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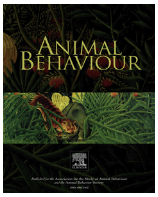

Sex roles in parental care in a species with precocial offspring and frequent brood desertion

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Biparental care can be favoured when offspring care by both parents provides a stronger fitness incentive to parents than deserting their offspring. In species with precocial offspring, the burden of care is expected to be comparatively low, facilitating desertion by one parent and uniparental care by the abandoned partner. However, care patterns can vary widely between and within precocial species, with some parents deserting their offspring, while other families remain biparental. Understanding the details of the care delivered by males and females in families before desertion is important to provide insight into the mechanisms that influence the stability of biparental care. Here we used detailed behavioural observations from the brood care period to investigate the balance of care between male and female parents in a well-studied precocial shorebird, the Kentish plover, *Charadrius alexandrinus*, both within families where females subsequently deserted and within families that remained biparental until the offspring were independent. We found that both males and females expressed all care behaviours (brooding, vigilance and brood defence) characteristic of precocial species, and we utilized quantitative mutual entropy analyses to show that the division of parental labour (i.e. care task specialization) was unrelated to the maintenance of biparental care. We also found that while males and females provided broadly similar levels of care, there were subtle differences: females typically delivered slightly more care than males across offspring development, suggesting that sex differences in self-maintenance may underlie sex differences in care. Together our results indicate minor differences in the care patterns of males and females, consistent with theoretical predictions that the division of labour should be limited in populations with frequent desertion and uniparental care.

Parental care can benefit parents by increasing the condition, survival and subsequent reproductive success of their offspring (Clutton-Brock, 1991; Royle et al., 2012). However, caring for offspring can be costly in terms of time and energy, or because of increases in parental predation risk, which may be traded against future reproductive success (Alonso-Alvarez & Velando, 2012; Li & Jackson, 2003; Santos & Nakagawa, 2012). Importantly, while both parents can benefit from either parent's investment in care, parents pay the costs of caring independently (Houston et al., 2005; Lessells, 2012; Székely, 2014). Biparental care thus represents a form of cooperation and provides scope for conflict between parents, where each parent may benefit by having their partner invest more in care while reducing their own level of care, potentially even deserting their offspring and leaving all care to their partner (Harrod & Mumme, 2021; Houston et al., 2005; Korpimäki et al., 2011; Lessells, 2012; McDonald et al., 2023; Székely, 2014). Understanding patterns of desertion is central to understanding the diversity of uniparental and biparental care in nature and has key consequences for our understanding of patterns of population productivity, given parental care can impact offspring survival (Dudeck et al., 2018; Holman & Kokko, 2013; Székely, 2014; Székely et al., 1996).

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Biparental care may be maintained by natural selection when care by both parents provides a stronger fitness benefit to parents than could be attained by deserting their offspring and instead investing in greater self-maintenance or seeking new reproductive opportunities (Alonso-Alvarez & Velando, 2012; Dall et al., 2004; Houston et al., 2005). For example, biparental care is expected to be more common in avian species with altricial young, where the high demands of raising offspring make it challenging for single parents to care for offspring successfully alone (Long et al., 2022; Thomas & Székely, 2005). Additionally, biparental care should be favoured if care by both parents provides synergistic effects, leading to greater benefits to offspring when both parents care together versus alone (Barta et al., 2014; Pilakouta et al., 2018). In such cases, the costs to parents of not caring may be larger than the benefits of abandoning offspring (e.g. to save resources for future breeding opportunities, Benowitz & Moore, 2016; Székely & Cuthill, 1999). Environmental conditions may also modulate the requirement for cooperative biparental care, where species in nutrient-poor environments or harsh climates are forced to cooperate to raise young effectively (Brown et al., 2010; Emlen, 1982; Vincze et al., 2017; Włodarczyk & Minias, 2015). In species with precocial offspring, however, the overall burden of parental care is typically expected to be reduced compared to species with altricial offspring, opening opportunities for one parent to desert (Thomas & Székely, 2005). For example, in several sex-role-reversed jacanas (family Jacanidae), males typically care for precocial young alone, while females desert to acquire future matings and provide limited or no posthatching care (Fresneau et al., 2021; Thomas et al., 2007). Despite this, however, observed patterns of care in both altricial and precocial species are highly diverse (Bulla et al., 2017; Clutton-Brock, 1991; Furness & Capellini, 2019; Gonzalez-Voyer et al., 2022; Goymann et al., 2016; Gross & Sargent, 1985; Long et al., 2022). For example, precocial swans and geese show biparental care irrespective of whether they breed in harsh or temperate conditions (Włodarczyk & Minias, 2015). Conversely, in other birds, insects, amphibians and fishes, including those with altricial young, parents may abandon their offspring and leave their partner to care alone (Ahnesjo, 1992; Amat et al., 1999; Beissinger & Snyder, 1987; Delia et al., 2017; Griggio & Pilastro, 2007; Harrod & Mumme, 2021; Keenleyside, 1983; Osorno & Székely, 2004; Szentirmai et al., 2007; Ward et al., 2009). Moreover, patterns of care can vary even within the same population, such as in some shorebirds (Székely et al., 2024), including the killdeer, *Charadrius vociferous* (Johnson et al., 2006) and the snowy plover, *Charadrius nivosus* (Carmona-Isunza et al., 2017; Cruz-López et al., 2017; Halimubieke et al., 2019), where families within the same population may be deserted by either males or females, or remain biparental until offspring fledge.

How much each parent cares for offspring in biparental families is expected to be subject to behavioural negotiations, where each parent may monitor the care of its partner and adjust levels of care accordingly (Johnstone et al., 2014; Kavelaars et al., 2019; Lessells & McNamara, 2012; McNamara et al., 2002, 2003). However, the specifics of how these interactions play out in nature are not known in detail (Székely, 2014; van Dijk & Székely, 2008). Understanding the details of the parental care delivered by males and females before desertion can provide insights into the patterns of negotiation and cooperation that influence the stability of biparental care. For example, in the rock sparrow, *Petronia petronia*, both parents initially care for their nestlings together; however, approximately 25% of males and 10% of females desert their broods before fledging, leaving all subsequent care to the deserted partner (Baldan & Griggio, 2019; Griggio et al., 2005). Importantly, in the rock sparrow pairs in which no desertion occurs, parents alternate and synchronize their nest visits more than pairs in which one parent deserts (Baldan & Griggio, 2019), consistent with suggestions that effective coordination of parental duties increases the stability and duration of biparental care (Bebbington & Groothuis, 2023; Johnstone & Hinde, 2006; Johnstone & Savage, 2019). Despite the utility of studies in systems with multiple care patterns (i.e. including families where one parent deserts and families where no parent deserts), relatively few studies have comprehensively studied the balance of care between males and females across families with and without desertion (van Dijk et al., 2012). Moreover, existing studies have typically focused on single care traits such as nest attendance or nestling provisioning (e.g. Eurasian penduline tits, *Remiz pendulinus*, van Dijk et al., 2012; rock sparrows, Griggio & Pilastro, 2007; although see snail kites, *Rostrhamus sociabilis*, Beissinger, 1987).

However, care often requires multiple different behaviours, including provisioning, defence from predators and sheltering offspring from environmental extremes (Barta et al., 2014; Itzkowitz et al., 2001; Royle et al., 2012). Importantly, when the costs of investing in different care behaviours are nonadditive (e.g. reduced parental food intake due to chick brooding may increase a parent's injury or mortality risk when aggressively defending offspring) or when costs of care behaviours are sex specific (e.g. the smaller sex pays a higher cost in offspring defence), specialization of males and females to perform specific care duties may be favoured (Barta et al., 2014). When parents within a family specialize on different care tasks this may give rise to a division of labour in parental care (i.e. within-individual consistency in which care tasks are performed but variability between parents in which tasks they perform, Kreider et al., 2022; Ulrich et al., 2018). A division of labour may stabilize biparental care because male and female care become complementary, providing synergistic benefits to offspring and reducing the relative effectiveness of uniparental care (Barta et al., 2014; Henshaw et al., 2019). Some level of sex-specific specialization in parental care has been identified in a variety of species, including insects, birds and fish (Barta et al., 2014; Emlen & Wrege, 2004; Iserbyt et al., 2017; Itzkowitz et al., 2001; Trumbo, 2012; Walling et al., 2008; Włodarczyk & Minias, 2015). However, the extent to which patterns of specialization facilitate the maintenance of biparental care remains unknown. Moreover, while quantitative measures of specialization and division of labour are common in the context of group living in social insects (Jeanson et al., 2007; Kreider et al., 2022), these measures have rarely been applied in the context of biparental care. A key first step is therefore to investigate the extent to which variation in patterns of parental specialization exists among families and whether these patterns are associated with desertion and the stability of families.

