partially biparental = 4/37 males rebreeding, Table S1, online supplementary material). Similarly, of the eight deserting males, six males were ringed and none of these ringed males were observed rebreeding.

Costs of desertion

Families deserted by females did not produce fewer fledglings compared to families in which females did not desert ($N = 54$ broods, $F_{1,47} = 2.867$, $p = .097$, Figure 2B). Families that hatched later in the season produced fewer fledglings ($N = 54$ broods, $F_{1,47} = 7.525$, $p = .009$), however, the number of fledglings produced by families was not related to year or site ($N = 54$ broods, year: $F_{3,47} = 0.669$, $p = .576$, site: $F_{1,47} = 0.002$, $p = .970$). Repeating the latter analysis focusing only on broods
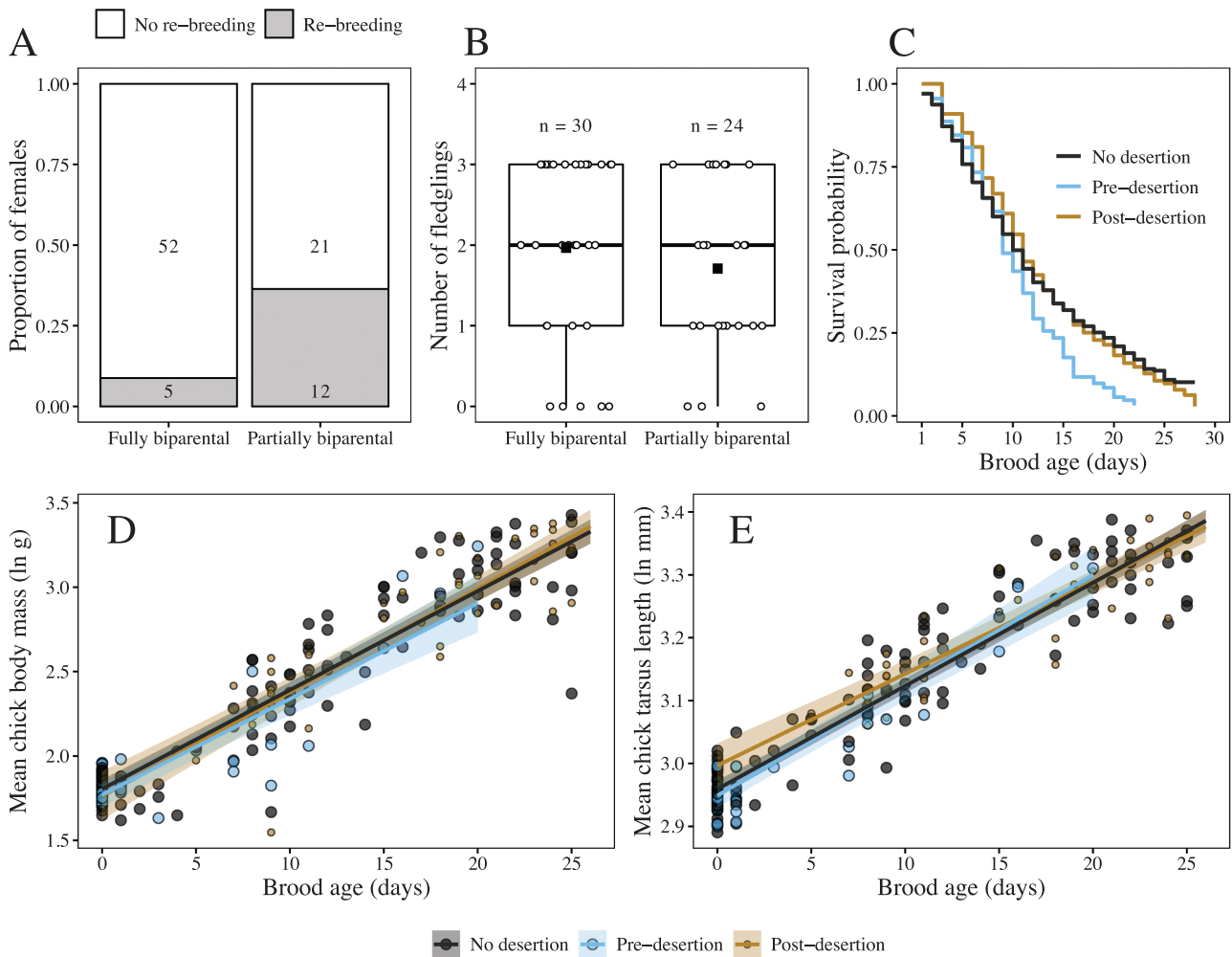
Figure 2. Reproductive consequences of brood desertion. (A) The proportion of females from fully biparental families and deserting females from partially biparental families observed initiating subsequent breeding attempts within the same season (rebreeding, filled bars) or not (no rebreeding, open bars). Counts are provided within bars. (B) Boxplots of the number of fledglings produced by fully biparental families and partially biparental families where females deserted. Black squares depict mean values. White points show raw data. (C) Chick survival probabilities for partially biparental families before (blue line) and after female desertion (yellow line) and in fully biparental families (black line). (D, E) The relationship between the age of broods and natural log-transformed mean chick mass in grams (D) and mean chick tarsus length in millimeters (E) for families before female desertion (Pre-desertion; blue), after female desertion (Post-desertion; yellow) and for families where no parent deserted (No desertion; black). Lines show predictions (± 95% CI) from maximal models. The intensity of point shading indicates point overlap.

