The evolution of parental sex roles

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The research presented in this thesis was carried out at the Theoretical Research in Evolutionary Life Sciences group (TRÊS) and the Behavioural and Physiological Ecology group (BPE) from the Groningen Institute for Evolutionary Life Sciences (GELIFES) of the University of Groningen (The Netherlands). Part of this research was also carried out at the Evolution and Biodiversity research group, which is part of the Department of Biology & Biochemistry of University of Bath (UK).

Xiaoyan Long received a PhD-grant from China Scholarship Council (CSC grant NO. 201606380125). Part of the work in this thesis was funded by the European Research Council (ERC Advanced Grant No. 789240) under the European Union's Horizon 2020 research and innovation programme. The printing of this thesis was funded by the University Library and the Graduate School of Science and Engineering of the University of Groningen.

Cover design: 廖志荣 (Zhirong Liao), 龙晓燕 (Xiaoyan Long)

Cover Illustration: 廖志荣 (Zhirong Liao)

Figures: All by 龙晓燕 (Xiaoyan Long), except for the pictures on the chapter title-pages by 廖志荣 (Zhirong Liao).

Layout and printing: Mercedes Benjaminse | proefschriftmaken.nl

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university of
groningen

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PhD thesis

to obtain the degree of PhD at the
University of Groningen
on the authority of the
Rector Magnificus Prof. C. Wijmenga
and in accordance with
the decision by the College of Deans.

This thesis will be defended in public on

Tuesday 17 May 2022 at 14.30 hours

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To my beloved mom, dad and grandma

献给我挚爱的爸爸，妈妈和外婆

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Chapter 1

Introduction

Xiaoyan Long

One of the most fascinating and conspicuous behaviours in animals is parental care[1]. Rather than simply supplying proteins and yolk lipids to eggs, parents of many animals provide extensive care to increase the survival and growth of their offspring, from nest construction to egg attendance and food provision (Clutton-Brock, 1991; Smiseth et al., 2012). For these elaborate forms of care, the extent to which each sex is involved differs remarkably between species (Balshine, 2012; Trumbo, 2012). The term *parental sex roles* has been coined to refer to the way parental care is distributed over the female and male parent.

In mammals, females are typically the primary caregivers for their offspring (Kleiman & Malcolm, 1981; Balshine, 2012). In many species, the female warms, protects and feeds her young until they become independent (e.g., Russell, 1982; Pal, 2005). In approximately 10% of mammalian genera, such as some rodents and primates (Dewsbury, 1985; Fernandez-Duque et al., 2009), males assist females with caring chores (Kleiman & Malcolm, 1981; Balshine, 2012). In most avian taxa, both parents participate in parental care activities, such as nest building, egg incubation, chick defence, and chick feeding (Cockburn, 2006; Balshine, 2012). Only in a few species (e.g., some shorebirds (Székely et al., 2007)) does one of the parents undertake all care tasks. In fishes where parents provide parental care, males often care for their offspring alone, whereas female-only care and biparental care are less prevalent (Blumer, 1979; Mank et al., 2005). When it comes to parental care in amphibians, parents abandon newly deposited eggs in most species. However, in some species parents display conspicuous parental behaviour, such as guarding eggs and carrying tadpoles in/on their bodies (Lehtinen & Nussbaum, 2003). In those where parents do care, female-only care is just as common as male-only care, while biparental care is very rare (Balshine, 2012; Furness & Capellini, 2019). Likewise, most reptiles do not take care of their offspring. In species whose parents provide parental care (e.g., guarding the nests), female-only care is the most widespread pattern, except for a few species of crocodilians providing biparental care (Shine,1988; Balshine, 2012). Finally, invertebrates also offer a wide range of care to their progeny, ranging from egg attendance to food provisioning (Trumbo, 2012; Wong et al., 2013). In most species, females provide the vast bulk of care, with only a few species exhibiting exclusive male care or biparental care (Trumbo, 2012).

Diversity in how parental care is distributed over the female and male parent exists not only at the interspecific level, but also at the intraspecific level. In some species, such as Eurasian penduline tits (*Remiz pendulinus*) (Szentirmai et al., 2007; Van Dijk et al., 2012) and Johnstone's whistling frogs (*Eleutherodactylus johnstonei*) (Bourne,

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[1] Throughout this thesis parental care is defined as any behaviour that is directed towards offspring with the intention of increasing offspring fitness, and that exhibits after gamete supply (Clutton-Brock, 1991; Klug et al., 2012).

1998), female-only care coexists with male-only care in the same population. In some other species, such as Chinese penduline tits (*Remiz consobrinus*) (Zheng et al., 2018), Rock sparrows (*Petronia petronia*) (Griggio & Pilastro, 2007), Galilee St Peter's fishes (*Sarotherodon galilaeus*) (Balshine-Earn, 1997) and burying beetles (*Nicrophorus vespilloides*) (Eggert, 1992; Smiseth & Moore, 2004), all three types of care pattern—female-only care, biparental care, and male-only care—exist side by side.