Here we investigated the balance of parental care between males and females in a wild population of a small shorebird, the Kentish plover, *Charadrius alexandrinus*, which typically breeds along the shores of salt-pans, saline lakes and coastal habitats (Fraga & Amat, 1996; McDonald et al., 2020, 2022). Male and female Kentish plover parents both incubate their clutch of eggs (AlRashidi et al., 2011; Székely, 2019). However, after incubation, brood care may be conducted by both parents or alternatively one parent may desert the brood and leave its partner to conduct all brood care alone, resulting in uniparental and biparental care within the same population (Székely & Cuthill, 1999; Székely et al., 2006). Kentish plover chicks are self-feeding and care by parents includes identifying threats including predators and conspecifics, defending offspring from those threats, leading offspring to safer and more suitable feeding territories, and performing essential thermoregulation of chicks by brooding (Fraga & Amat, 1996; Kosztolányi et al., 2007; McDonald et al., 2023; Székely & Cuthill, 1999). We previously showed that almost half of Kentish plover families were deserted by one parent before fledging and that the majority of these desertions were by females (McDonald et al., 2023).

Moreover, research has indicated that deserting Kentish plover parents frequently remate with a new partner, particularly early in a breeding season when there may be sufficient time remaining to produce a new brood (Amat et al., 1999; McDonald et al., 2023; Székely & Lessells, 1993; Székely & Williams, 1994). Such desertion may be favoured due to increased offspring production as result of these subsequent breeding attempts (McDonald et al., 2023; Székely et al., 1999). However, despite this, the absence of desertion in approximately 50% of broods, and the observation that both deserting and nondeserting female strategies can occur widely throughout a breeding season (McDonald et al., 2023), suggests that other factors may influence the probability that a parent abandons its partner and deserts its brood. As a result, the Kentish plover system provides an excellent opportunity to investigate how the balance of parental care delivered by males and females varies across families before female desertion versus families that stay together, and therefore to shed light on the behavioural mechanisms influencing the stability of biparental care.

We first characterized the care budgets of male and female parents across three key care behavioural axes, brooding, defence and vigilance, within families that remained biparental until the chicks fledged (fully biparental families) and within families in which females subsequently deserted their offspring (partially biparental families). We then utilized quantitative measures of specialization to assess the potential role of the division of labour in facilitating the maintenance of biparental care. If a division of labour (e.g. males specialize in offspring defence and females in offspring brooding) facilitates the maintenance of biparental care, we would expect stronger division of labour across care behaviours within families that remained together (fully biparental) compared to families that subsequently broke apart (partially biparental). Second, because patterns of care may be dynamic across offspring development, we assessed how the balance of care between males and females in partially and fully biparental families varied over brood development, while controlling for the potential roles of seasonality, time of day and brood size in shaping rates of care. If reduced coordination and an imbalance in average care rates influences desertion, we would expect stronger sex differences in the frequency of care behaviours among partially biparental families compared to fully biparental families. Finally, we assessed the frequency that male and female parents spent feeding themselves rather than caring for young to explore whether differences in parental self-maintenance may give rise to any sex differences in care rates.

METHODS

Study Population and Patterns of Parental Care

We studied Kentish plover families in their natural habitats surrounding Tuzla lake in Turkey between 1996 and 1999 (Székely & Cuthill, 1999, 2000; Székely et al., 1999). We utilized data from 66 previously studied families for which detailed behavioural observations on parental care were available and where families either were biparental over the whole brood care period or became uniparental at a variable time during brood care after the female parent deserted (see McDonald et al., 2023). As male desertion is rare in this population (McDonald et al., 2023), we focused only on female desertion and the current data set of 66 families included 28 families in which females deserted their offspring before fledging (partially biparental, Fig. A1) and 38 families in which neither parent deserted (fully biparental, Fig. A1).

All families were studied near Tuzla village, and we followed previous studies by defining two sites within our study area: site A which was close to Tuzla village and site B which was more distant from the village (McDonald et al., 2023; Székely & Cuthill, 1999). Most families were identified at the nesting stage ($N = 54$) and their hatching date was determined by repeat visits to the nest every 1–2 days over the last few days of incubation (Székely & Cuthill, 1999). A subset of families ($N = 12$) were identified after hatching, and the age of the brood was estimated from tarsus length measurements via previously defined linear growth rates of chicks (Székely & Cuthill, 1999). We aimed to monitor each family to determine the parental status and number of chicks present (‘brood records’) for up to 25 days after hatching (approximate age of chick fledging, Dos Remedios et al., 2015; Székely & Lessells, 1993). To do so, we searched for families every 2–3 days; we recorded the care type (uniparental male, uniparental female or biparental) of the family and the number of chicks present (Székely & Cuthill, 1999, 2000; Székely et al., 1999; Székely & Kosztolányi, 2006). Across all 66 families we obtained 778 brood records, with a mean (±SD) of 11.8 ± 3.8 records per family.

Each family was then scored as partially or fully biparental based on the sequence of brood records as in McDonald et al. (2023; for similar categorizations also see Beissinger, 1987; Beissinger & Snyder, 1987; Harrod & Mumme, 2021; Kupán et al., 2021). Partially biparental families were those families where the female deserted the brood before 25 days of brood care (i.e. before approximate fledging age, Fig. A1). Desertion was determined by two or more consecutive uniparental care recordings (e.g. two male-only care recordings in a row) with no further observations that indicated care by the female parent. For desertion to occur before 25 days, the first of these consecutive uniparental observations must have occurred before day 25 of brood care. The day of desertion was determined as the midpoint (rounded upwards to the nearest integer day number) between the dates of the last biparental and first uniparental record. For families with no biparental observations, the midpoint between the hatch date (day 0) and the first uniparental record was used as the desertion day. Among partially biparental families, females deserted at a mean brood age (±SD) of 10.8 ± 6.95 days. Fully biparental families were those families in which no desertion was recorded before 25 days of brood care (Fig. A1). All studied families had a minimum of two brood records and at least one record prior to 25 days.

Parental Behaviour Observations

For each family we conducted detailed behavioural observations during a subset of brood records. Because our aim was to understand patterns of care prior to desertion, behavioural observations that occurred after female desertion (postdesertion, Fig. A1) were excluded from further analyses. In two of our 66 families, observations only occurred after desertion and so our final data set included 64 families (26 partially biparental families where females deserted and 38 fully biparental families).

Our behavioural observation data across the final 64 families comprised 231 observations each of 1 h, with a mean (±SD) of 3.6 ± 1.70 behavioural observations per family. For each 1 h observation we recorded behaviour as described in McDonald et al. (2023). Briefly, during each observation we scan sampled the behaviour of all present parents every 30 s (120 scans per 1 h observation, Kosztolányi et al., 2006; Székely et al., 1999; Székely & Cuthill, 1999, 2000). If a parent was absent from the brood or obscured from view, their behaviour was not scored.

We categorized key parental behaviours into three parental care categories: brooding, defence and vigilance. Brooding by parents is key for shorebird chick thermoregulation and may include warming the chicks in cold weather and shading them in hot weather (Visser & Ricklefs, 1994). Brooding thus included all cases where parents brooded or shaded their chicks (McDonald et al., 2023). Defence included all cases where parents aggressively defended their territories or chicks through fighting and/or chasing of conspecifics and heterospecifics (Fraga & Amat, 1996), as well as specific brood defence behaviours such as injury feigning behaviours that function to distract potential predators from chicks (de Framond et al., 2022; Simmons, 1951). Vigilance included all cases where parents extended their neck upwards, which was associated with scanning the environment. In addition, we used substrate pecking by parents as an indicator of the time spent by parents feeding themselves (McDonald et al., 2023). For a full list of all behaviours recorded during observations see Table A1.

Specialization and the Division of Labour

If the division of labour impacts on the stability of biparental care, we predict there to be stronger specialization of parents into different care tasks within families that remain together (fully biparental) compared to families that subsequently break apart (partially biparental; Fig. 1a–d). There are at least three mechanisms in which a greater division of labour in fully versus partially biparental families may be expressed. First, (1) task specialization in fully biparental families may be sex specific, i.e. males specialize in performing the same subset of tasks across different families while females consistently perform a different subset of tasks across families (Fig. 1a). Alternatively, (2) parents within fully biparental families may specialize in performing different tasks, but the tasks that each sex performs may differ between families (Fig. 1b). In this case, division of labour may be high in fully biparental families, but the tasks that individual males and females specialize on will differ between families (Fig. 1b). For both (1) and (2) we expect a comparably lower division of labour in partially biparental families, such that the tasks performed by parents within a pair largely overlap, either because parents in these families are not specialized (Fig. 1c) or because parents specialize on the same care tasks (Fig. 1d). Third, (3) it is possible that the level of female specialization is unimportant and instead patterns of female desertion may relate only to male specialization. For example, females may be less likely to desert when male partners are more specialized in their care repertoire and therefore more limited in the types of care they express, but more likely to desert when their male partners perform a wider range of care behaviours. For (3) only the level of male specialization will be expected to differ between fully and partially biparental families (i.e. higher male specialization in fully biparental families).