that fledged at least one chick successfully (excluding observations indicating that all chicks died, i.e., complete brood failure), provided broadly similar results ($N = 46$ broods, care type: $F_{1,39} = 2.864$, $p = .099$, hatch date: $F_{1,39} = 0.400$, $p = .531$, year: $F_{3,39} = 1.674$, $p = .188$, site: $F_{1,39} = 1.494$, $p = .229$). We found no evidence that fledgling numbers were impacted by nest manipulations (see online supplementary material).

Similarly, chick mortality rates did not differ between fully biparental families and partially biparental families either before or after female desertion (No desertion-Post-desertion; HR = 0.760, 95% CI = [0.360, 1.607], No desertion-Pre-desertion; HR = 0.582, 95% CI = [0.265, 1.277], Pre-desertion-Post-desertion; HR = 1.307, 95% CI = [0.839, 2.035]; Figure 2C; Table S2, online supplementary material). Moreover, we found no evidence that either the chick body mass, tarsus length, or rate of growth in these traits were different between fully biparental families and partially biparental families before or after female desertion (Figure 2D and E; Tables S3 and S4, online supplementary material). These latter results

were robust to controlling for nest manipulations (see online supplementary material).

Behavioral dynamics of brood desertion

Deserted chicks received less brooding at young ages but received slightly more brooding at older ages than chicks cared for by both parents, suggesting uniparental males slightly over-compensated for the lack of female care later in chick development (Figure 3A, Table 1; Tables S5 and S6, online supplementary material).

