

RESEARCH ARTICLE

Effects of season length and uniparental care efficacy on the evolution of parental care

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Handling Editor: A. Bradley Duthie**Abstract**

1. Parental care patterns differ enormously among and even within species. This is exemplified by Chinese penduline tits *Remiz consobrinus*, where biparental care, female-only care, male-only care and biparental desertion all occur in the same population; moreover, the distribution of these care patterns differs systematically between populations. The eco-evolutionary determinants of this diversity are largely unknown.
2. We developed an individual-based model that allows us to investigate the effects of season length and offspring needs (expressed by the efficacy with which a clutch can be raised by a single parent) on the evolution of parental care patterns. The model is largely conceptual, aiming at general conclusions. However, to keep the model realistic, its set-up and the choice of parameters are motivated by field studies on Chinese penduline tits. Exploring a wide range of parameters, we investigate how parental care patterns are affected by season length and offspring needs and whether and under what conditions diverse parental care patterns can stably coexist.
3. We report five main findings. First, under a broad range of conditions, different care patterns (e.g. male care and biparental care) coexist at equilibrium. Second, for the same parameters, alternative evolutionary equilibria are possible; this can explain differences in care patterns across populations. Third, rapid evolutionary transitions can occur between alternative equilibria; this can explain the often-reported evolutionary lability of parental care patterns. Fourth, season length has a strong but nonmonotonic effect on the evolved care patterns. Fifth, when uniparental care efficacy is low, biparental care tends to evolve; however, in many scenarios uniparental care is still common at equilibrium. In addition, our study sheds new light on Trivers' hypothesis that the sex with the highest prezygotic investment is predestined to invest more postzygotically as well.
4. Our study highlights that diversity in parental care can readily evolve and it shows that even in the absence of environmental change parental care patterns can be evolutionary labile. In the presence of directional environmental change, systematic shifts in care patterns are to be expected.

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KEYWORDS

alternative stable states, behavioural polymorphism, individual-based model, parental sex roles, penduline tits

1 | INTRODUCTION

In many animals, parents commonly devote considerable time and energy to care provided to their offspring. However, parental care systems are highly diverse (Clutton-Brock, 1991). Across and within species, there is large variation in the amount of parental care and the involvement of the two parents. In biparental care species, both parents make a substantial effort, although the sexes may differ in the amount of care provided and in the distribution of tasks (Eldegard & Sonnerud, 2009; Pilakouta et al., 2018). In uniparental care (either female-only care or male-only care), one of the parents deserts the young and leaves the parental workload to the remaining partner (Henshaw et al., 2019). These parental care types indicate different evolutionary pathways among animals. However, despite intense research efforts, the evolution of parental care diversification is not well understood (Furness & Capellini, 2019; Remeš et al., 2015). The reason is that the evolution of parental care is governed by a complex interplay of cooperation and conflict: on the one hand, the parents have a common interest in ensuring that their offspring survive in good condition, but on the other hand, the parents have conflicting interests on who should do most of the caring (Clutton-Brock, 1991).

Empirical studies revealed that both ecological and environmental factors play important roles in the evolution of parental care (Furness & Capellini, 2019; Remeš et al., 2015). Parental cooperation may be enforced by high predation pressures or a scarce/scattered food supply, as in such situations two interacting parents can be much more efficient in raising the offspring than a single parent (Eldegard & Sonnerud, 2009; Pike et al., 2016). Uniparental care can be sufficient in species with protected nests providing good thermal conditions, or in precocial species where the offspring are relatively independent early on (Kupán et al., 2021; Pogány et al., 2008). Seasonality is also an important factor influencing parental care (Halupka & Halupka, 2017). In rock sparrows *Petronia petronia*, for example, the experimental shortening of the breeding season resulted in a higher rate of offspring desertion (Griggio, 2015). In other bird species, the opposite pattern has been observed: those individuals that arrive earliest on the breeding grounds (and thus have the longest breeding season) have the highest tendency to desert their offspring (Jankowiak & Wysocki, 2016; Székely et al., 1999).

Species exhibiting variation in parental care patterns are ideal for exploring how external factors affect parental care. Many such species exist in the animal kingdom. For example, biparental care, male-only care and female-only care coexist in many fish species (Balshine-Earn, 1997; Brown Blumer, 1986), male-only and female-only care coexist in various reptiles and amphibians (Bourne, 1998), and female-only and biparental care coexist in some mammals (Rymer & Pillay, 2018). Birds are particularly well-studied

in this respect. Different care patterns do coexist in little egrets *Egretta garzetta* (Fujioka, 1989), rock sparrows *P. petronia* (Griggio & Pilastro, 2007), Tengmalm's owls *Aegolius funereus* (Eldegard & Sonnerud, 2009) and various species of plovers *Charadrius* spp. (Eberhart-Phillips et al., 2018). Arguably, penduline tits *Remiz* spp. are a model example for both the diversity of parental care systems and the difficulty to explain this diversity. Multiple types of parental care (including female-only care, male-only care, biparental care and even biparental desertion) coexist in this genus and parental care patterns vary across species (Ball et al., 2017; Pogány et al., 2008). Chinese penduline tits *Remiz consobrinus* exhibit the most flexible parental care pattern, which varies not only within the same population but also between populations (Zheng., 2022; see [Supporting Information S1](#) for an overview).

Taking Chinese penduline tits as our exemplar species, we here analyse an evolutionary model that allows us to investigate how the evolution of parental care decisions is affected by season length and factors that determine the efficacy of single parents to successfully raise a brood. Starting with the classical articles of Maynard Smith (1977) and Houston et al. (1985), a broad spectrum of modelling studies investigated various aspects of the evolution of parental care strategies, using diverse theoretical tools such as evolutionary game theory (McNamara & Weissing, 2010; Van Dijk et al., 2012), dynamic programming (McNamara et al., 2000; Webb et al., 2002) adaptive dynamics (Klug et al., 2013) and selection gradient methods (Fromhage & Jennions, 2016; Kokko & Jennions, 2008). Modelling the evolution of parental care decisions is not straightforward, as the fitness implication of each decision does not only depend on what the other parent is doing but also on the state of the population as a whole (McNamara et al., 2000). There are methods to derive evolutionarily stable parental strategies (Fromhage & Jennions, 2016; McNamara et al., 2000), but these methods often fail in situations where diversifying selection leads to individual variation in parental strategies (Long, 2022). Therefore, we develop a model that shares many features with the model in McNamara et al., 2000, but instead of using a fitness-based analytical approach, we investigate the model by systematically running a large number of individual-based evolutionary simulations. With this method, we address the question: how does the sex-specific decision on whether to desert the current clutch of offspring depend on season length and the efficacy of uniparental care?