To investigate mechanisms (1) and (2) we used normalized mutual entropy (NME) (Gorelick et al., 2004; Jeanson et al., 2007) to systematically compare the level of division of labour within fully and partially biparental families. NME calculated for each male and female pair measures the degree to which parents are specialists and the extent to which they specialize on different tasks. To calculate NME, we constructed a separate 2 × 3 matrix for each

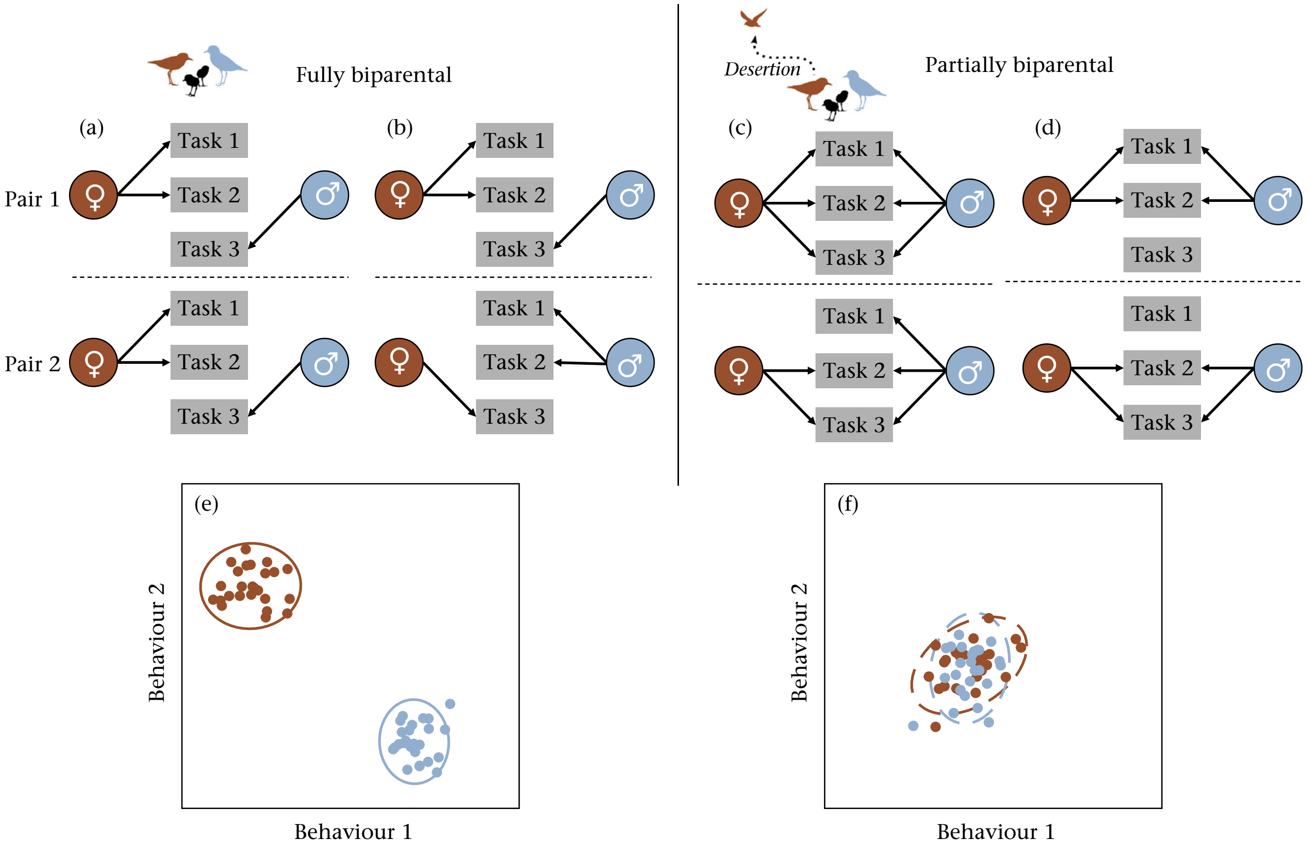

Figure 1. Division of labour in parental care. (a-d) Hypothetical patterns of different levels of division of labour across three parental care behaviours (tasks 1, 2 and 3) for two breeding pairs (pair 1 and 2) of male (blue) and female (brown) Kentish plovers. In fully biparental families where no desertion occurs, parents show a division of labour in parental care where either (a) the sexes specialize in different tasks (i.e. sex-specific division of labour) or (b) parents divide tasks within pairs but the sex performing each task differs between pairs. In partially biparental families where females subsequently desert their offspring, parents show little or no division of labour and the parental care patterns of males and females within pairs largely overlap either because (c) parents show no specialization or (d) males and females within pairs are specialized on the same tasks. (e, f) Alternative representation of hypothetical patterns of a sex-specific division of labour (i.e. Fig. 1a, c) in a population of Kentish plovers, where parents can perform two parental care behaviours (behaviour 1 and 2). (e) In fully biparental families, males (blue) and females (brown) tend to specialize in performing different tasks across families (i.e. males specialize in performing the same care behaviour across different families while females consistently perform a different care behaviour across families). In contrast (f) in partially biparental families where females subsequently desert their offspring, males and females largely overlap indicating no consistent sex-specific specialization across families.

observation of a given family where columns correspond to the sexes and rows to the three care behaviours (i.e. brooding, defence and vigilance). The counts within the matrix represent the number of scan samples in which each parent performed the given care task. We included only those 1 h observations in which both parents were present during observations so that all observations of males and females within a pair were matched for the stage of brood development (i.e. 17 of the 231 observations where only one parent was observed with the brood were excluded, leaving 214 observations over 62 families). In families that were observed multiple times, we summed these matrices so we had one 2 × 3 matrix for each pair which represents the pooled counts of each care behaviour. To avoid infinite values in the calculation of NME, caused by cells with zero counts, we added a value of one to all cells. Each matrix was then normalized so that all cells summed to one. Calculation of the mutual entropy over the joint distribution of parents (X) and care tasks (Y) across each cell in the matrix was done as described by Gorelick et al. (2004). This involves first calculating mutual entropy as $I(X,Y) = \sum_{x\in X, y\in Y} p(x,y)\log\left[\frac{p(x,y)}{p(x)p(y)}\right]$, where $p(x,y)$ is the proportion a given individual performs a given task and $p(x)$ and $p(y)$ are the row and column totals of the 2 × 3 matrix, before dividing by the square root of the product of Shannon's indexes (H) for both parents and all three tasks, as $\mathrm{NME} = I(X,Y)\,/\sqrt{H(X)H(Y)}$. The final NME measure ranges from zero to one where a value of zero represents no division of labour. We then used a linear model to compare NME between partially and fully biparental families, where NME was arcsine square-root transformed and explanatory variables included care type (partially and fully biparental families) as a two-level factor, the Julian hatch date of the clutch, a two-level factor for the site of brood care and a four-level factor for year.

Importantly, while calculating NME is an essential step in determining the extent of division of labour across partially and fully biparental families, it is insufficient alone to distinguish between mechanisms (1) and (2) above. For example, a higher NME in fully biparental families cannot identify whether task division is consistent across families (Fig. 1a) or whether the way tasks are divided between males and females varies between families (Fig. 1b). Therefore, we also visualized the behavioural composition of parents across all three care behaviours in two dimensions using nonmetric multidimensional scaling (NMDS) based on dissimilarities in the mean proportional frequency with which each parent performed each behaviour (Anderson, 2001; Warton et al., 2012). If the division of labour was stronger in fully versus partially biparental families and this was due to consistent sex differences in task specialization across fully biparental families (Fig. 1a), we would expect the centroids of males and females over the two nonmetric multidimensional scaling axes to be more different in fully versus partially biparental families (Fig. 1e, f). For NMDS, mean proportions for each behaviour for all males and females were calculated by first calculating the relative proportion for which each care behaviour (brooding, defence and vigilance) was observed in each 1 h observation, where the proportions of brooding, defence and vigilance summed to one in each sex. We again included only those observations in which both parents were present during observations. In one case, a male parent was present during observations but did not express any of the three care behaviours and this parent was given a proportion of zero for all three care behaviours. Mean proportions for each male and female were then calculated across all observations for each pair. We then calculated the pairwise distance matrix between all males and females based on these mean proportions using Bray–Curtis dissimilarities and visualized these distances in two dimensions using nonmetric multidimensional scaling ordination using the package ‘vegan’ (Oksanen et al., 2022) and R statistical software (version 4.2.1, R Core Team, 2022).