In addition to being remarkably diverse between and within species, parental sex roles are also evolutionarily labile. By using recent advances in molecular phylogenies and statistical techniques, researchers discovered that transitions between female-only care, biparental care, and male-only care happen frequently in animals (Reynolds et al., 2002; Gilbert & Manica, 2015). Interestingly, transitions in care patterns are not always unidirectional, as they can occur in the opposite direction. In primates, female-only care has switched to biparental care on several occasions, and *vice versa* (Reynolds et al., 2002). In shorebirds, there have been transitions from biparental care to male- or female-only care, with approximately equal probability (Reynolds et al., 2002). In cichlid fishes, the most typical transition is from biparental care to exclusive female care, while a few transitions occur in the opposite direction (Goodwin et al., 1998; Reynolds et al., 2002). In neotropical poison frogs, male-only care has switched towards female-only and biparental care sporadically (Summers & McKeon, 2004; Summer & Tumulty, 2014). And in holometabolous insects, biparental care has been found to evolve from female-only care and no care. However, biparental care is relatively unstable since, once established, it tends to shift back to female-only care (Gilbert & Manica, 2015).

This stunning diversity in parental care patterns poses a considerable challenge to evolutionary theory. Why do both parents care for their offspring in some species (or at some times), while only one parent cares for the offspring in other species (or at other times)? In case of parental asymmetry, which factors decide whether the male or the female parent does most of the caring? The answers to these questions have implications beyond parental care, because parental care patterns interact with other key components of animal life, such as sexual selection (Trivers, 1972; Kokko & Jennions, 2008; Alonzo, 2012), mating systems (Ligon, 1999; Alonzon, 2010), life histories (Klug & Bonsall, 2010; Klug et al., 2013), social environment (Rebar et al., 2020) and sex allocation (Rosenheim et al., 1996; Komdeur, 2012). In the remainder of the introduction, I will briefly review what we currently know about the two aforementioned questions.

BIPARENTAL CARE

Biparental care, where the male and female parent work together to nurture their offspring, is relatively rare in animal species, but it has evolved recurrently in a variety of taxonomic groups, most notably in birds (Cockburn, 2006; Balshine, 2012). Except in a few animal taxa where biparental care evolves directly from no care (in, e.g., some holometabolous insects (Suzuki, 2013; Gilbert & Manica, 2015) and ray-finned fishes (Mank et al., 2005)), biparental care is more likely to develop when one of the sexes already provides parental care (Reynolds et al., 2002, Gilbert & Manica, 2015). In general, the ancestors of mammals, birds and insects were characterised by exclusive female care; biparental care occurs when males participate in care activities alongside the caring females (Burley & Johnson, 2002; Reynolds et al., 2002; Tullberg et al., 2002; Gilbert & Manica, 2015). On the contrary, exclusive male care is the primitive pattern in some amphibians, and thus, the occurrence of female parental care is crucial for the evolution of biparental care (Summers & Earn, 1999; Furness & Capellini, 2019).

One long-established hypothesis posits that biparental care should be expected in hostile and challenging environments (harsh environment hypothesis, Wilson, 1975; Carey, 2002). In harsh conditions, living costs can be exceedingly high due to a possible shortage of food, intense predation pressure, and unpredictable weather; as a result, a single parent may not be able to provide adequate parental care to ensure offspring survival and growth, and thus both parents are required for the offspring (Wesolowski, 1994). This harsh environment hypothesis has been investigated in a wide range of species (Bredy et al., 2007; Brown et al., 2010; AlRashidi et al., 2011; Vincze et al., 2013; Remeš, et al; 2015; Cole & Rosengaus, 2019; Vági et al., 2020; Moss & Moore, 2021; Gonzalez-Voyer et al., 2022), and phylogenetic comparative studies found that some environmental factors are associated with biparental care while others are not. For example, phylogenetic studies in frogs and toads (Anura) demonstrate that biparental care is strongly correlated with nutrient scarcity (Brown et al., 2010) and/or desiccation risk (Vági et al., 2019), but not with harsh and unpredictable climates (Vági et al., 2020). Also in birds, no association was found between climate conditions and parental care patterns (Remeš et al., 2015; Gonzalez-Voyer et al., 2022); however, there are other “harshness” factors, such as high risk of predation and limited food resources, that may be related to biparental care. In **Chapter 2**, I will investigate whether environmental factors that reflect food availability and predation pressure are correlated with care patterns in birds using the most comprehensive dataset and state-of-the-art phylogenetic techniques.

Once biparental care is established, conflicts of interest between the male and female parents on how much care each should contribute inevitably arise unless there is life-long monogamy (Trivers, 1972; Parker et al., 2002; Houston et al., 2005; Lessells, 2012). This is because care provided by either parent benefits the offspring, and thus the reproductive success is shared by both parents; however, only the caring parent pays the costs of its own effort in terms of remating opportunities. Therefore, in attempting to maximise lifetime reproductive success, each parent should ensure the success of current reproduction and optimise future reproductive potential. Consequently, each parent benefits the most when its partner does most of the caring. In face of such conflict, why, then, is stable biparental care able to evolve and maintain in some animal species?