Individual-based simulation models have the advantage that they can easily be tailored to a particular empirical system. Here, we consider a model that makes quite generic assumptions, but which is parameterized in such a way that it resembles the situation in Chinese penduline tits (Zheng et al., 2018). This makes the model more realistic and allows us to compare the model outcomes with empirical

findings. Perhaps most importantly, we can address one conspicuous aspect of parental care in penduline tits: before deciding on whether to care for the offspring or to desert the clutch, both parents have already made a substantial investment by constructing an elaborate and sophisticated nest and by producing a clutch of eggs (Pogány et al., 2008; Zheng et al., 2018). According to a hypothesis by Trivers (1972), the sex with higher prezygotic investment should also care more once the offspring have been produced. Although Trivers' line of argument was flawed (Dawkins & Carlisle, 1976; Kokko & Jennions, 2008), his prediction may still be largely correct, be it for different reasons than envisaged by Trivers (Alonzo, 2010; Long, 2022). Our model can shed new light on this question. In the model, males have a higher prezygotic investment than females (as they do most of the nest-building). We would therefore expect that males are predestined to care for the offspring.

With the model described in detail below, we will address the following questions: (1) How consistent is the outcome of evolution for a given parameter setting? Can different care patterns evolve under identical environmental and ecological circumstances? (2) How is the evolutionary outcome affected by season length and uniparental care efficacy? (3) How does a sex bias in prezygotic investment affect the evolution of postzygotic investment? Do females show more postzygotic care to compensate for the higher prezygotic investment of their mates? (4) To what extent do the model outcomes correspond to empirical findings on penduline tits?

2 | MATERIALS AND METHODS

2.1 | Model overview

We consider an individual-based simulation model that allows us to study the evolution of parental care patterns in relation to the length of the breeding season (S , measured in days) and the relative efficacy of uniparental care (U , expressed as the percentage of brood survivorship achieved by a single parent in comparison to biparental care). The model has two timescales: the within-generation 'behavioural timescale' of the breeding season, where individuals engage in activities like nest-building, mating, egg-laying, incubating and caring for the young, and the across-generation 'evolutionary timescale', on which the parental care strategies change due to the interplay of mutation and natural selection. The parental care strategies considered are simple: each parent has a fixed sex-specific propensity D to desert the clutch once egg-laying is completed. Clutch desertion has an obvious effect on fitness, as it affects the balance between current and future reproductive success: it typically reduces the number of fledglings to be expected from the current clutch (as the other parent might desert the clutch as well or otherwise be less efficient in raising the young on its own), but it may enable the deserting parent to start a new clutch, thus potentially increasing the lifetime number of clutches initiated. Individuals differing in their desertion propensity D will, on average, differ in their lifetime production of fledglings, depending on the behaviour of the parental partner (does he/she

desert as well?), the efficacy of uniparental care and the length of the breeding season (how many broods fit in a breeding season). As parents with a higher fledgling production transmit their desertion strategy to more offspring (subject to rare mutations), the distribution of D changes over the generations. The distribution of parental care patterns (biparental care, male-only care, female-only care and biparental desertion) will change along with the (sex-specific) distribution of D . A graphical overview of the model can be found in [Supporting Information S2](#).

2.2 | Events within a season

Our model is mainly conceptual, but in order to be concrete (and realistic), the structuring of the breeding season is inspired by the breeding biology of Chinese penduline tits (Zheng et al., 2018, see [Supporting Information S1](#) for details). The season consists of S days, and various events can happen on a single day. At the start of the season, 500 males and 500 females are drawn at random from the fledglings that were produced in the previous season. These individuals arrive asynchronously during the first 10 days of the season (10% arriving each day), and they immediately enter the 'mate search stage'. In this stage, the females search for a male partner. The males incrementally build a nest (at a rate of one unit per day) and wait to meet and pair up with a female. For a given male, the probability P of meeting and pairing up with a female on a certain day depends on the availability of females in the mate search stage. More precisely, P is proportional to the fraction of females among the individuals in the mate search stage. Throughout, we chose $1/3$ as the constant of proportionality, as this value roughly reproduces the speed of male mate acquisition in Chinese penduline tits (Zheng et al., 2021, about 3–4 days for males to pair up). However, as shown in [Supporting Information S6](#) the exact value does not matter much for the model outcome. If a male does not pair up within 15 days, it will pause nest-building (as male penduline tits do) and wait for a female to pair up with. Once a male gets paired, a female in the mate search stage is assigned at random to this male; both individuals leave the mate search stage and are transferred to the 'paired stage'. In this stage, both partners first complete the nest (now at a rate of two units per day); the nest is considered complete when in total 20 units of work have been invested in nest-building. Immediately thereafter, egg-laying starts, which lasts for 5–8 days (for each nest the exact number of days is drawn at random from a uniform distribution). After egg-laying is completed, both members of the pair make a decision on whether to stay and care for the young or whether to desert the clutch. Each parent makes its decision (independently of its partner) based on its inherited sex-specific desertion probability (see below). If an individual deserts the clutch, it immediately enters the mate search stage again. If an individual decides to care, it enters the 'caring stage', which lasts for 35 days (15 days of incubation, followed by 20 days of nestling feeding), irrespective of whether a single parent or both parents care for the clutch. Hence the total period from the start of egg-laying to fledging lasts between 40 and 43 days (as in

Chinese penduline tits). In the case of biparental care, F fledglings are produced on average; the actual number is drawn from a Poisson distribution with mean value F . In the case of uniparental care, the number of fledglings is drawn from a Poisson distribution with mean value $U \cdot F$, where U is the uniparental care efficacy. At the end of the season, all adult individuals are removed; the adult population of the next season is randomly selected from the fledglings of the current season (500 males and 500 females).