In principle, it is possible to statistically test whether the multivariate centroids across the three care behaviours differ between males and females from different care types using a permutational MANOVA (PerMANOVA). However, PerMANOVA may provide spurious results when there is heterogeneity in the multivariate dispersions among groups (Anderson & Walsh, 2013; Warton et al., 2012). We identified borderline nonsignificant differences in dispersion between the four sex × care type (fully biparental, partially biparental) groups (permuted dispersion tests: $F_{3,120} = 2.604$, $P_{perm} = 0.058$, 10 000 permutations), driven by a significantly larger multivariate dispersion in partially biparental families than in fully biparental families (permuted dispersion tests: $F_{1,122} = 8.173$, $P_{perm} = 0.004$, 10 000 permutations; Fig. 2a) and therefore we did not conduct PerMANOVA analyses.

Finally, if the above NME analyses excluded the role of mechanisms (1) and (2), it would still be possible that mechanism (3), i.e. male-only differences in specialization, influences the maintenance of biparental care. To investigate the role of mechanism (3), we calculated normalized entropy for males only, in both fully and partially biparental families. Male normalized entropy (H_M) was calculated using the pooled matrices for males used to calculate NME described above as $H_M = -\sum_{i=1}^{N} p_i \log p_i / \log N$, where p_i is the proportion of scans in which a male performed the i_{th} care task and $\log N$ represents the maximum entropy for N tasks. Male entropy ranges from zero to one, where zero represents maximum entropy (i.e. strong specialization). We then used a linear model to compare male entropy between partially and fully biparental families, where entropy was arcsine square-root transformed and explanatory variables included care type as a two-level factor, the Julian hatch date of the clutch, a two-level factor for the site of brood care and a four-level factor for year.

Dynamics in Care and Self-maintenance over Brood Development

To assess how relative differences in male and female care change throughout brood development, as well as whether differences in parental care may be due to greater investment in self-maintenance (i.e. feeding rates), we fitted generalized linear mixed-effects models (GLMMs) with binomial error structures for each behaviour (brooding, defence and vigilance and substrate pecking) separately. Each model included the proportion of scans in which each behaviour was observed at a given observation for males and females as a response variable. Proportions for each behaviour were calculated across all scans and all possible behaviours, not only among those scans in which the four response variables (i.e. brooding, defence and vigilance and substrate pecking) were observed, and therefore represent proportional frequencies across a parent's overall time budget. Explanatory variables included care type (partially and fully biparental families), sex (male or female), brood age in days, all two-way interactions (Care type * Sex, Brood age * Sex, Care type * Brood age) and the three-way interaction (Care type * Brood age * Sex) to explore how behavioural rates vary between the sexes, between families of different care types and over brood development, as well as differential changes in behaviour between the sexes and care types across brood development. In addition, each model included the Julian date of the observation, a linear and quadratic term for the time of the observation in decimal hours, a two-level factor for the site of brood care, a four-level factor for year and the brood size (i.e. number of chicks recorded as alive at the time of the observation, see McDonald et al., 2023 for further details). Models included a random effect for family identity to account for repeated measures

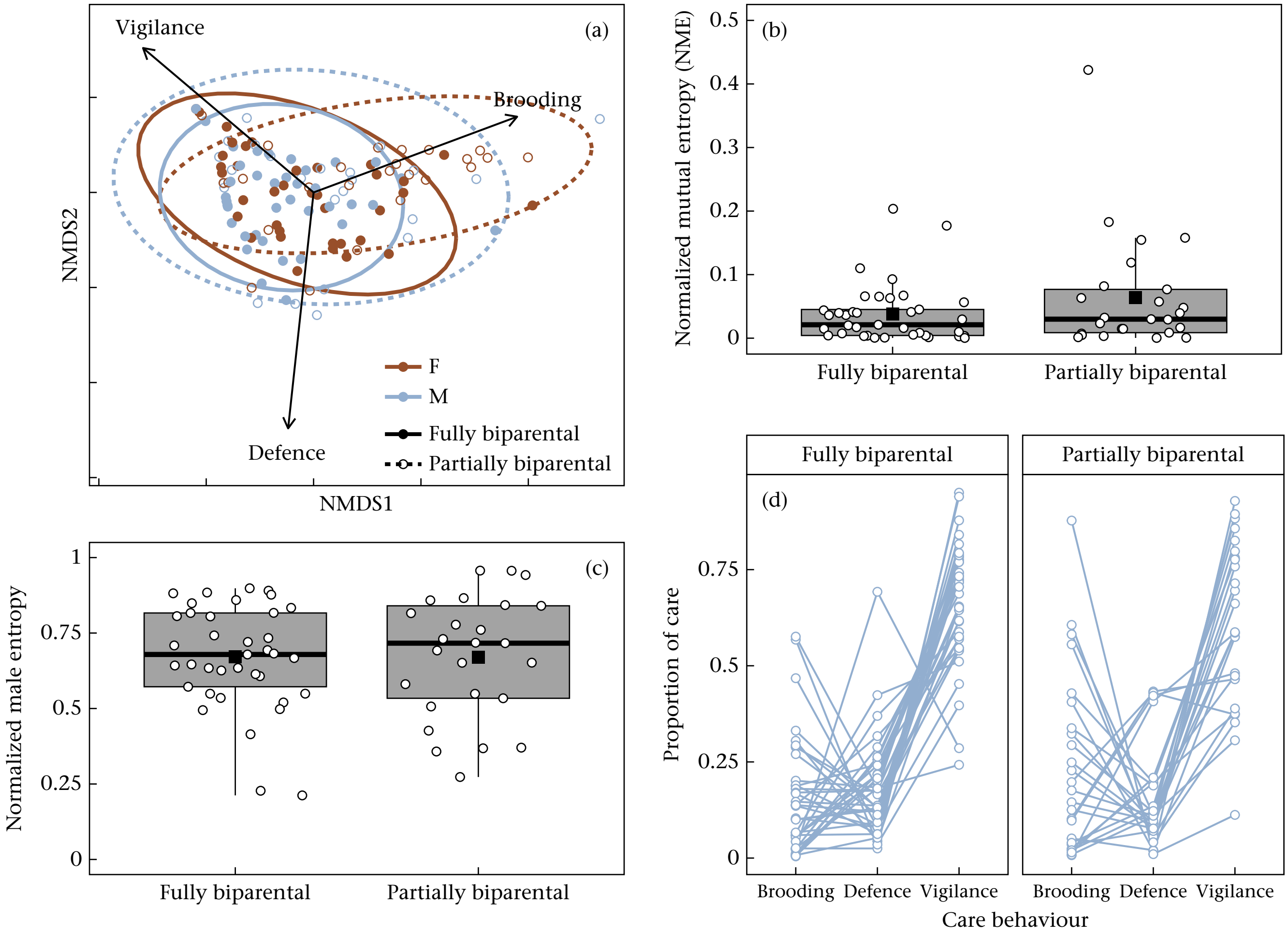

Figure 2. Sex differences in parental care. (a–d) Observed patterns of specialization in Kentish plover families in three parental care behaviour categories (brooding, defence and vigilance) for partially and fully biparental families. (a) Results of two-dimensional nonmetric multidimensional scaling (NMDS) of the mean proportion in which males and females were observed conducting the three parental care behaviour categories (stress = 0.032). Arrows indicate the direction in which each care behaviour maps on to the NMDS axes (NMDS1 and NMDS2). Ellipses show 95% confidence intervals of centroids. NMDS plots are dimensionless; shorter distances between pairs of points indicate that they are more similar in their proportional composition across the three parental care behaviour categories. Box plots show (b) the levels of normalized mutual entropy (NME) within pairs of males and females and (c) levels of specialization for males only (male entropy) for fully and partially biparental families. Box plots show the median (horizontal line), the mean (black squares), interquartile range (IQR) from the lower (Q1) and upper (Q3) quartiles. Whiskers extend from Q1 and Q3 to the lowest and largest values that lie within Q1-(1.5 × IQR) and Q3+(1.5 × IQR), respectively. White circles show the individual values. (d) The mean proportion of care performed by individual males for three parental care behaviour categories (brooding, defence and vigilance) for fully and partially biparental families.

of males and females from the same family over brood development. In addition, all models included an observation level random effect to account for overdispersion. As this analysis included the stage in brood development (i.e. brood age) as a variable, we included those cases where one parent was absent during observations for both fully biparental families and partially biparental families before desertion. We then used an Akaike information criterion (AIC) model comparison approach to determine the top model set (Grueber et al., 2011), where the top models are those with a ΔAICc (i.e. difference between a given model and the model with the lowest AICc) < 2. Throughout we treat the inclusion of a given parameter in top models as strong evidence for a relationship between parameter and response variable.

All GLMMs were constructed in R using the package 'glmmTMB' version 1.1.7 (Brooks et al., 2017).

Ethical Note

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 where T.S. was affiliated at the time of fieldwork.

Handling time during captures was minimized and birds were released in their natural habitat after ringing and taking measurements. Repeated brood visits and behavioural observations were done from a distance to avoid disturbing the birds, as our aim was to record their natural behaviour.