It has been suggested that biparental care can be stabilised in populations when it has synergistic (rather than additive) effects on offspring fitness (Barta et al., 2014; Fromhage & Jennions, 2016; Alger et al., 2020). In this case, the male and female parents exhibit complementary parental behaviours, benefiting their offspring more than twice as much as a single parent would (Maynard Smith, 1977; Grafen & Sibly, 1978; Yamamura & Tsuji, 1993). Synergistic benefits of biparental care can arise when male and female parents specialise in different care duties (e.g., in Boreal owls (*Aegolius funereus*), females incubate and brood the young while males feed their mate and offspring (Korpimäki, 1981; Zárybnická, 2009)) or when parents take turns participating in the same care activity (e.g., in Great tits (*Parus major*), parents take turns feeding the young (Johnstone et al., 2014)). By applying these strategies, parents might experience weakened sexual conflict over care and hence have a stronger proclivity to care jointly. In **Chapter 3** of this thesis, I will systematically investigate how parental synergy influences the evolution of parental care, and I will show that parental synergy does, under certain conditions, lead to biparental care, but that this is not always the case.

In situations where a single parent is able to provide all the care needed by the offspring, sexual conflict is especially intense. Biparental care may shift towards uniparental female care or uniparental male care. This will be the focus of next section which attempts to summarise ultimate factors promoting the evolution of uniparental care and, more importantly, identifies which sex should care under various circumstances.

UNIPARENTAL CARE—WHO SHOULD CARE?

One of the fascinating observations in nature is that the female typically, but not always, provides most of the caring (Balshine, 2012; Trumbo, 2012; Klug et al., 2012; Kokko & Jennions, 2012). In an influential paper that lays the groundwork for modern studies of the evolution of parental care, Trivers (1972) claimed that this phenomenon can be attributed to anisogamy, the ubiquitous finding that females produce much larger gametes than males. According to Trivers, the female parent has already made a greater investment in each offspring than the male parent, and hence has more to lose if the offspring do not survive. Therefore, Trivers argues, females should be more strongly selected than males to engage in the subsequent parental care (i.e., post-zygotic parental care). This argument was refuted by Dawkins and Carlisle (1976), who stated that investment decisions should be based on *future* costs and benefits, rather than on investments made in the past. While agreeing with this critique, some studies pointed out that Trivers' prediction can be resurrected when other factors are taken into account, such as costly competitive traits and uncertainty of paternity (Queller, 1997; Kokko & Jennions, 2003; 2008; 2012; Klug et al., 2012; Fromhage & Jennions, 2016). Thus, whether or not sex role divergence can ultimately be traced back to anisogamy is still debated in the literature. In **Chapter 3** of this thesis, I will show that there might be causal links from pre- to post-zygotic parental sex roles even when the sexes do not differ in other aspects. In fact, a small asymmetry in pre-zygotic parental investment can induce a large asymmetry in post-zygotic investment, but the relationship between the two types of asymmetry is more complicated than previously thought.

Anisogamy is characterised by pronounced sexual asymmetry not only in terms of gamete size, but also in terms of gamete number. In general, the number of sperms far outweighs the number of eggs, which can result in sperms from multiple males competing for one egg produced by a single female. As a consequence, males may often be uncertain of their paternity as they may not be the genetic father of all offspring in a brood (Alonzo & Klug, 2012). It has been argued that, because of this uncertainty, males should generally offer less, if any, care (Trivers, 1972; Queller, 1977; Kokko & Jennions, 2008). Although this argument seems straightforward, it has been hotly debated in the literature. The early model studies of Maynard Smith (1977) and Grafen (1980) directed the attention to the fact that a male's paternity should be equally uncertain in future breeding attempts as in the current one and concluded that uncertainty about paternity alone is not sufficient to explain care decisions in males. Some authors, however, pointed out an important gap in the arguments of Maynard Smith (1977) and Grafen (1980): any paternity a male loses must be gained by another male (Queller, 1997; Houston & McNamara, 2002; 2005). When the model ensures self-consistence, the prediction of Maynard Smith (1977) and Grafen (1980) no longer holds true (Queller, 1997; Houston & McNamara, 2002; Kokko & Jennions, 2008; Fromhage & Jennions, 2016). Moreover, the negative correlation between uncertainty of paternity and male care may not be the norm (Kempenaers & Sheldon, 1997; Sheldon, 2002; Houston & McNamara, 2002; Alonzon, 2010). For example, when individual males differ in their ability to obtain extra-pair matings, low-quality males may find it difficult to engage in extra-pair matings; just because their alternative options are restricted, they should put a lot of effort into each mating that they can achieve, even if their paternity is low (Houston & McNamara, 2002). Taken together, these studies indicate that the relationship between certainty of paternity and male care is more nuanced than originally predicted, and that how males adjust their parental effort in response to uncertainty of paternity is likely to be conditional on a variety of factors (Alonzo & Klug, 2012). Although a systematic investigation of the effect of uncertainty of paternity on sex-specific parental care behaviour is beyond the scope of my thesis, it is a fascinating and vital topic that I intend to study in greater depth in the future.