Assessing parent-brood proximities (i.e., distance from chicks to their nearest parent) revealed that chicks who were deserted by their mother were consistently more isolated than chicks cared for by both parents (Figure 3B, Table 1; Tables S5 and S6, online supplementary material) indicating that during biparental care, if males are distant from chicks, females bridge the gap, however in families where females desert, males do not (or cannot) compensate.
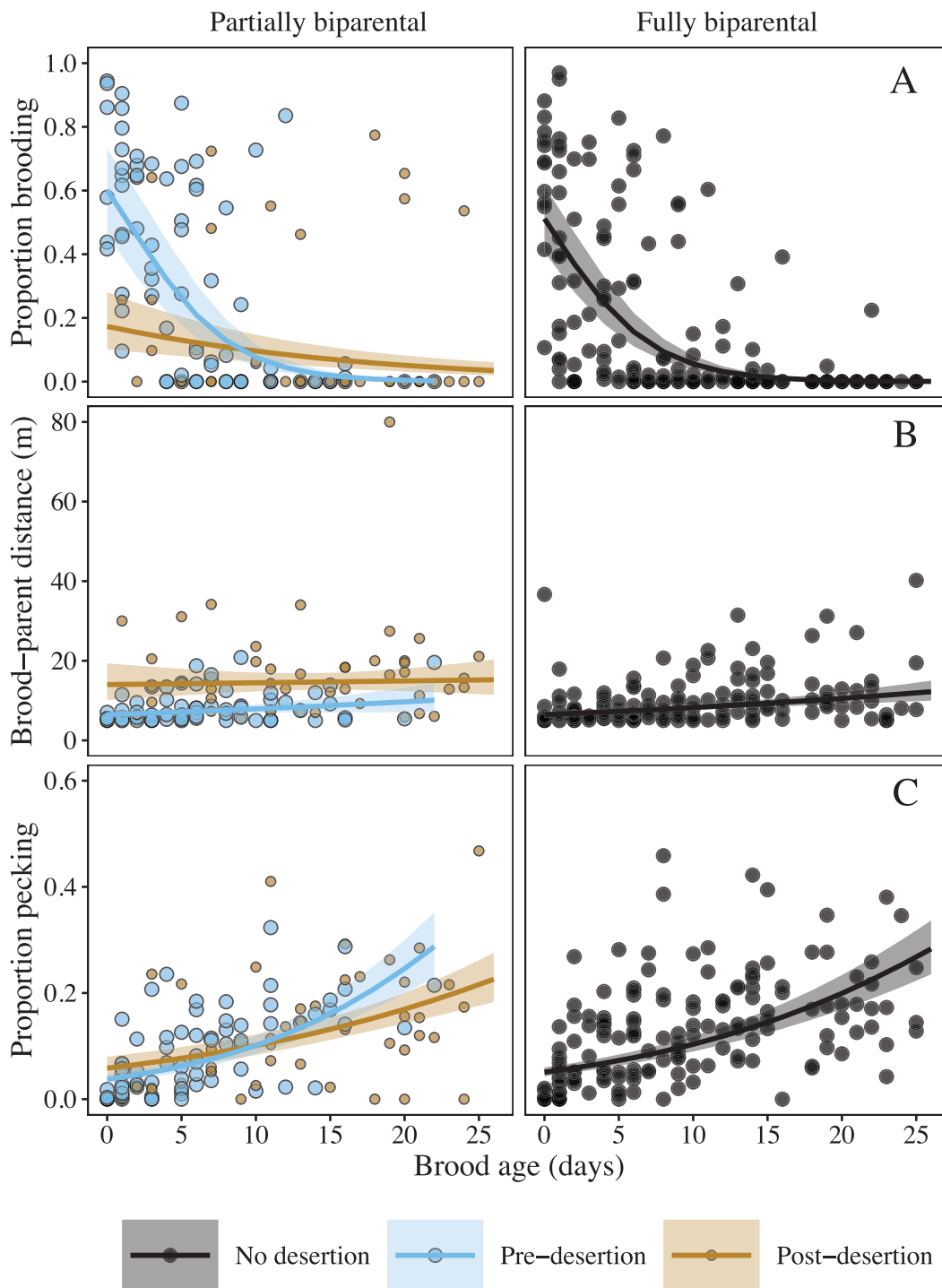
Figure 3. Behavioral dynamics of brood desertion. The relationship between the age of broods and (A) the proportion of observations chicks were engaged in brooding, (B) mean distance in meters between parents and broods and (C) the proportion of observations chicks were engaged in foraging (substrate pecking). Data shown for partially biparental families before female desertion (Pre-desertion; blue), after female desertion (Post-desertion; yellow) and for fully biparental families where no parent deserted (No desertion; black). Lines show predictions (± 95% CI) from maximal models. The intensity of point shading indicates point overlap.

Chicks increased pecking as they grew older at a slightly faster rate in partially biparental families pre-desertion and at the slowest rate post-desertion (Figure 3C, Table 1; Tables S5 and S6, online supplementary material), indicating that feeding rates of chicks increased slightly faster in families before desertion but that this rate is not maintained after desertion.

Discussion

Our work examines the costs and benefits of parental care and brood desertion in a wild population wherein desertion and sequential mating produce multiple care patterns within the same population (Székely et al., 1996). Our results show that almost half of broods were deserted by one parent and

Table 1. Behavioural dynamics of brood desertion in Kentish plovers.