RESULTS

Sex-specific Care Rates and Specialization

Males and females performed all three care behaviours. Across observations, where both parents were present, males spent a median (interquartile range) of 12.2% (2.7–25.1%) of time brooding offspring, 13.2% (7.8–19.8%) on defence and 69.3% (58.4–80.2%) on vigilance, whereas females spent 20.9% (5.4–39.7%) of time brooding offspring, 11.8% (6.0–20.6%) on defence and 62.1% (50.7–77.5%) on vigilance.

Normalized mutual entropy (NME) was typically low for both fully and partially biparental families, indicating little division of

Table 1

Dynamics of male and female parental care and self-maintenance over brood age in families with different care types (fully biparental families versus partially biparental before desertion)

Response	Model rank	Site	Year	Time (h)	Time^2 (h)	Date	Brood size	Brood age (days)	Sex	Care type	Care type * Sex	Brood age * Sex	Care type * Brood age	Care type * Brood age * Sex	ΔAICc
Proportion brooding	1		+	−0.404	1.278	−0.270	0.452	−2.311	+						0.000
	2		+	**−0.408**	**1.290**		**0.489**	**−2.432**	+						**0.628**
Proportion defence	**1**		+	**−0.087**	**−0.206**			**0.560**		+			+		**0.000**
Proportion vigilance	1		+	0.319	−0.494		−0.144	0.244							0.000
	8			**0.315**	**−0.493**			**0.278**							**1.268**
Proportion pecking	1		+	−0.148	−0.138	−0.206		0.531	+						0.000
	2		+	**−0.264**		**−0.208**		**0.534**	+						**0.394**

Models are ranked by AICc (Akaike information criterion corrected for small sample size) and models with the lowest AICc are model rank 1. If the most parsimonious top model (i.e. model with fewest parameters and within 2 AICc of model rank 1) is not model 1, this is also shown. Most parsimonious top models are highlighted in bold. Date = Julian date of observation, brood size = number of chicks alive in the brood at the time of observation, site = the site of brood care and time = time of observation in decimal hours.

labour (mean NME ± SE; fully biparental = 0.038 ± 0.008, partially biparental = 0.064 ± 0.019; Fig. 2b). Moreover, NME did not differ significantly between fully and partially biparental families ($F_{1,55} = 1.466$, $P = 0.231$), indicating that neither a division of labour that was (1) consistent across families in which tasks each sex performed (Fig. 1a) nor a division of labour that was (2) inconsistent across families in which tasks each sex performed (Fig. 1b) was associated with the maintenance of biparental care. Similarly, NME was not significantly associated with the site of brood care ($F_{1,55} = 0.394$, $P = 0.533$), year ($F_{3,55} = 0.615$, $P = 0.609$) or Julian hatch date ($F_{1,55} = 0.002$, $P = 0.962$). Given that NME analyses indicated no differences in the division of labour between fully versus partially biparental families, we would not expect nonmetric multidimensional scaling (NMDS) to show a larger distance between the centroids of male and female care patterns in fully versus partially biparental families. Consistent with this, NMDS visualizations revealed a large overlap in care repertoires of males and females and similarly high levels of overlap between partially and fully biparental families (Fig. 2a).

Normalized male entropy was typically high in both fully and partially biparental families, indicating low levels of male task specialization (mean entropy ± SE; fully biparental = 0.671 ± 0.028, partially biparental = 0.670 ± 0.041; Fig. 2c) and did not differ significantly between males from fully and partially biparental families ($F_{1,55} = 0.184$, $P = 0.670$). This is because males in both care categories usually performed all three care behaviours (Fig. 2d). In addition, normalized male entropy was not significantly associated with the site of brood care ($F_{1,55} = 0.967$, $P = 0.330$), year ($F_{3,55} = 1.511$, $P = 0.222$) or Julian hatch date ($F_{1,55} = 1.049$, $P = 0.310$).

Dynamics in Care over Brood Development

Mixed-effects models controlling for the stage in brood development showed that females and males reduced brooding over offspring development, although males tended to brood offspring at a slightly lower rate than females (Tables 1, 2, Fig. 3). Rates of brooding did not differ between partially and fully biparental families (Tables 1, 2, Fig. 3).

Males and females tended to perform defence behaviours at a similar rate and parents increased their rates of defence over brood development (Tables 1, 2, Fig. 3). Compared to parents in fully biparental families, parents in partially biparental families performed defence slightly less frequently early in care but also increased their rates of defence behaviours more rapidly over the course of brood development (Tables 1, 2, Fig. 3).

Males and females spent the same proportion of time being vigilant and both sexes increased vigilance rates as broods developed (Tables 1, 2, Fig. 3). Rates of vigilance did not differ between partially and fully biparental families (Tables 1, 2, Fig. 3).

Finally, the number of chicks present in each family was associated with an overall increase in brooding, although this effect was overall weak (Tables 1, 2). The time of day consistently impacted rates of care behaviours (Table 1). Parents had higher rates of brooding earlier and later in the day, whereas rates of defence and vigilance tended to be lower at these times (Tables 1, 2, Fig. A2). In addition, rates of brooding and offspring defence varied between study years (Tables 1, 2). Full results from model comparisons are presented in Table A2.

Dynamics in Self-maintenance over Brood Development

Males were observed pecking the substrate (i.e. feeding) at a higher frequency than females, and both sexes increased their rate of feeding as broods developed (Tables 1, 2, Fig. 3). Rates of pecking did not differ between partially and fully biparental families and

Table 2
Predictors of male and female parental care dynamics and self-maintenance

Model	Fixed effect	Estimate	SE	95% CI	*z*
Proportion brooding	Intercept (1996, Female)	−7.871	0.859	−9.555−−6.187	−9.163
Random effects:	Brood size	0.489	0.253	−0.007−0.986	1.931
family identity $\sigma^2 = 0.00$,	Year (1997)	0.878	0.538	−0.175−1.932	1.634
observation identity $\sigma^2 = 6.28$,	Year (1998)	2.068	0.48	1.126−3.009	4.304
residual $\sigma^2 = 9.57$,	Year (1999)	1.057	0.445	0.185−1.930	2.375
No. of observations = 445,	Brood age (days)	−2.432	0.208	−2.840−−2.025	−11.698
No. of families = 64	Sex (Male)	−0.872	0.291	−1.442−−0.303	−3.001
	Time (h)	−0.408	0.215	−0.829−0.013	−1.897
	Time^2 (h)	1.29	0.186	0.925−1.655	6.931
Proportion defence	Intercept (1996, PB)	−2.277	0.249	−2.765−−1.789	−9.143
Random effects:	Year (1997)	−0.455	0.291	−1.026−0.116	−1.561
family identity $\sigma^2 = 0.10$,	Year (1998)	−1.214	0.266	−1.736−−0.692	−4.559
observation identity $\sigma^2 = 1.73$,	Year (1999)	−0.366	0.224	−0.805−0.073	−1.634
residual $\sigma^2 = 5.02$,	Care type (FB)	0.101	0.183	−0.258−0.459	0.552
No. of observations = 445,	Brood age (days)	0.56	0.17	0.227−0.893	3.296
No. of families = 64	Time (h)	−0.087	0.11	−0.302−0.128	−0.793
	Time^2 (h)	−0.206	0.096	−0.393−−0.018	−2.151
	Care type (FB) * Brood age	−0.469	0.187	−0.836−−0.102	−2.506
Proportion vigilance	Intercept (PB)	0.058	0.083	−0.105−0.220	0.697
Random effects:	Brood age (days)	0.278	0.044	0.192−0.364	6.325
family identity $\sigma^2 = 0.11$,	Time (h)	0.315	0.066	0.185−0.445	4.747
observation identity $\sigma^2 = 0.68$,	Time^2 (h)	−0.493	0.057	−0.605−−0.380	−8.601
residual $\sigma^2 = 3.97$,					
No. of observations = 445,					
No. of families = 64					
Proportion pecking	Intercept (1996, Female)	−4.175	0.229	−4.624−−3.726	−18.223
Random effects:	Year (1997)	0.731	0.322	0.100−1.362	2.272
family identity $\sigma^2 = 0.22$,	Year (1998)	0.161	0.29	−0.408−0.729	0.554
observation identity $\sigma^2 = 1.25$,	Year (1999)	0.640	0.251	0.147−1.133	2.544
residual $\sigma^2 = 4.54$,	Brood age (days)	0.534	0.082	0.372−0.695	6.483
No. of observations = 445,	Sex (Male)	0.641	0.126	0.393−0.889	5.071
No. of families = 64	Time (h)	−0.264	0.071	−0.403−−0.125	−3.721
	Date	−0.208	0.104	−0.412−−0.004	−1.997

Full results are shown for the most parsimonious top models predicting the behaviour of parents including the proportion of time spent brooding, in defence, in vigilance and pecking (i.e. feeding). Julian date, time and brood age are scaled to have a mean of zero and standard deviation of 1. PB = partially biparental and FB = fully biparental. Date = Julian date of observation, brood size = number of chicks alive in the brood at the time of observation and time = time of observation in decimal hours. Estimates are provided alongside their 95% confidence intervals (95% CI).

decreased later in the day (Tables 1, 2, Fig. 3). In addition, rates of pecking varied between years and were lower later in the breeding season (Tables 1, 2, Fig. 3).