The fact that smaller and more numerous sperms compete for fertilization of larger and fewer eggs may lead not only to uncertainty of paternity, but also to sexual selection on males (Andersson, 1994, Jones & Ratterman, 2009). Sexual selection is well-known for driving the evolution of conspicuous characteristics in males, such as brilliant colour patterns, elaborate calls and songs, and exaggerated weapons, all of which can be detrimental to viability and fecundity but auspicious for winning intrasexual competition for mates (Darwin, 1871; Andersson, 1994). Trivers (1972) was the first to point out that sexual selection may be intrinsically linked to the evolution of parental care, and this idea makes a step forward in our understanding of sex role evolution. Numerous studies have demonstrated a strong correlation between sex differences in parental care and sexual selection, with exclusive female care being associated with strong sexual selection on males (e.g., Liker et al., 2015) and exclusive male care being associated with strong sexual selection on females (e.g., Amundsen & Forsgren, 2001; Cunha et al., 2017). Nevertheless, the causal relationships between sexual selection and parental care strategies are not yet clear. On the one hand, sexual selection may be a driver of sex-specific parental sex roles. The underlying idea is that the sex subjected to sexual selection has a greater variance in mating success than the other sex (Bateman, 1948; Wade, 1979). As some individuals of the sex exposed to sexual selection are more likely to find a mate than others, they benefit more from seeking additional mating opportunities rather than caring for the offspring (Kokko & Jennions, 2012). Moreover, there might be a trade-off between parental and mating effort (Magrath & Komdeur, 2003). When individuals allocate more resources into traits that enhance mating opportunities (e.g., armament and ornamentation), there is a corresponding reduction in the amount of time and energy spent providing parental care. Consequently, the sex engaged in intense mating competition is selected against providing care, which induces the other sex to be choosy and to offer care. On the other hand, sexual selection might be a consequence rather than a cause of parental care strategies (Trivers, 1972; Arnold & Duvall, 1994). When one of the sexes undertakes all caring responsibilities, the accessibility of that sex on the mating market is dramatically decreased, resulting in intense competition among members of the non-caring sex for access to the limited number of mates. The resulting strong competition in the non-caring sex, in turn, diminishes the incentive for this sex to care, as indicated above. To disentangle the causality between sexual selection and parental care patterns, in **Chapter 3** of this thesis I will allow female preferences and male ornaments to coevolve with parental strategies, and I will show the relationship between parental strategies and mating strategies is more intricate than typically assumed in verbal argumentation.

Following on from the preceding point, the strength of mating competition is determined by the relative abundance of males and females on the mating market, which refers to an important component in the evolution of sex roles, namely the ‘operational sex ratio’ (OSR, the ratio of males to females among those individuals that are ready for mate) (Emlen & Oring, 1977). Traditionally, the OSR has been expected to play a pivotal role in the evolution of parental care (Emlen & Oring, 1977; Clutton-Brock, 1991). The greater the degree of bias in the OSR, the more intense the mating competition among members of the overrepresented sex. It has been argued that, as a result, the sex overrepresented in the OSR should place more emphasis on competitiveness on the mating market than on parental care (Emlen & Oring, 1977; Clutton-Brock, 2017). However, this argument has been criticised. According to Kokko and Jennions (2008), when the OSR is sex-biased, members of the majority sex on average have a lower chance of finding a mate, and hence each mating becomes more valuable, favouring a greater parental investment in current reproduction. So, to what extent and in what ways does the OSR influence parental care patterns? In **Chapter 4** of this thesis, I will give an answer to this question.

Another sex ratio, the adult sex ratio (ASR, the ratio of males to females in the adult population) has recently attracted a lot of attention. Various studies have argued that the ASR may be a more accurate predictor of parental sex roles than the OSR (Kokko & Jennions, 2008; 2012; Székely et al., 2014; Schacht et al., 2017). The main reason is that the ASR is subject to the so-called “Fisher condition”. Fisher (1930) argued that in diploid sexually reproducing organisms each offspring has one adult father and one adult mother, hence the *total* number of offspring produced by each sex must be equal. If there is any bias in the ASR (e.g., because the two sexes have different mortality rates), the *per capita* number of offspring must differ between the sexes: a member of the more common sex in the adult population produces on average fewer offspring than a member of the rarer sex. As a consequence, each mating event is relatively more important for a member of the majority sex than for a member of the minority sex, making the members of the majority sex more inclined to invest more time and energy in the resulting brood. Thus, female-biased care is predicted to occur when the ASR is female-biased, and male-biased care is expected arise when the ASR is male-biased. However, this argument has largely ignored feedback between the ASR and parental care asymmetry. If parental care is a high-risk activity (e.g., conspicuous care behaviours may attract predators (Smith & Wootton, 1995; Reguera & Gomendio, 1999)), members of the caring sex will die at a higher rate, thus reducing (or even reversing) the ASR bias inducing them to care (Fromhage & Jennions, 2016, Jennions & Fromhage, 2017). Accordingly, it becomes difficult to distinguish cause and consequence when addressing the relationship between the ASR and parental care strategies. In **Chapter 4** of this thesis, I will study the causal relationship between ASR and parental care using a comprehensive evolutionary model.