2.3 | Inheritance of parental care strategies

For simplicity, we assume that the individuals in our model are haploid. There are two gene loci A and B , with infinitely many possible alleles (ranging from 0 to 1) at each locus. The combination of alleles (D_A, D_B) at the two loci determines the sex-specific clutch desertion probabilities of the individual harbouring these alleles: D_A (resp. D_B) specifies the probability of deserting a given clutch if the individual happens to be the male (resp. the female) parent. We assume that the gene loci are not linked and that an offspring with parents of genotypes (D_A, D_B) and (D'_A, D'_B) will, with equal probability, be of genotype (D_A, D_B), (D_A, D'_B), (D'_A, D_B), or (D'_A, D'_B). After assigning the offspring's genotype, mutations with a small effect size can occur. At each of the two loci, a mutation occurs with probability $\mu=0.01$. The mutational step size is drawn from a normal distribution with mean zero and standard deviation 0.05 and added to the allelic value inherited from the parent. If the value thus obtained is smaller than zero (resp. larger than one), it is set to zero (resp. to one). As the genetics underlying nest desertion is unknown, these assumptions are somewhat arbitrary. Following standard practice in evolutionary modelling (Botero et al., 2010; DeAngelis & Mooij, 2005; Fromhage & Jennions, 2016; Long, 2022), we chose an implementation that is as little as possible affected by genetic constraints and interaction effects.

2.4 | Simulation details

We systematically varied two parameters: the season length was changed from $S=80$ days to $S=180$ days (in steps of 10 days), and the efficacy of uniparental care was changed from $U=60\%$ to $U=100\%$ (in steps of 10%). For each parameter combination, we ran at least 40 replicate simulations. We report on 60 scenarios, but many more simulations were run to check for the robustness of our results (see Supporting Information S3–S6). Each simulation was run for at least 100,000 seasons, ensuring that a stable equilibrium was reached (see Supporting Information S4, which considers a timescale of 1,000,000 seasons). All simulations started with a monomorphic population where all individuals were of genotype (D_A, D_B)=(0.5, 0.5), that is, each individual had an initial clutch desertion probability of 50% (but see Supporting Information S5, which indicates that the simulation outcome is only marginally affected by initial conditions). The simulation code is written in C++20 and is freely available; the

simulation data were analysed and visualized by R-4.2.2. This theoretical study did not require ethical approval.

3 | RESULTS

3.1 | Polymorphism of care strategies and alternative stable outcomes

To illustrate the evolution of parental care strategies in our model, Figure 1 shows two representative simulations for a season length of 140 days and a uniparental care efficacy of 80%. We ran 40 replicate simulations for this scenario; eight of these closely resembled the simulation in Figure 1a (top) while 32 resembled the simulation in Figure 1b (bottom). Supporting Information S3 shows the consistency across replicates and a comparison between selected and neutral gene loci. The simulation in Figure 1a illustrates how an apparently stable parental care pattern can persist for an extended period of time, followed by a rapid switch to a very different pattern. In the first 50,000 generations, the male desertion alleles fluctuate around a value of 0.19 (implying that males will desert the clutch on average in about 19% of all breeding attempts), while the female desertion alleles fluctuate around 0.62 (Figure 1a1). As a consequence, male-only care occurs in about 52% of all breeding attempts, biparental care in about 29%, female-only care in about 7% and biparental desertion in about 12% of all cases (Figure 1a3, first 50,000 generations). Around generation 50,000, this pattern changes completely: in the second half of the simulation, male desertion alleles approach the value of 1.0 (100% desertion), while female desertion alleles approach the value of 0.0 (no nest desertion). As a result, female-only care is the dominant pattern (Figure 1a3, last 50,000 generations). Figure 1a2 shows the distribution of male and female desertion alleles in the final generation of the simulation. Due to mutation and genetic drift, the male desertion alleles are not fixated at 1.0, and the female desertion alleles are not fixated at zero. Accordingly, biparental care and biparental desertion occur at low frequency.

Rapid switches from one pattern to another one are an indication that a system has two alternative stable states (Long, 2022; also see Supporting Information S4). In the present case, one of these states is female-only care, as illustrated in Figure 1a. The other stable outcome is illustrated by the simulation in Figure 1b, which resembles the first half of the trajectory in Figure 1a: the average values of the male and female desertion alleles fluctuate around 0.16 and 0.58 respectively. Notice, however, that the standard deviation of the female desertion alleles in the population is very large, indicating a broad distribution of alleles in the population. Panel (b2) shows how the desertion alleles are distributed in the final generation: the male alleles are clustered around the value 0.14, while the distribution of female desertion alleles is bimodal: about 32% of the female desertion alleles are close to 0.0, while 68% of the alleles are close to 1.0. In other words, there are two types of females in the population: 32% of the females will (almost) never desert the nest, while 68% will always desert. As the males will care for most of the time, the resulting care system is dominated by male-only care and biparental care.

3.2 | Effect of uniparental care efficacy

For a season length of 110 days, Figure 2 illustrates how the evolutionary outcome depends on the relative efficacy of uniparental care (when compared to biparental care). We found that

whenever uniparental care efficacy is very low, biparental care evolves (Figure 2, first panel, $U = 60\%$). If uniparental care efficacy increases to 70%, females continue to care while the male part of the population becomes polymorphic: when averaging over the generations, about 32% of the males desert their clutch, while the remaining