DISCUSSION

Conflict and cooperation between parents are some of the fundamental processes that drive the evolution of reproductive strategies and family dynamics (Parker et al., 2002). Understanding the details of parental care delivered by males and females in families before desertion is key to provide insights into the patterns of negotiation and cooperation that influence the stability of biparental care. However, relatively few studies have comprehensively investigated the share of care between males and females across families with and without desertion (van Dijk et al., 2012), and these studies have not systematically measured levels of division of labour across different care patterns. Here we investigated the balance of parental care between males and females in a well-studied bird population where parents frequently desert their precocial offspring, resulting in uniparental and biparental care patterns within the same population.

Our results show that a division of labour in parental care is not associated with variation in the maintenance of biparental care across families and that males and females expressed all measured care behaviours regardless of whether they were in partially biparental families before female desertion or in fully biparental families where no parent deserted. However, controlling for dynamic changes in care as offspring developed revealed subtle differences in care rates, indicating that, while both parents cared for the family, females were typically engaged slightly more in care. Our results suggest differences in self-maintenance may underlie sex differences in care rates as male parents also spent a comparably larger proportion of time feeding themselves rather than caring.

Task specialization is expected to facilitate the maintenance of biparental care when parents specialize in different care tasks, so that the parental care delivered by both parents becomes complementary (i.e. a division of labour, Barta et al., 2014; Henshaw et al., 2019). In such cases, uniparental care may be rendered less effective because single parents are unable to efficiently provide all forms of care. Our results indicate no division of labour in care across vigilance, defence and brooding in both fully and partially biparental families. Importantly, observational studies such as the present study are unable to determine whether any difference in the division of labour across fully and partially biparental families arises from a parent's decision to desert rather than being a driver of desertion. For example, while mating with more, or less, specialized males may influence female desertion decisions, it is also possible that females that are likely to desert choose less specialized male partners. However, the lack of division of labour observed across fully and partially biparental families in our study indicates that specialization is neither a key consequence of decisions to desert nor a driving force determining why some families remain biparental and other families break apart. Future studies that follow our approach and identify a division of labour in more stable families should seek to disentangle whether this

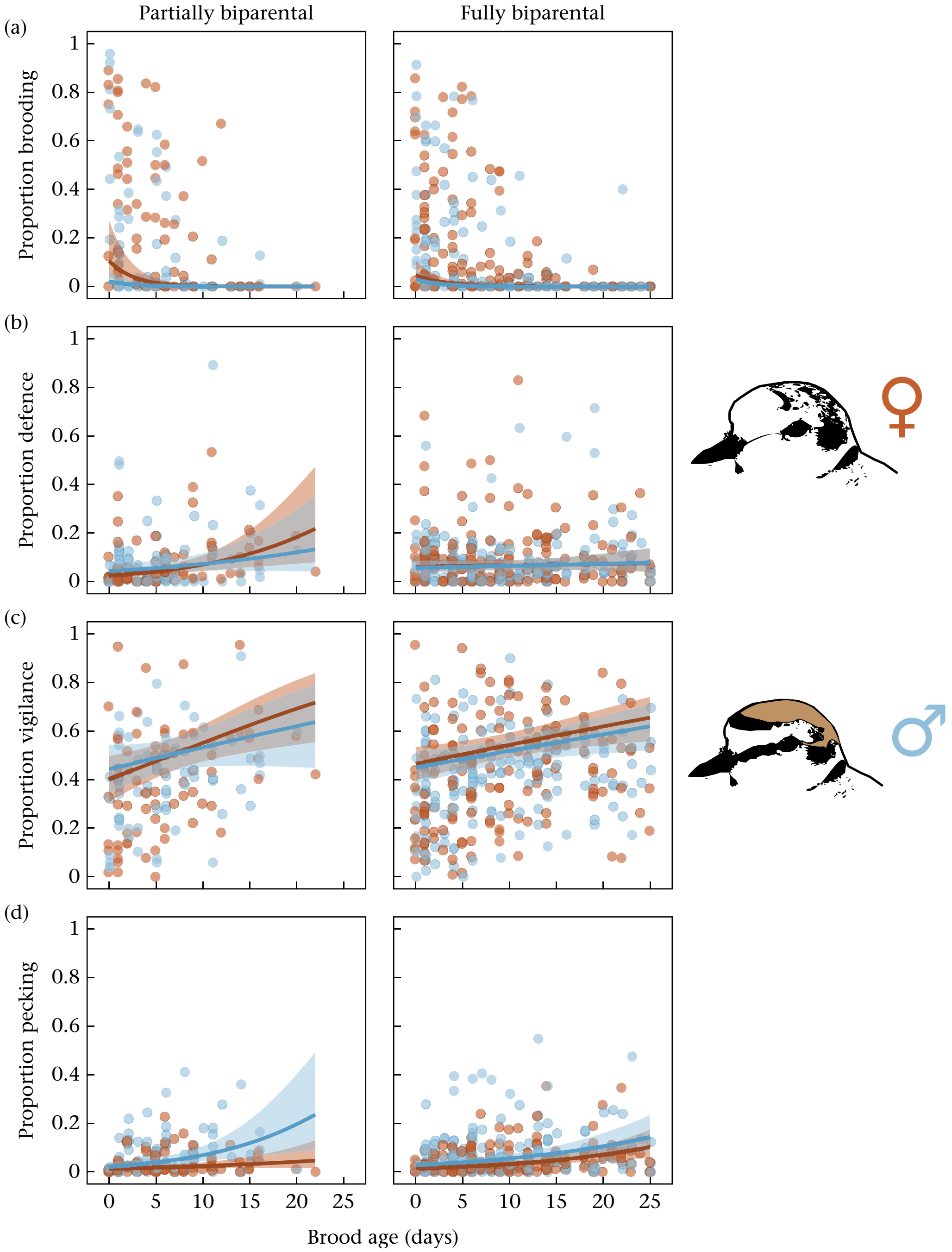

Figure 3. Dynamics of sex differences in parental care. Data are shown for male and female parents in partially biparental families before female desertion and fully biparental families where no desertion occurred. Panels show the relationship between the age of broods in days and the proportion of observations parents were engaged in (a) brooding, (b) defence behaviours, (c) vigilance and (d) feeding (substrate pecking). The intensity of point shading indicates point overlap. Lines show predictions (±95% confidence interval) from the maximal models.

specialization is a cause or consequence of variation in desertion. We suggest several potential routes to achieve this. First, if the relationship between individual characteristics (e.g. body size or condition) and the breadth of a parent's care repertoire is known, experiential studies may be able to manipulate these characteristics, and thus the care profiles of male and female partners, to experimentally examine whether greater specialization reduces family stability. Second, longer term studies in species with flexible uni- and biparental care may allow researchers to characterize the typical care profiles and desertion strategies of both partners prior to pair formation and reproduction. Such studies may allow researchers to ask whether individual levels of specialization in past episodes of reproduction with previous partners predict care profiles and pair stability in current reproductive episodes with different partners.

The lack of clear specialization in our study is in contrast to a number of biparentally caring insects, including bark beetles and dung beetles (Trumbo, 2006, 2012; Walling et al., 2008), as well as multiple avian species (Barta et al., 2014) where males and females show distinct roles in terms of care. For example, raptors typically show a clear division of labour, with females almost exclusively incubating and brooding offspring, while males provide food (Sonerud et al., 2014). While our results do not indicate a role for specialization in determining the stability of biparental care within a population, our results remain consistent with the idea that across species, those species with frequent uniparental care should exhibit a lower division of labour compared with species in which care is almost exclusively biparental and desertion is infrequent. Future research should explore the extent to which the division of care labour covaries with the frequency (risk) of desertion across populations. Such studies may use a multipopulational approach, combined with quantitative measures of specialization as employed here, to assess the prediction that populations or species in which desertion is rare should show stronger sex-specific specialization and division of labour compared to populations or species in which desertion is common and parents have evolved care strategies under the risk of desertion.