While various studies have attempted to examine the role of OSR and ASR in the evolution of parental care, far less attention has been paid to the role of the most fundamental sex ratio, i.e., the primary sex ratio (PSR, the sex ratio of males to females at conception). In general, the PSR is supposed to be unbiased according to the Fisher condition (Fisher, 1930): all else being equal, the more common sex in the PSR has a lower *per capita* reproductive output (i.e., the expected number of lifetime matings), thus favouring parents to produce more members of the minority sex until the PSR reaches the point where the number of males and females is equal. However, the PSR can be biased if the costs of raising male offspring and female offspring are not equal. The reason for this is that parents have a tendency to allocate their reproductive resources equally between the production of sons and daughters ('Fisher's principle of equal allocation'), which results in an overproduction of the 'cheaper' sex (Fisher, 1930; West, 2009). Therefore, a number of questions arise, including whether a bias in the PSR has a long-lasting effect on parental sex roles, whether parental decisions have a feedback effect on the PSR, and, perhaps most importantly, whether Fisher's principle of equal allocation still holds when the PSR evolves in tandem with parental care. This topic will be covered in greater depth in **Chapter 5** of this thesis.

THIS THESIS

This thesis strives to explain the remarkable diversity in parental sex roles of males and females. As a starting point, I conduct a comprehensive phylogenetic analysis to explore why various parental care systems are observed across a broad spectrum of avian species. Then, in order to gain a better understanding of the causes and effects of sex role evolution, I develop theoretical models utilizing mainly individual-based evolutionary simulations. Such a simulation approach is highly valuable for checking the results of analytical analysis, which has been well establish in sex role theory (for example, Kokko and her colleagues have developed a comprehensive and elegant modelling framework to study the role of numerous factors involved in the evolution of parental care (see Kokko & Jennions, 2008; Fromhage & Jennions, 2016)). Moreover, the simulation approach makes it simple to model complicated scenarios in a realistic manner. For example, sexual selection can be implemented in a more natural fashion (see Chapter 3 for more details) than in Kokko and Jennions (2008)'s model, in which sexual selection was restricted to a set of fixed parameters that cannot evolve in concert with parental care. Last but not least, simulation studies can directly track phenotype for each individual in a population, making them capable of dealing with changing patterns of phenotypic variation, which has been shown to have substantial evolutionary implications. Given the strengths of individual-based simulations, I employ simulation models as a primary focus, with analytical analysis as a supplement. By combining both approaches (albeit simulations are the main focus), I aim to provide robust results and general insights under more realistic assumptions. Below I give an overview of each chapter of this thesis.

In **Chapter 2**, I apply phylogenetic comparative study to investigate the extent to which environmental factors and life-history characteristics influence parental strategies in birds. Bird species differ considerably in their parental care patterns (e.g., intensity of care, sex differences in parental roles). Researchers have linked these patterns to differences in ecological factors and life histories, but a robust empirical test of the importance of these predictors is still lacking. Here, I collect the most comprehensive dataset of parental care patterns in birds (including 1101 bird species from 119 families). By means of a phylogenetic analysis, I investigate how parental care patterns is associated with ecological parameters (e.g., food type, nest structure and coloniality) and life history characteristics (e.g., chick development mode and body size). I show that colonial and altricial species provide more biparental care than solitary and precocial species, respectively, and that food type, nest structure, and body size do not correlate with parental care patterns in birds. Moreover, I show that in a specific taxonomic group, i.e., shorebirds, there is a higher level of biparental cooperation during pre-hatching phase than during the post-hatching phase, suggesting that parental sex roles at different breeding phases may also be highly diverse between and within species.

In the remainder of this thesis, I adopt individual-based simulations to explore the effect of a variety of factors on the evolution of parental sex role. Theoreticians have built numerous mathematical models to investigate the evolution of sex differences in parental roles over the last two decades. However, these analytical models are only tractable if numerous simplifying assumptions are made. To overcome this limitation, I use the simulation approach to study the evolution of parental care. In particular, in this thesis, I complement the mathematical analyses of Kokko and Jennions (2008) and Fromhage and Jennions (2016) with simulation studies that make use of a very similar modelling framework.