Response	Model rank	Site	Year	Care type	Brood age	Observation time (hrs)	Date	N chicks	Care type × brood age	ΔAICc
Proportion brooding	**1**			+	+	+		+	+	0.000
Average brood-parent distance (ln m)	**1**		+	+	+					0.000
	4			+	+					1.448
Proportion pecking	**1**		+	+	+	+			+	0.000

Note. Best performing models predicting the behavior of chicks. For all behaviors, the model with the lowest AICc across all possible models is shown (model rank 1). If the best minimal model was a more parsimonious model within two AICc of model rank 1 (ΔAICc < 2), this is also shown. Best minimal models are in bold. A + indicates that a variable was retained in the model. Care type represents a 3-level factor (No desertion, Pre-desertion, and Post-desertion). For full AICc model comparisons and best minimal model results see Tables S5 and S6, online supplementary material.
Note. AICc = Akaike Information Criterion corrected

the majority of these desertions were by females. Our results confirm experimental research in the same population suggesting that females benefit from desertion via an increased probability of remating (Székely et al., 1999). However, contrary to previous experimental research, our results indicate that females do not pay a cost of desertion in terms of the growth or survival of offspring (Székely & Cuthill, 1999), indicating that under natural conditions females may tailor their desertion strategies to minimize costs to their brood, whilst capitalizing on mating opportunities

We show that females may benefit from desertion by remating within the same season while their male partner cares for the abandoned brood, supporting recent indications in multiple populations of plover species (*Charadrius* spp.) (Halimubieke et al., 2019, 2020). Such strategies can substantially increase reproductive success, for example sequentially polyandrous female Tengmalm's owls (*Aegolius funereus*) that abandon their brood—leaving it to be cared for by their male partners while they remate with another male—raise 73% more fledglings than females that do not desert (Korpimäki et al., 2011). While not all females that deserted in our study remated, it is also possible that there are additional benefits associated with desertion, such as saving resources for subsequent breeding seasons or otherwise allowing females to optimize preparation for, or the timing of, migration (Harrod & Mumme, 2021; Kelly & Kennedy, 1993). Such alternative benefits of desertion may become more important toward the end of the breeding season when the remaining time window of conditions suitable to raise an additional second brood become more limited. The benefits of continued uniparental care are likely bolstered for male Kentish plovers by low rates of extra-pair paternity and high paternity assurance (Maher et al., 2017). Similarly, the bias toward female versus male desertion is likely facilitated by strongly male-biased adult sex ratios, providing higher remating opportunities for females than for males (Grant & Grant, 2019; Liker et al., 2013). In the studied population, estimates of adult sex ratios indicate over six times more males than females (Kosztolányi et al., 2011), and remating times for experimentally widowed males were estimated to be almost five times longer than females (Székely et al., 1999). This strong adult-sex ratio bias may explain the relatively low frequency of male desertion. Only 8 males deserted of the 121 families studied and we did not observe any remating among these males, suggesting that caring males face relatively low opportunity costs of not deserting due to low remating probabilities. Changes in the proportion of males ready to breed (i.e., the operational sex ratio) may also be one potential explanation for the identified

seasonal decline in female rebreeding probabilities—if an increase in uniparental caring males as the season progresses reduces the male bias in the operational sex ratio. Given deserting Kentish plovers often disperse large distances before remating (Székely et al., 1999; Székely & Lessells, 1993), our results likely underestimate the benefit of desertion, since several deserting parents may have dispersed and remated outside of our study site. Since females often disperse further than males, the underestimation of remating benefits is therefore likely higher for females relative to males (Székely et al., 1999; Székely & Lessells, 1993). Together these results support suggestions that male-biased adult sex ratios are associated with a bias toward male care in birds (Liker et al., 2013) and are consistent with theoretical expectations (Fromhage & Jennions, 2016; Kokko & Jennions, 2008; Székely et al., 2014).

The advantages of desertion also depend on the behavior of the abandoned partner and the deserted offspring. We, therefore, compared the behavior of parents and their offspring before female desertion, after female desertion, and in families that remained biparental. Biparental care should be favored when the fitness benefits to both parents exceed the costs caused by missed future breeding opportunities (Pilakouta et al., 2018). For example, in the burying beetle *Nicrophorus vespilloides*, care by both parents operates to synergistically increase offspring growth and survival compared to uniparental families (Pilakouta et al., 2018) and in the related *Nicrophorus orbicollis*, biparental families raise more offspring than uniparental families (Benowitz & Moore, 2016). However, low costs of desertion may arise if abandoned parents can effectively provide parental care alone (Houston et al., 2005). When abandoned parents can fully compensate for their absent partner, offspring raised in uniparental families may fare equally well, or even better, when compared to biparental families (Griggio & Pilastro, 2007; Houston et al., 2005; McNamara et al., 2003; Royle et al., 2002). In such cases, deserting strategies may incur modest costs but accrue large benefits in terms of remating, thus reducing the frequency of biparental care.