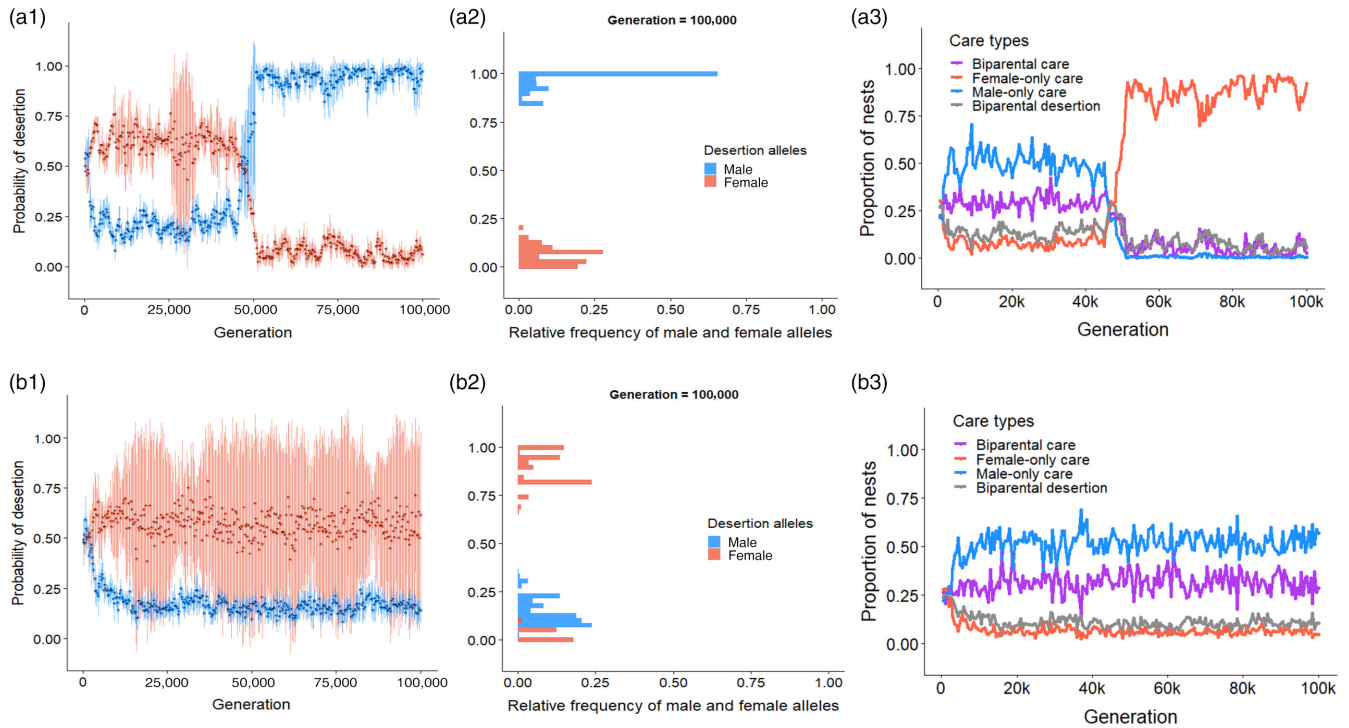


FIGURE 1 Two replicate simulation runs illustrating alternative outcomes of evolution. (a) and (b) present two simulation runs for a season length of 140 days and 80% efficacy of uniparental care. The left panels (a1 and b1) show how the values of the alleles (mean \pm SD) determining the probability of clutch desertion in males (blue) and females (red) evolve in the course of time; the middle panels (a2 and b2) show histograms of the distribution of male and female desertion games at the end of the simulation (generation 100,000); the right panels (a3 and b3) show how the proportions of different types of parental care change over the generations. In (a), a mixture of male-only care and biparental care dominates the first half of the simulation; around generation 50,000, the system suddenly switches to female-only care. In (b), male desertion stays at a low level (about 10%) while the female population is polymorphic: about 40% of the females almost never desert, while 60% of the females have a high desertion probability. This results in a parental care system dominated by a mixture of male-only care (about 50%) and biparental care (about 30%).

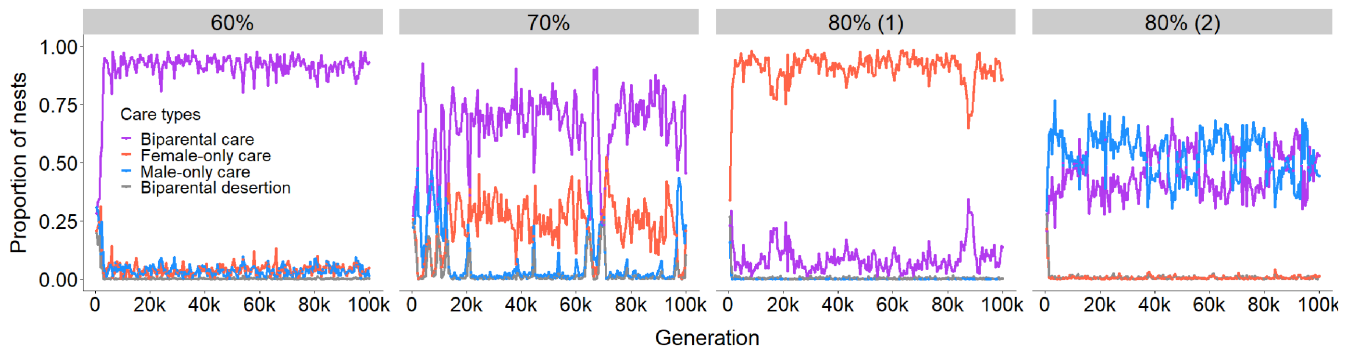


FIGURE 2 Effect of uniparental care efficacy on the outcome of evolution. For a season length of 110 days, the four panels show the evolution of parental care patterns for a uniparental care efficacy of 60%, 70% and 80%. In the case of 60% uniparental care efficacy (first panel), all simulations resulted in biparental care; in the case of 70% uniparental care efficacy (second panel), all simulations resulted in a mixture of biparental care and female-only care. In the case of 80% uniparental care efficacy, our model has two alternative attractors: 40% of our simulations resulted in female-only care (third panel), while 60% of the simulations resulted in a mixture of male-only care and biparental care (fourth panel).