In **Chapter 3**, I show that simulation outcomes are surprisingly different from earlier mathematical predictions, despite the fact that very similar assumptions to those used in analytical models are made. The reason for this is that the main analytical approaches (e.g., selection gradient methods) used to derive these results are based on the assumptions of a monomorphic population, while my simulations show that parental conflict drives the population to a polymorphic state with very different properties than those of a monomorphic population. In addition, I show that sex roles can be evolutionary labile (with rapid switches between alternative stable equilibria in the absence of any external change), that the interplay of parental care and sexual selection is more intricate than suggested by current theory (the evolution of asymmetric care precedes the evolution of mate choice, rather than being driven by sexual selection), that synergistic benefits of biparental care do not always induce egalitarian biparental care (small synergy results in fluctuating polymorphism in both sexes, with some individuals offering a high level of care while others do not care at all), and that sex differences in pre-zygotic parental investment have a predictable effect on parental sex roles in post-zygotic care.

In **Chapter 4**, by systematically changing life history characteristics (e.g., maturation rate, mortalities at different life stages) in a sex-specific manner I study how the two sex ratios (i.e., OSR and ASR) match to evolved parental sex role. The main conclusion is that neither OSR nor ASR are drivers of parental sex roles, as the same parental patterns evolve under diverse combinations of OSR and ASR. In contrast, sex differences in life history characteristics are a good predictor of sex differences in parental care: typically, but not always, the sex with the lower mortality or the faster maturation is selected to provide most (or all) of the care.

In **Chapter 5**, I consider a model where the investment per son and daughter is an evolvable property that coevolves with the PSR. I show that Fisher's equal allocation principle, one of the most basal results of evolutionary theory, ceases to hold when the PSR does not evolve in isolation but in concert with parental investment. In some scenarios, the more expensive sex is even overproduced (rather than underproduced, as predicted by Fisher's principle). Moreover, I demonstrate that polymorphic populations occur under some circumstances, with some parents predominantly producing and caring for sons while the other parents focus their care on daughters. In addition, I show that cost differences between male and female offspring can be an important determinant of parental sex roles, a factor that has been largely overlooked.

Bringing everything together, I show that simulation outcomes are quite different from the standard analytical predictions. To further understand the causes of these discrepancies, I will highlight some essential components that are overlooked in earlier mathematical models in **Chapter 6.** Finally, I will close with some thoughts on the evolutionary implications of these components. With this I intend to offer some important and thought-provoking insights that will spur more in-depth research into sex role evolution.

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Chapter 2

Does ecology and life history predict parental cooperation in birds? A comparative analysis

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Under review at Behavioral Ecology and Sociobiology

ABSTRACT

In animals, species differ remarkably in parental care strategies. For instance, male-only care is prevalent in teleost fishes, while biparental care predominates in birds and female-only care is widespread in mammals. Understanding the origin and maintenance of diversified parental care systems is a key challenge in evolutionary ecology. It has been suggested that ecological factors and life-history traits play important roles in the evolution of parental care, but the generality of these predictions has not been investigated across a broad range of taxa. Using phylogenetic comparative analyses and detailed parental care data from 1101 avian species that represent 119 families of 26 orders, here we investigate whether parental strategies are associated with ecological variables (i.e., food type, nest structure and coloniality) and life-history characteristics (i.e., chick development mode and body size). We show that parental care strategies are in relation to coloniality (solitary, semi-colonial, colonial) and chick development mode (altricial vs. precocial). Colonial and altricial species provide more biparental care than solitary and precocial species, respectively. In contrast, food type (plant, invertebrate, vertebrate), nest structure (open vs. closed) and body size do not covary systematically with parental care patterns in birds. Taken together, our results suggest that living in groups and/or having high-demand offspring are strongly associated with biparental care. Towards the end, we discuss future research directions for the study of parental care evolution.

SIGNIFICANCE STATEMENT

Animal species differ remarkably in the amount of care parents provide to their offspring and in the distribution of care tasks over the parents. In birds, for example, the young of some species are quite independent from the start, while the young of other species are helpless after hatching, requiring a lot of care. Moreover, either the female or the male does most of the caring some species, while the parental tasks are shared equally in still other species. To understand the diversified parental care patterns, we applied advanced comparative methods to a large data set comprising over 1000 bird species. The analysis reveals that the parents tend to share their care duties equally when they live in groups and/or have offspring that are born helpless, and that parental care patterns are not associated with diet, nest type or body size. Hence, living in groups and having high-demand offspring seem to play important roles in the evolution of parental care.

Keywords
Parental care, food type, nest structure, coloniality, chick development mode, body size

2.1 INTRODUCTION

Biparental care, a form of cooperation between the male and female parent, is observed across many animal taxa including insects, fishes, amphibians, birds and mammals (Balshine, 2012; Trumbo, 2012; Vági et al., 2019). When parents collaborate in caring, the offspring have a better chance of surviving, especially in situations where one parent cannot raise the young successfully (Brown et al., 2010; Pilakouta et al., 2018). However, conflicts over how much care each parent should provide are inescapable, because parents share the benefits of joint care while each parent pays its own costs of caring (e.g., time and energy); consequently, the sexes can typically not maximise their reproductive success simultaneously (Parker et al., 2002; Houston et al., 2005; Lessells, 2012). Therefore, biparental care is an excellent system for investigating cooperation and conflict in animal societies (McNamara et al., 2000; Van Dijk et al., 2012; Barta et al., 2014).