While we observed no division of labour in brood care, previous work in Kentish plovers has indicated a more subtle temporal division of labour during incubation. In Kentish plover populations, males and females specialize in the timing of incubation care, where males largely incubate at night and females mostly incubate during the day (AlRashidi et al., 2011; Fraga & Amat, 1996). Previous work has suggested that such sex-specific incubation schedules in birds may be associated with sex-specific costs of incubation via differences in predation risk associated with sexual dichromatism, where brighter and more colourful males typically incubate clutches at night (Ekanayake et al., 2015). Male Kentish plovers are also typically more ornamented than females during breeding (i.e. males have black frontal head bars and eye stripes and more colourful crowns, Argüelles-Ticó et al., 2016). Such sex-specific costs are one of the key mechanisms thought to drive the emergence of a division of labour (Barta et al., 2014). Our results suggest these potential sex differences in costs of ornamentation do not influence an overall division of labour during brood care in Kentish plovers. However, how such differences in ornamentation may impact the timing schedules of brood care has received less attention, and is made challenging by the difficulty in conducting brood observations at night compared to conducting incubation studies at night (e.g. via the use of infrared nest cameras, St Clair et al., 2010). While our results here indicate daily patterns in brood care, that is, more brooding early and late in the day, we were unable to observe patterns of brooding at night. Future work is needed to assess the potential for a temporal division of labour in brood care and the possibility that brood care patterns mirror the care patterns during incubation.

Despite no division in labour, our results show that females typically brooded offspring more than males, consistent with an overall bias towards female care across taxa (Royle et al., 2016), although these differences were typically small, and males and females also performed similar rates of defence and vigilance. Regardless, the overall tendency for similar or slightly more female care across both partially and fully biparental families suggests female desertion is not related to poor body condition limiting their ability to care (Barta et al., 2002). Instead, previous work in Kentish plovers suggests that deserting females are more likely to initiate a second breeding attempt within the same season, when compared to females that do not desert (McDonald et al., 2023), indicating that immediate remating benefits, rather than low reserves, influence female desertion (Amat et al., 1999; McDonald et al., 2023; Székely et al., 1999). The benefits of such desertion strategies are often expected to be largest early in the season, when deserting parents have sufficient time to raise a second brood to fledging before the seasonal decline in suitable breeding conditions (Amat et al., 1999; McDonald et al., 2023; Székely & Lessells, 1993). However, the observation that deserting and nondeserting female strategies can occur widely throughout a breeding season (McDonald et al., 2023) still suggests that other factors may influence the probability that parents abandon their brood. More recent work in the closely related snowy plover has suggested that females may desert their broods based on offspring needs, where females desert offspring only if their care is unlikely to have a strong impact on offspring survival (Kupán et al., 2021). For example, high investment in parental care by females may be less likely to alleviate chick mortality driven by flooding or starvation, and as a result females may instead choose to desert low-value broods affected by such mortality (Kupán et al., 2021). Future work should further investigate such possibilities in Kentish plovers by investigating the causes of chick mortality between families. While identifying the causes of chick mortality in highly mobile shorebird chicks is challenging, recent work in other shorebird species suggests that detailed radiotelemetry tracking of chicks may provide a promising route to assign chick mortality (Lees et al., 2019).

Rates of care behaviours were dynamic as broods developed. Overall, parents brooded less as chicks grew larger and became better able to thermoregulate independently (Visser & Ricklefs, 1993, 1994). Instead, rates of vigilance and defence tended to increase over the period of brood care, suggesting a trade-off between brooding and other care behaviours and that brooding may limit other aspects of care early in brood development. Alternatively, it may be that vigilance may simply become a more important component of care at later stages in development, whereas brooding becomes less important. Given distances between chicks, and between parents and chicks, may increase as shorebird chicks age (Colwell et al., 2007; Lenington, 1980; McDonald et al., 2023), higher levels of vigilance may emerge as a response by parents to better observe more dispersed broods. Importantly, however, while the benefits of brooding are directed towards chicks, vigilance and defence behaviours may also benefit parents directly via competitive access to resources and predator avoidance. Thus, a greater investment in these behaviours by parents later in offspring development may also indicate increases in self-maintenance rather than offspring care. Our results indicate that rates of care by males and females were typically similar in fully versus partially biparental families, suggesting that the probability of female desertion is not instigated by inequality in the share of care between parents. Previous studies examining associations between care imbalances and desertion have typically focused on altricial species where parents feed offspring (Baldan & Griggio, 2019; Johnstone & Savage, 2019). We suggest future work should further explore the generality of our results among precocial species that do not feed their offspring, and where the costs of care may be overall lower and the importance of imbalances in care in shaping desertion decisions may be weaker.

Surprisingly, our results also revealed a weak relationship between brood size and care behaviour in Kentish plovers. Brood size is often assumed to have comparably low impact on rates of care in precocial species because parents do not feed young and other key care behaviours are not expected to depreciate with increases in brood size (Sandercock, 1994). However, we show that more chicks in a brood are associated with increased rates of brooding, which may reflect a greater investment in larger and more valuable broods and/or differences in parent quality (Sandercock, 1994). While behaviours such as vigilance are expected to represent a shared investment in offspring (i.e. the benefits of vigilance are likely shared equally across all offspring), we suggest brooding may in some cases represent an unshared investment as only those offspring being brooded at any point accrue the benefits (Lazarus & Inglis, 1986). If parents are unable to efficiently brood all chicks simultaneously, either due to physical or physiological constraints or because offspring differ in when brooding is requested, each chick (or some of the chicks) may need to be brooded in turn. As a result, parents with larger broods may spend a higher proportion of time brooding and potentially suffer a greater cost of care because parents cannot simultaneously feed themselves and brood offspring (Beintema & Visser, 1989). To further examine the generality of the relationship between brood size and care behaviour among precocial species, we encourage more detailed studies of brood care behaviour. However, given the mobility and often cryptic behaviour of shorebird families during brood rearing, studies in the wild will remain challenging.

Finally, we investigated the mechanisms that may drive differences and similarities in rates of male and female care, via patterns of self-maintenance. We showed that males spent more time feeding themselves in both partially and fully biparental families, which may account for the overall lower rates of male versus female care (i.e. brooding). Such differences in feeding rates could be driven by higher feeding and physiological demands of males versus females. For example although sex differences in body size in Kentish plovers are typically small (Fraga & Amat, 1996), males are significantly larger than females (Küpper et al., 2009). A limitation of most previous studies, however, is that the behaviour of parents, including feeding, is rarely quantified while they are away from the brood. Recent advances in movement ecology have the potential to fill this gap by providing detailed information on the location of parents alongside inferred parental behaviours from biologging sensors (Giuggioli & Bartumeus, 2010; Jetz et al., 2022; Williams et al., 2020).

Conclusions

In summary, our study provides a detailed analysis of parental care in a precocial shorebird, both in families that remain biparental and in families where one parent deserts. We found an absence of a division in care labour, suggesting that differential sex-specific specialization across families is not a key force determining why some families remain biparental. Despite no division of labour, our results indicate that females tended to care for offspring slightly more than males, even in families where females soon deserted. Moreover, our results underline the need to assess differences in male and female care behaviours over time as they change dynamically across the duration of offspring development. Future work should examine the generality of a low division of labour among families within species and populations with frequent offspring desertion.

Author Contributions

Grant C. McDonald: Conceptualization, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Barbara A. Caspers:** Writing – review & editing. **Zoltán Barta:** Methodology, Writing – review & editing. **András Kosztolányi:** Conceptualization, Investigation, Methodology, Writing – review & editing. **Tamás Székely:** Conceptualization, Investigation, Writing – review & editing

Data Availability

Data are provided as Supplementary material.

Declaration of Interest

Authors declare no conflicts of interest.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2024.06.007.

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Appendix

Table A1
The behaviours of Kentish plover parents recorded during behavioural observations

Behavioural category	Observed behaviours	Description
Brooding	Brooding or Shading	Brooding or shading of chicks by parents, where chicks are at least partially hidden by the adult's breast feathers and under wings
Vigilance	Head Up	Standing individuals with head raised, typically scanning the area
	Extreme Head Up	Exaggerated vigilance, alerted individuals scanning the area with vertically elongated neck
Defence	Fighting conspecifics	Chasing or fighting with conspecifics
	Fighting heterospecifics	Chasing or fighting with other species e.g. little terns, *Sterna albifrons*, and spur-winged plovers, *Vanellus spinosus*
	Injury Feigning	Multiple parental defence behaviours typically expressed in response to potential predators, including distraction displays such as injury feigning and false brooding (parent mimicking brooding but without chicks)
	False Brooding	
	Flight Calling	
	Crouched Standing	
	Rodent Running	
	Wing Flapping	
	Injured Flight	
	Upright Running	
	False Pecking	
Pecking	Pecking	Foraging for food by pecking the substrate
Other	Running	Other behaviours that add to the overall denominator in proportions of individual behavioural budgets, including general movement, standing, preening and courting behaviours (e.g. nest scraping)
	Sitting/Standing	
	Flying	
	Preening	
	Courting	

At each scan, each behaviour was recorded whether occurring or not; only one behaviour could be scored per individual per scan.