68% stay caring. As a consequence, the population exhibits a mixture of biparental care and female-only care (Figure 2, second panel). When the efficacy of uniparental care increases even further, there are two alternative evolutionary outcomes. The third and fourth panels show these outcomes for the case $U=80\%$. In 16 of 40 simulations, female-only care was the dominant care strategy (with 7% biparental care when averaged over the generations; third panel); the remaining 24 simulations resulted in a mixture of male-only care and biparental care in similar proportions (52% male-only care, 47% biparental care; fourth panel). The latter outcome reflects a situation where males never desert the nest, while the females are polymorphic for the always-desert and the always-care strategy. If the efficacy of uniparental care is further increased ($U \geq 90\%$, Figure 4), the simulations either resulted in male-only care or female-only care.

In our model, males have to spend time on initializing a new nest. As our model is time based, males have a higher prezygotic investment than females. The question therefore arises whether and how this initial asymmetry results in a postzygotic care asymmetry in a consistent manner. The case $U=70\%$ (Figure 2, second panel) suggests that females tend to invest more in parental care than males (all females care, while 32% of the males desert the nest). This, however, is not a general outcome. As illustrated by the two alternative outcomes for $U=80\%$, either all the females care and the males desert (third panel) or all the males care and a substantial fraction of the females desert the nest (fourth panel). Accordingly, in this latter case, males invest more than females in parental care, both pre- and postzygotically.

3.3 | Effect of season length

Figure 3 illustrates the effect of season length on the evolutionary outcome for $U=60\%$. Although the uniparental care efficacy is very low, biparental care is not necessarily the predominant care pattern. For a season length of 90 days (first panel) and 150 days (third panel), all four care patterns (biparental care, female-only care, male-only care

care, biparental desertion) occur in similar frequencies. The outcome for a season length of 120 days (second panel) is remarkably different, as biparental care is the only care pattern. Biparental care is also predominant, be it to a lesser extent, in case of a season length of 180 days (fourth panel): in the first 20,000 generations, about 89% of all clutches are being cared for by both parents; this percentage suddenly drops to about 58% around generation 25,000, when the male population shifts from a monomorphic no-desertion strategy to the polymorphic coexistence of the no-desertion strategy with the always desertion strategy. As a result, the population exhibits a mixture of biparental care and female-only care.

There seems to be a periodicity in the evolved breeding patterns: a season length of 90 days has similar implications as a season length of 150 days, while a season length of 120 days is reminiscent of a season length of 180 days. This 60-day periodicity roughly corresponds to the duration of one breeding cycle, which encompasses nest-building (10 to 17.5 days per male; 2.5 to 10 days per female) and the period from the start of egg-laying to fledging (between 40 and 43 days).

3.4 | Combined effects of uniparental care efficacy and season length

Figure 4 shows in a comprehensive manner how the evolutionary outcome in our simulations depended on uniparental care efficacy (ranging from 60% to 100%) and season length (ranging from 80 days to 180 days). Several conclusions can be drawn from this overview. First, biparental care is the predominant strategy only when the efficacy of uniparental care is low ($U=60\%$, 70%, and to a lesser extent $U=80\%$). But even when the efficacy of uniparental care is low, biparental care only evolves as the dominant strategy for some season lengths, and in most cases, uniparental care coexists with biparental care (as illustrated in Figure 3). Second, uniparental care is the dominant strategy when the efficacy of uniparental care is very high ($U=90\%$ or 100%). In these cases, female-only care and male-only

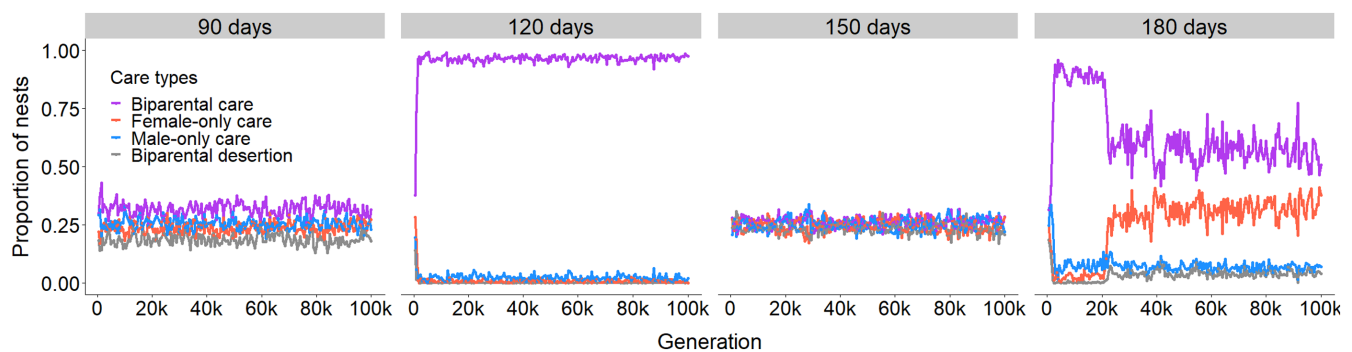


FIGURE 3 Effect of season length on the outcome of evolution. For a uniparental care efficacy of 60%, the four panels show the evolution of parental care patterns for a season length of 90, 120, 150 and 180 days. For a season length of 90 days or 150 days (first and third panel), all simulations resulted in an outcome where all four care types occur in similar proportions. For a season length of 120 days (second panel), all simulations resulted in biparental care. In the case of a season length of 180 days (fourth panel), all simulations resulted in a mixture of biparental care and female-only care; this care pattern is caused by a distribution of desertion alleles similar to the one in Figure 1b2: this time, however, females never desert while the males are polymorphic for either 'never desert' or 'always desert'.