Recent work including experimental manipulations (Tumulty et al., 2014; Pilakouta et al., 2018), field-based studies (AlRashidi et al., 2011) and comparative analyses (Brown et al., 2010; Remeš et al., 2015) has furthered our understanding of the evolution of parental cooperation. Here, we define parental cooperation as a parental strategy that increases the reproductive success of caregivers' partner, ranging from egalitarian biparental care where the two parents equally share in the parental duties, to partial biparental care where one of the parents cares to a much higher extent than the other, and uniparental care where the parents do not share the care tasks and only one of the parents cares for the young (Cockburn, 2006; Remeš et al., 2015). It has been suggested that sexual selection (e.g., sexual size dimorphism), demography (e.g., adult sex ratio), and mating systems are associated with parental cooperation (Székely et al., 2014; Remeš et al., 2015; Vági et al., 2020). Ecological variables and life-history traits have also been put forward to explain parental cooperation (Wilson, 1975; Klug & Bonsall, 2010), but little is known about the generality of these predictions.

That ecological factors predict parental care strategies has been the subject of considerable discussion (Cockburn, 2006; Wong et al., 2013). One long-established hypothesis posits that a high level of parental cooperation can be expected in harsh and challenging conditions (Wilson, 1975; Carey, 2002). To investigate this hypothesis, we here look at the impact of three ecological factors on parental strategies: food type, nest structure and coloniality. First, scarcity of food is supposed to be associated with biparental cooperation (Andersson, 2005; Eldegard & Sonerud, 2009). It is argued that biparental care can be expected in species where parents have to catch large and dispersed prey (e.g., amphibians, fishes and mammals) in order to provision their young (Crook, 1964; Slagsvold & Sonerud, 2007). This could be because juveniles are not yet be capable of finding and catching this type of prey (Newton, 1979; Hunt et al., 2012), necessitating a higher level of care from their parents under such conditions. Therefore, parental cooperation may be required to guarantee a consistent food supply and to protect the nest when one parent is absent. In contrast, species that feed on plant materials (e.g., fruits, seeds and nectar) might exhibit a greater prevalence of uniparental care, as such food resources tend to be seasonally abundant and one parent should suffice to efficiently provision the young (Lack, 1968; Morton, 1973; Barve & La Sorte, 2016).

Second, nest structure is suggested to be related to the extent of parental cooperation, as it is crucial in determining breeding success (AlRashidi et al., 2011). Open nests such as scrapes and platforms are exposed to environment while closed nests such as cavities and burrows are covered by roofs and only accessible by a small entrance (Collias & Collias, 1984; Hansell, 2000). Previous studies have shown that open nests provide less protection from predators and lead to harsher microclimate than closed nests (Deeming, 2011; Martin et al., 2017). Therefore, species that build open nests may exhibit higher levels of parental cooperation after nest construction than species that build closed nests.

Third, colonial breeding where individuals together occupy a territory which only consists of nesting sites might also be associated with biparental cooperation (Perrins & Birkhead, 1983). Individuals living in colonies may benefit from sharing of information (e.g., foraging sites) and increasing anti-predator behavior (Brown & Brown, 2001). However, leaving the young alone in a colony with high nest density might be dangerous, as the young can easily get lost (they have many stimuli attracting them away from the nest), and as they are vulnerable to attacks of neighbours and predators (Brown & Brown, 2001; Ashbrook et al., 2008). Therefore, both parents may be required to raise the young successfully in colonies.

Life-history characteristics are also anticipated to be associated with parental care patterns (Stearns, 1976; Kolm et al., 2006; Gilbert & Manica, 2010; Klug & Bonsall, 2010; Klug et al., 2013). One central concept of life-history theory is that parental strategies are constrained by the trade-off between current and future reproduction (Williams, 1966). Here, we focus on two life-history variables that may influence the trade-off: chick development mode and body size. In empirical studies, both factors are often included as confounding variables (Liker & Székely, 2005; Liker et al., 2015; Remeš et al., 2015); only a few small-scale studies tested directly whether body size or chick development mode has an impact on parental care behavior (Thomas & Székely, 2005). Therefore, it is unclear whether life-history traits are associated with parental care in a broader range of taxa.

First, offspring demands differ between altricial and precocial species, corresponding to distinct care decisions (Vleck et al., 1979; Starck & Ricklefs, 1998; Thomas et al., 2006). In altricial species chicks are unable to obtain food and regulate the body temperature on their own. Therefore, a deserting parent might pay a great cost in terms of growth and survival of the current brood (Vleck et al., 1979; Starck & Ricklefs, 1998). Accordingly, a high level of biparental cooperation can be expected in altricial species. On the contrary, offspring of precocial species require relatively little care as hatchlings are adept at feeding themselves (Vleck et al., 1979; Starck & Ricklefs, 1998), with the result that one parent might be able to raise the young efficiently (Lack, 1968; Bennett & Owens, 2002) and the deserting sex benefits more from seeking new mates (Olson et al., 2008).