Our results reveal a complex pattern of male compensation for their absent partner, where males at least partially compensated for the lack of female care in terms of brooding, supporting patterns of compensation predicted from sexual conflict theory (Houston & Davies, 1985; McNamara et al., 2003), as well as previous empirical work in birds, amphibians, fish and insects that has indicated abandoned parents increase their investment in care (Cantarero et al., 2019; Harrison et al., 2009; Hunt & Simmons, 2002; Lavery &

Reebs, 1994; Osorno & Székely, 2004; Ringler et al., 2015; Royle et al., 2002). Specifically, we show that deserted males on average maintain a higher frequency of brooding across later brood ages compared to males in fully biparental families. However, the magnitude of this later stage compensation was overall low. Given the importance of brooding in terms of chick thermoregulation is largest within the earlier days of shorebird development when chicks are most thermally dependent (Beintema & Visser, 1989a), the benefit to chicks of this later stage brooding may be comparably low. However, when chicks were young, uniparental males appear unable to compensate for their absent partner. Behavioral compensation by males thus changed over brood care and when chicks were older uniparental males over-compensated and deserted chicks received more brooding than biparental broods. These results provide similar patterns to those in hooded warblers (*Setophaga citrina*), where females who were deserted by their male partners compensated for nestling provisioning rates differentially based on chick age (Harrod & Mumme, 2021). This work on hooded warblers suggested that females were unable to compensate for the absence of males when chicks were young as a result of time constraints imposed by need to brood young offspring. However, when chicks were older and brooding demands are lower, females were able to over-compensate and feed older chicks at a higher rate (Harrod & Mumme, 2021). In Kentish plovers, parents do not feed their chicks, however in shorebirds brooding offspring may incur thermoregulatory costs to parents and can trade off with both chick and parental foraging (Beintema & Visser, 1989a; Walters, 1984). It may be that the costs associated with maintaining the high rates of brooding we observed in biparental families when chicks are young are prohibitively high for uniparental males. However, overcompensation at later stages of brood care, when overall brooding demands are lower, may be more attainable. While the level of compensation by males was overall low, future research should aim to assess to potential costs of uniparental care to males, such as via reductions in male body condition when compared to males from biparental families.

Despite evidence for male compensation in terms of brooding, we show that deserted chicks remained more isolated from parents than chicks cared for biparentally. These results parallel previous work in snowy plovers (*Charadrius nivosus*) that indicate distances between chicks and parents increase with age but are not related to fledging success (Colwell et al., 2007). Moreover, our behavior analyses indicate that the rate of increase in chick feeding rates was fastest in families before desertion, whereas these rates of increase in chick feeding were lower in families after female desertion. While observed differences in the rate of change in feeding rates is relatively minor, such differences in feeding behavior may indicate a possible mechanism underlying female desertion. For example, faster increases in chick feeding rates may reflect suitable conditions to re-nest with another partner or for male parents to care alone for the brood. Females may therefore assess such suitable conditions to desert either directly from the environment or indirectly via chick feeding behavior. Together these results indicate a complex pattern of compensation, where male compensation for brooding is dependent on the age of chicks and males do not fully compensate in terms of their average proximity to chicks.