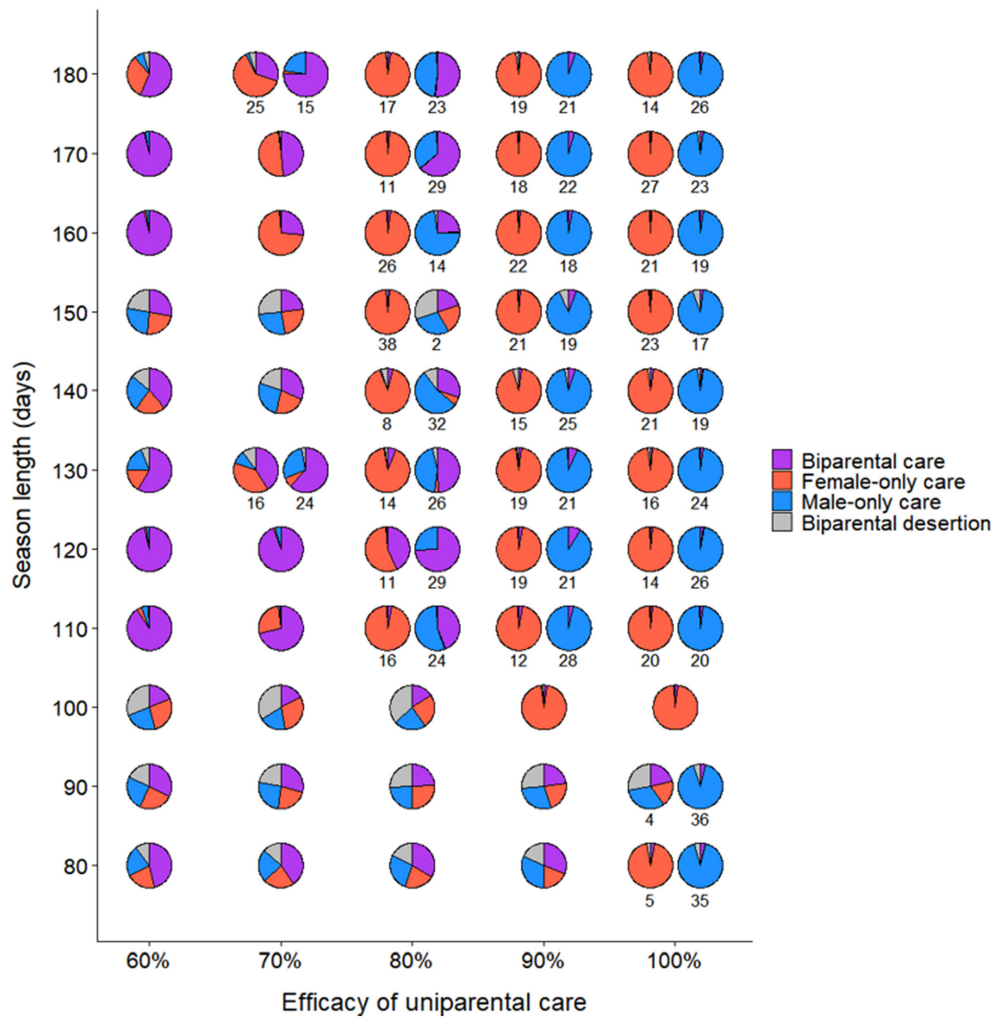


FIGURE 4 Overview of all simulation outcomes. For 11 season lengths (ranging from 80 to 180 days) and five values of uniparental care efficacy (ranging from 60% to 100%), we ran 40 replicate simulations. A single pie chart for a given parameter combination indicates that all 40 simulation runs resulted in the same outcome. The area of the four slices of the pie corresponds to the relative frequency of the four care types at the end of the simulation (after 100,000 generations). For many parameter combinations, two alternative simulation outcomes were observed, which are represented by two pie charts. The numbers below these pie charts indicate how many of the 40 replicate simulations resulted in one or the other outcome.

care are typically alternative outcomes. Which of these outcomes is more likely seems to depend on season length in a complicated way. The shorter season lengths differ somewhat from this general pattern, again in a nonintuitive manner. For example, female-only care is the only outcome for a season length of 100 days and $U=90\%$ or 100% , while a season length of 90 days leads to a mixed breeding system when $U=90\%$ and to male-only care (in most simulations) when $U=100\%$. Third, biparental desertion occurs regularly in case of a short season (80, 90 or 100 days) and for some season lengths (140 or 150 days) in combination with a low uniparental care efficacy ($U=60\%$ or 70%). Fourth, the most variable outcomes occur for an intermediate efficacy of uniparental care ($U=80\%$; see also Figure 1). For season lengths above 100 days, there are typically two alternative outcomes: female-only care and a mixture of biparental care and male-only care. The first case corresponds to parental division of labour: by building the nest, males make a high prezygotic

investment, while females make a high postzygotic investment by caring for the fledglings. In contrast, the second case is a system where the males provide most of the prezygotic and postzygotic care and females split up into caregivers and deserters. Which of the two outcomes is more likely to occur depends on season length in a complicated way.

3.5 | Effect of sex differences in uniparental care efficacy

Figure 5 illustrates how the parental care pattern evolves when males and females provide uniparental care with different efficiencies. We take the scenario in Figure 1 as our point of departure (season length = 140 days, $U=80\%$), but we now consider the four cases where only one parent has a uniparental care efficacy of 80%, while