Table A2
Dynamics of male and female parental care and self-maintenance over brood age in families with different care types (fully biparental families versus partially biparental before desertion)

Response	Model rank	Site	Year	Time (h)	Time^2 (h)	Date	Brood size	Brood age (days)	Sex	Care type	Care type * Sex	Brood age * Sex	Care type * Brood age	Care type * Brood age * Sex	ΔAICc
Proportion brooding	1		+	−0.404	1.278	−0.270	0.452	−2.311	+						0.000
	2		**+**	**−0.408**	**1.290**		**0.489**	**−2.432**	**+**						**0.628**
	3		+	−0.403	1.277	−0.295		−2.425	+						1.102
	4		+	−0.411	1.287		0.513	−2.398	+	+					1.861
	5		+	−0.406	1.277	−0.246	0.468	−2.304	+	+					1.902
Proportion defence	**1**		**+**	**−0.087**	**−0.206**			**0.560**		**+**			**+**		**0.000**
	2		+	−0.088	−0.206		0.178	0.644		+			+		0.331
	3		+	−0.085	−0.209	0.109		0.480		+			+		0.916
	4		+	−0.086	−0.209	0.114	0.179	0.562		+			+		1.205
	5	+	+	−0.089	−0.201			0.561		+			+		1.888
	6		+	−0.087	−0.206			0.562	+	+			+		1.976
Proportion vigilance	1		+	0.319	−0.494		−0.144	0.244							0.000
	2			0.317	−0.491		−0.139	0.244							0.412
	3			0.318	−0.491	0.099	−0.131	0.201							0.485
	4		+	0.321	−0.494	0.080	−0.137	0.209							0.669
	5			0.316	−0.493	0.105		0.230							1.054
	6		+	0.318	−0.495			0.279							1.114
	7	+	+	0.322	−0.498		−0.139	0.244							1.220
	8			**0.315**	**−0.493**			**0.278**							**1.268**
	9		+	0.320	−0.496	0.087		0.239							1.480
	10		+	0.319	−0.493		−0.145	0.243	+						1.547
	11	+		0.320	−0.497		−0.135	0.244							1.818
	12		+	0.320	−0.493		−0.147	0.240		+					1.888
	13			0.316	−0.491		−0.139	0.244	+						1.942
Proportion pecking	1		+	−0.148	−0.138	−0.206		0.531	+						0.000
	2		**+**	**−0.264**		**−0.208**		**0.534**	**+**						**0.394**
	3	+	+	−0.144	−0.147	−0.220		0.536	+						0.632
	4		+	−0.146	−0.137	−0.212	−0.124	0.504	+						1.068
	5	+	+	−0.267		−0.221		0.538	+						1.346
	6		+	−0.260		−0.214	−0.126	0.506	+						1.410
	7		+	−0.141	−0.143			0.439	+						1.687
	8	+	+	−0.142	−0.146	−0.226	−0.116	0.510	+						1.836

Models are ranked by AICc (Akaike information criterion corrected for small sample size). Model with the lowest AICc is model rank 1. All models within 2 AICc of model rank 1 are shown. The most parsimonious top model (i.e. the model with fewest parameters and within 2 AICc of model rank 1) is highlighted in bold. Date = Julian date of observation, brood size = number of chicks alive in the brood at the time of observation, site = the site of brood care and time = time of observation in decimal hours.

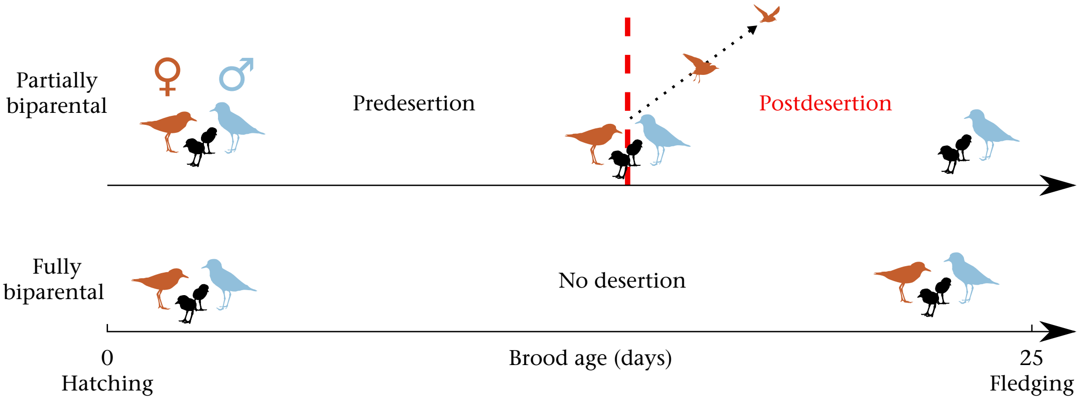

Figure A1. Diagram outlines the patterns of parental care and desertion in Kentish plover families that were analysed in the current study. Families may remain biparental until chicks fledge (fully biparental) or become uniparental after females (brown) desert their family, leaving males (blue) to care for the brood alone. All care behaviour in partially biparental families after desertion were excluded from behaviour analyses as our aim was to understand patterns of care prior to desertion.

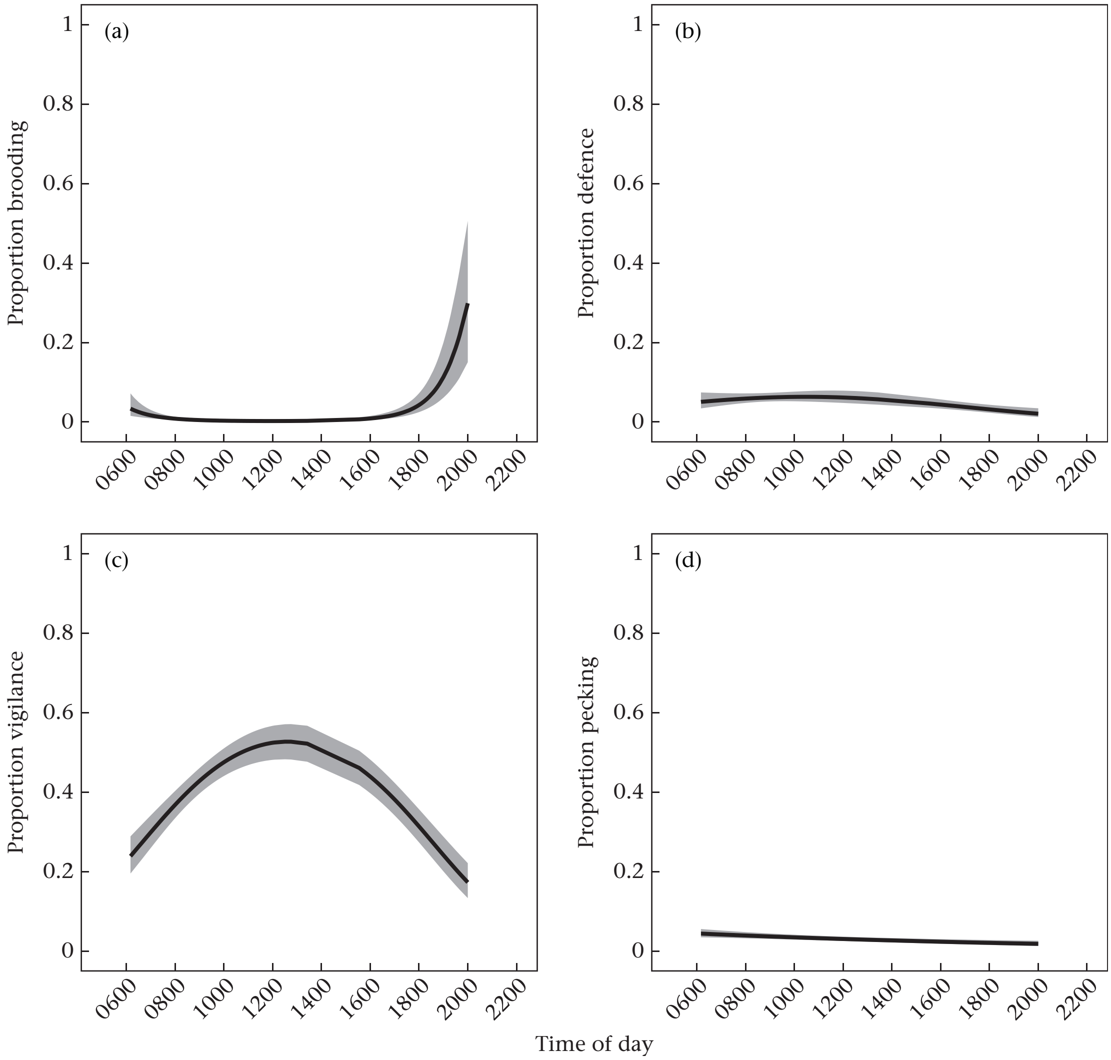

Figure A2. The effects of the time of day in decimal hours on rates of parental care across both fully and partially biparental Kentish plover families, for (a) brooding, (b) defence, (c) vigilance and (d) feeding (substrate pecking). Lines show predictions (±95% confidence intervals) from the most parsimonious top models.