Despite only partial male compensation in terms of behavioral rates of care, by comparing between partially and fully biparental families, we demonstrate no costs of desertion to females in terms of chick growth or the number of fledglings produced, corroborating findings in other avian species including the closely related snowy plover (Harrod & Mumme, 2021; Kupán et al., 2021). However, it remains possible that costs of desertions may become apparent at later development stages (e.g., after fledging), for example, if chicks learn foraging or other skills better with both parents present, or are unable to learn sex-specific skills from the deserting parent. Our results contrast with previous studies in other species that indicate costs of desertion, such as via reduced effectiveness of uniparental offspring defence (Lehtonen et al., 2011; Zimmermann et al., 2021). Moreover, experimentally enforced desertion in Kentish plovers immediately after hatching of the eggs, similarly suggest that potentially high costs of desertion may arise via reduced effectiveness of uniparental offspring brooding and/or defence (Székely & Cuthill, 1999; Székely & Williams, 1995). While these experimental manipulations provide crucial insights into the mechanisms underlying biparental care, they are limited in their ability to shed light on the costs and benefits of naturally occurring parental strategies.

The difference in costs between the previous experimental work and our results here suggest that under natural conditions, females target desertion to those situations in which costs to their current brood are minimized and uniparental brood care is likely to be successful, such as (a) when local predation pressure and conflict with conspecifics are low—and the greater isolation of deserted chicks is less costly (Huang et al., 2013; Kosztolányi et al., 2006)—and (b) where feeding rates of offspring are comparably high and male partners are behaviorally able to compensate for at least some of the lost care by their deserted partner. Previous research has suggested that reductions in rates of parental care, including via offspring desertion, may have negative consequences for population productivity (Dudeck et al., 2018; Holman & Kokko, 2013; Szentirmai et al., 2007). Our results suggest that the frequent female desertion in our population is unlikely to negatively impact population productivity. While our study identifies remating as the primary benefit of desertion, if second clutches do not provide hatched eggs or fledglings this may not translate into fitness benefits. However, a more recent multipopulational study across eight *Charadrius* species has shown that deserting parents, including both females and males, produce a higher number of hatched offspring within a breeding year when compared to parents that stay together, and indicates that the increased number of hatchlings is at least partly driven by the hatching success of second clutches (Halimubieke et al., 2020). This research across populations provides support for the idea that second-breeding attempts may ultimately contribute to a higher total number of offspring produced for deserting parents (Halimubieke et al., 2020). In contrast, however, Kupán et al. (2021) demonstrated in a comparison between snowy plover females from 9 partially- and 5 fully-biparental families, that while the maximum number of fledglings produced by deserting females was higher, on average deserting females did not produce significantly more fledglings. The latter result indicates that repeat breeding by deserting females may not always translate into more fledglings. However, Kupán et al. (2021) also reported that female desertion was closely associated with chick mortality and a reduction in brood size in families before desertion. They suggest that the reasons for

brood desertion in snowy plovers may be twofold: (a) females may desert early in the season to increase their reproductive success by rebreeding later in the season, and (b) females may desert poorly performing families when chick mortality significantly reduces that the value of the brood. In contrast, we found no evidence for higher chick mortality before desertion in the Kentish plover. Future research should ultimately investigate whether the total number of recruited offspring differs between families with and without desertion, ideally, using several wild populations in which desertion is part of the natural care pattern.

In conclusion, our study helps further our understanding of the maintenance of biparental care and the fragmentation of families in nature by providing investigation of the costs, benefits, and behavioral mechanisms underlying variation in offspring desertion in a wild population. By investigating a species that exhibits a flexible parental care system, our results reveal that female brood desertion is favored by strong benefits of remating and we identified no costs of desertion in terms of brood growth and survival. Our results support previous indications that such parental care decisions are dynamic over the course of a reproductive period (Balme et al., 2017; Eldegard & Sonerud, 2009; Kosztolányi et al., 2006; Székely et al., 1999) and suggest that females tune their desertion behavior and desert more frequently early in the season, potentially when there is sufficient time for individuals to remate and a higher probability to raise another successful brood. This time-dependent desertion, and partial, rather than full compensation by the abandoned male, may contribute to the co-existence of both biparental and uniparental care strategies in the same population (Halimubieke et al., 2020; Houston & Davies, 1985).

Supplementary material

Supplementary material is available online at *Evolution* (https://academic.oup.com/evolut/qpac020).

Data availability

Associated data is available on Dryad at https://doi.org/10.5061/dryad.gf1vhhmt1 (McDonald et al., 2022).

Author contributions

G.C.M., A.K., I.C.C., and T.S. conceived the study. A.K. and T.S. collected the data. G.C.M. and A.K. analyzed the data. G.C.M. wrote the manuscript, with input from all authors.

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