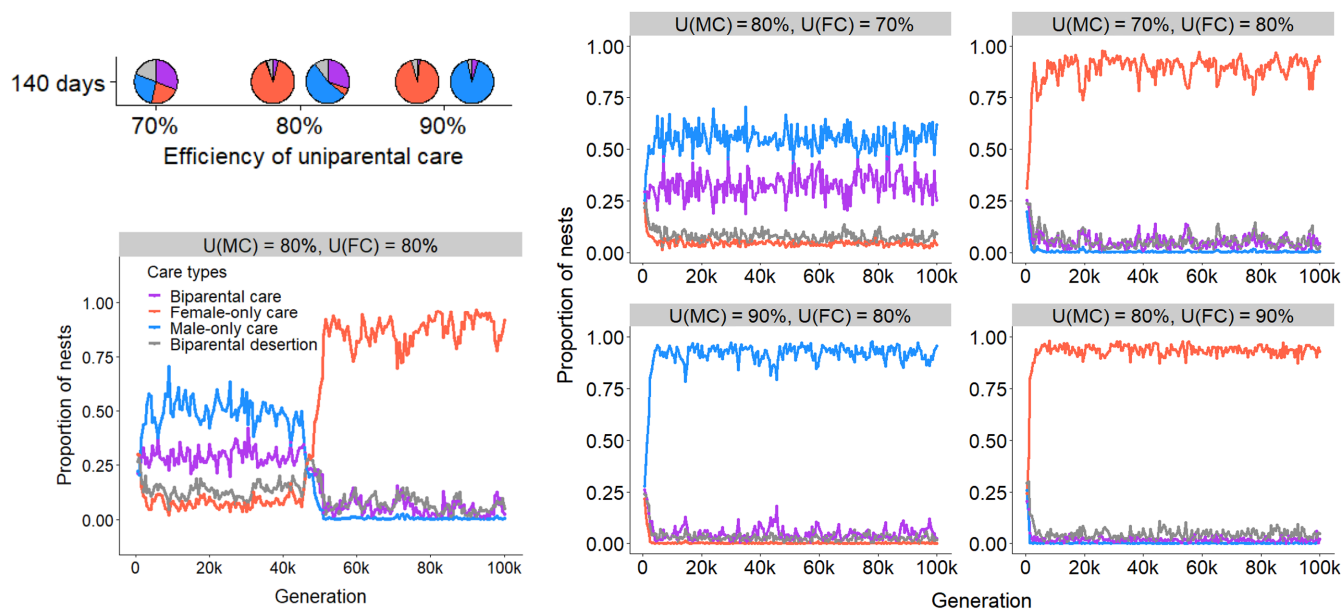


FIGURE 5 Effect of sex differences in uniparental care efficacy. For a season length of 140 days, the left panels show the evolutionary outcomes for our standard scenario that assumes that the male and the female parent have the same efficacy when caring uniparentally for their clutch. The pie charts in the upper left panel give an overview of outcomes for three efficiencies of uniparental care, while the lower left panel presents the simulation in Figure 1a3 again, as it illustrates both outcomes for a uniparental care efficacy of 80%. The other four panels show simulations where the efficacy of uniparental male care $U(\text{MC})$ differs from the efficacy of uniparental female care $U(\text{FC})$. All simulations with higher female uniparental care efficacy ($U(\text{FC}) > U(\text{MC})$, right panels) resulted in female-only care. The simulations with higher male uniparental care efficacy ($U(\text{MC}) > U(\text{FC})$, middle panels) resulted either in male-only care or in a mixture of male-only care and biparental care.

the other parent has a U value of either 70% or 90%. When the parents differ in U , we no longer observe alternative evolutionary outcomes: all simulations resemble those shown in Figure 5. In all these simulations, the parent with the higher uniparental care efficacy cares more than the parent with the lower efficacy. This is clearest for the cases where the female has a higher uniparental care efficacy than the male (Figure 5, right panels): female-only care evolved in all simulations. When the male has a higher uniparental efficacy than the female (Figure 5, middle panels), male-only care evolved when the male efficacy $U=90\%$, while a mixture of male-only care and biparental care evolved when the male efficacy $U=80\%$.

4 | DISCUSSION

Our study investigates an individual-based model for the evolution of sex-specific parental care and desertion decisions in a seasonal environment. We found first, evolution can, under the same conditions, lead to alternative outcomes: strikingly different parental care patterns can evolve for the same parameter settings and the same initial conditions. Therefore, our model provides an explanation for the fact that different populations of the same species can differ in their pattern of parental care, even if the populations live under similar ecological conditions. Second, in most cases evolution resulted in the coexistence of two different strategies ('always care' and 'never care') in one of the two sexes. As a result, the coexistence of different care patterns (often

biparental care and one form of uniparental care) is the rule, rather than the exception. Third, and not unexpectedly, biparental care mainly evolved when the efficacy of uniparental care is relatively low. When the efficacy of uniparental care is high, male-only care or female-only care are the dominant care patterns. By and large, both uniparental care patterns evolved equally frequently in our simulations, although our model incorporates the basal asymmetry that males have to make a relatively higher prezygotic investment (nest-building) than females. Fourth, season length has a strong effect on the evolutionary outcome. If uniparental care efficacy is low, a small change in season length can result in quite different parental care patterns. If uniparental care efficacy is intermediate ($U=80\%$), season length may strongly affect which of the two uniparental care patterns is most likely. In both cases, the dependence of the evolutionary outcome on season length is quite complex.

The joint evolution of male and female parental strategies is an intricate process with many facets (Fromhage & Jennions, 2016; Kokko & Jennions, 2008). On purpose, we kept our model as simple as possible, being aware that we left out potentially relevant factors. Perhaps most importantly, the individuals in our model cannot make their brood desertion decision dependent on the time within the season. We also did not consider conditionalities, such as making mate choice and brood care decisions depending on factors such as own condition, the condition of one's mate, the condition of the nest, the partner's desertion decision (see McNamara et al., 2000) or the local sex ratio (which determines the intensity of competition for

mates). As such condition-dependent strategies are notoriously difficult to implement in a generic way (McNamara & Weissing, 2010), we leave such model extensions to a future attempt. Even so, our model manifests that under very simple assumptions the evolution of the parental care system can be highly dynamic and can easily lead to the coexistence of different parental care patterns. For the time being, we will now discuss our findings in light of empirical evidence.

Our model resembles the breeding system of penduline tits *Remiz* spp. In Eurasian penduline tits *R. pendulinus*, all clutches are cared for by a single parent (either the female or the male, Pogány et al., 2008). Strikingly, more than 30% of all nests are deserted by both parents, despite the fact that the clutch is fully viable and the parents have invested a lot in nest construction and egg-laying (Pogány et al., 2015; Van Dijk et al., 2012). This empirical fact is in line with our finding that biparental desertion can be an evolutionary outcome coexisting with other patterns. Chinese penduline tits *R. consobrinus* show the most complex care system in this genus: uniparental care, biparental care and biparental desertion coexist in the same population; and two well-studied populations differ considerably regarding the parental care patterns (female-only care is the dominant pattern in one population, whereas biparental care prevails in the other, Zheng, 2022, see Supporting Information S1). These findings agree well with the predictions of our model: the season length in the two populations is about 110 days, and, as predicted in Figure 4, the population with lower uniparental care efficacy ($U=66\%$) mainly exhibits biparental care, while uniparental care is the most common pattern in the population with higher uniparental care efficacy ($U=76\%$).

Our model shows that alternative outcomes are also possible (and actually common; see Figure 4) for the same set of parameters. This implies that differences in parental care patterns across populations of the same species are not necessarily shaped by external factors. A second implication is that systems with alternative equilibria have, on a long timescale, the tendency to switch from one equilibrium state to an alternative one (Long, 2022). A famous example is geomagnetic reversal, the switch in polarity of the Earth magnetic field, which occurred repeatedly in the history of our planet (Singer et al., 2019). As shown in Supporting Information Figure S4, such transitions are also observed in our model: on a longer timescale, our model populations switch, seemingly spontaneously and very rapidly, from one parental care pattern (e.g. female care) to a very different one (e.g. a mixture of male care and biparental care). In other words, our model predicts that parental care patterns can be 'evolutionarily labile'. This is confirmed by recent phylogenetic studies, which conclude that species belonging to the same clade and having a similar social system, breeding system and similar ecological requirements often differ in their parental care pattern (Furness & Capellini, 2019; Remeš et al., 2015).

In our model, males invest more time in nest-building than females. As we neglect other forms of prezygotic investment (like the production of a clutch of eggs by females), we can use the model to test Trivers' (1972) ideas on parental investment. Trivers argued that the sex with the higher investment before fertilization has 'more to

lose' and should therefore be more readily selected to provide care than the other sex. This line of reasoning was criticized by Dawkins and Carlisle (1976), who argued that care decisions should not reflect past investments but future benefits. Our simulation results, summarized in Figure 4, do not support Trivers' theory. Although the prezygotic investment of males is, in our model, consistently higher than that of females, male-only care did not evolve more often than female-only care. Our results suggest that parental care decisions are not predestined by prezygotic investment, but mainly reflect other factors, such as season length.

It is generally thought that biparental care evolves under challenging ecological conditions, where a single parent is not able to provide sufficient care (Eldegard & Sonnerud, 2009; Remeš et al., 2015), while uniparental care is expected to evolve when a single parent is almost as efficient in raising the offspring as both parents are together (Thomas et al., 2007). Interestingly, a recent phylogenetic study on parental cooperation in birds did not find evidence for the general idea that the type of parental care (uniparental vs biparental) is associated with ecological factors, such as predation pressure (Long et al., 2022). Figure 4 shows that, by and large, the predictions of our model are in line with conventional wisdom: biparental care is the dominant pattern when uniparental care efficacy is low, and uniparental care is dominant for a high uniparental care efficacy. However, there are some interesting deviations from this general pattern. In some simulations, uniparental care became the dominant strategy although the efficacy of uniparental care was relatively low (e.g. 70%, 170 days). This resembles findings in some natural systems where uniparental care has evolved despite the fact that offspring mortality is quite high (Cruz-López et al., 2017; Griggio & Pilastro, 2007). In other simulations, biparental care became the dominant strategy although the efficacy of uniparental care was relatively high (e.g. 80%, 120 days). This corresponds to findings in species with biparental care, where the nestlings could survive well even after the removal of one of the parents (Bulla et al., 2017; Goymann, 2020). We would like to stress, however, that our results on biparental care should not be overinterpreted, as our simple model neither considers sexual conflict during parental care (e.g. Royle et al., 2002) nor synergistic effects arising from parental division of labour (Pilakouta et al., 2018).

Season length is important, as it determines the maximum number of successful breeding attempts in a given year. The time needed for activities like nest-building, egg-laying, incubation and caring for the nestlings until fledging are all relatively fixed, resulting in a species-specific breeding cycle. Animals with different cycle lengths may adjust their parenting strategy in different ways to changes in season lengths. In rock sparrows, the experimental reduction of season length induced a higher desertion rate of female parents before fledging (Griggio, 2015). In contrast, a shorter breeding season enhanced the tendency to care in Kentish plovers and blackbirds (Jankowiak & Wysocki, 2016; Székely et al., 1999). Additionally, the effects of season length on the two sexes can be asymmetric. In our model, males have to spend more time on nest-building than females. As a consequence, males experience a stronger selection pressure

than females to 'seize time' for more breeding attempts rather than to spend time on caring. This may explain why male desertion, but not female desertion, evolves when uniparental care efficacy is low ($U = 70\%$ in Figure 4) and the season is sufficiently long (≥ 110 days) to allow for two breeding attempts.

Climate change is expected to either expand or reduce season length, depending on the geographic region (Dunn & Møller, 2014; Hällfors et al., 2020). One could speculate whether this will lead to a mismatch between the 'old' parental care pattern and the 'new' season length and/or induce an evolutionary change to a new care pattern. However, predictions may be hampered by the fact that uniparental care efficacy most likely will be affected by climate change as well. For instance, passerines may either profit from a higher insect abundance under warmer conditions (Hidalgo Aranzamendi et al., 2019), or suffer from a lower food availability as they are no longer able to predict the annual abundance peak of their insect prey (Barras et al., 2021). In other words, climate change will induce a shift in both dimensions in Figure 4 (season length and uniparental care efficacy). If both types of the shift are known, models like the one discussed here can be used to discuss the likely repercussions of climate change on the parental care pattern. However, it is not obvious that general, overarching conclusions can be drawn. Climate effects on season length, uniparental care efficacy and their association will strongly depend on regional circumstances and species-specific peculiarities, such as food category and vulnerability to predation. More specific models designed by integrating characteristics of regions and clades will help to explore the implications of climate change on the evolution of parental care patterns.

AUTHOR CONTRIBUTIONS

Jia Zheng designed and implemented the model, analysed the simulation results and wrote and revised the manuscript. Jan Komdeur joined supervision and edited the manuscript. Franz J. Weissing provided the main supervision on the model design and graphic creation and revised the manuscript.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest to declare for this study.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.x3ffb7n0> (Zheng et al., 2023).

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SUPPORTING INFORMATION

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

Supporting Information S1. Breeding biology of Chinese penduline tits.

Supporting Information S2. Graphical overview of the simulation model.

Supporting Information S3. Consistency across replicates and comparison with genetic drift.

Supporting Information S4. Transitions between alternative evolutionary outcomes.

Supporting Information S5. Effect of initial conditions on the simulation outcome.

Supporting Information S6. Effect of the mating rate on the simulation outcome.

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