Second, stable parental cooperation is probably much easier to achieve in species with large body size (Remeš et al., 2015; Vági et al., 2019). Species with large body size have relatively low metabolic rates, and thus take a long period to develop and become independent (West et al., 2001). Moreover, large-bodied species are long-lived, leading to prolonged pair-bonding (Lindstedt & Calder, 1976; 1981; Choudhury, 1995; Jeschke & Kokko, 2008); consequently, mating opportunities are probably limited after desertion. Taken together, providing care to current broods is more beneficial, and thus biparental care may be selected in species with large body size. In contrast, species with small body size are short-lived, thus may tend to exhibit uniparental care more frequently.

Although previous studies offered insights into how some of the related factors (e.g., nesting density, developmental duration) might explain diversified care patterns (Owens, 2002; Cooney et al., 2020), no study has yet investigated all of these hypotheses across a broad range of taxa and estimated their importance. To understand to what extent and in what way do ecological conditions (e.g., food type, nest structure and coloniality) and the life-history traits (e.g., chick development mode and body size) may explain parental cooperation, we here apply phylogenetic comparative methods to the most comprehensive dataset on parental cooperation, including 1101 avian species representing 26 orders and 119 families (Fig. 1). Birds are ideal organisms for investigating the evolution of parental cooperation on the grounds that avian taxa are characterised by an extraordinary diversity in the distribution of care tasks over the two parents (Remeš et al., 2015), and data on ecological factors, life-history traits and parental behaviour are available across a broad spectrum of species. In particular, here parental care behaviour is studied at two breeding stages: pre-hatching stage (i.e., any parental behaviour displayed before the chick hatches) and post-hatching stage (i.e., any parental behaviour exhibited after the chick hatches). Previous research has discovered that parents tend to make different decisions between these two stages (Liker et al., 2015), suggesting that these two stages might be related to ecological and life-history traits in different ways. Moreover, some of the variables we are interested in might only be relevant in one of the stages. For example, one may expect food type to be correlated with parental strategies during the post-hatching stage rather than the pre-hatching stage.

Specifically, using phylogenetic comparative analyses the following predictions are investigated. First, carnivorous species should show higher level of cooperation between parents than plant-eating species. Second, species which breed in open nests should provide biparental care more frequently than those that build closed nests. Third, colonially breeding species should exhibit a higher degree of biparental cooperation than solitary breeding species. Four, biparental care should be more common in altricial species than in precocial species. Last, parents are expected to cooperate to a greater extent in species with large body size.

2.2 METHODS

2.2.1 Data collection

We collected data from reference works (e.g., The Birds of the Western Palearctic, The Birds of North America, Handbook of Australian, New Zealand and Antarctic Birds), pre-existing datasets (see below) and primary literatures by using Web of Science and Google Scholar. We added more species with available data on parental behaviour to an existing dataset used by Liker et al. (2015). Then we augmented the dataset with expanded information on parental roles by extracting data of ecological and life-history traits (food type, nest structure, coloniality, chick development mode and body mass). The final dataset included 1101 species (26 orders and 119 families) representing a broad spectrum of avian diversity. For cooperatively breeding birds (132 of 1101 species; 1.2%), we collected the data on the parental behaviour of the sexes only when parents raise the offspring without helpers. Detailed information on parental cooperation, ecology and life history was collected for most of all species, but sample size varies for different traits as data on each trait were not available for all species. Sample size for each variable is shown in Supplementary Table S1.

2.2.2 Parental care variables

Bird species exhibit diverse forms of parental care, ranging from the preparation for the nest to nutrition provision. Here, we investigate eight types of avian parental behavior: nest building, nest guarding, incubation, chick brooding, chick feeding, chick guarding, post-fledgling feeding and post-fledgling guarding. For each type of parental behavior, we followed the most well-established and widely-used protocol (see, for example, Liker et al., 2015; Remeš et al., 2015) to quantify the extent of parental cooperation. Hence, the results can be comparable to the greatest extent across studies, and the considerable diversity in parental care patterns in birds can be systematically investigated. According to the 'standard' scoring system, here the extent of parental cooperation was scored on a 3-point scale, 0: uniparental care by females or males (no cooperation between parents: 0% or 100% male care); 1: partial biparental care (low and intermediate level of cooperation: 1-33% or 67–99% male care); 2: egalitarian biparental care (high level of cooperation: 34–66% male care). Therefore, the lowest level of cooperation is uniparental care (score 0), while the highest level of cooperation is egalitarian biparental care (score 2). Scoring was necessary as quantitative data were not available for many species. For such quantitative data, it is necessary to establish arbitrary cut-off points, with the threshold being assumed prior to the data collection and analysis. When quantitative data were not available, we used the information from verbal descriptions. For instance, when a source declared "only the female incubates eggs", incubation was scored as zero.

We then divided the parental activities into (i) pre-hatching activities, which involved nest building, nest guarding and incubation and (ii) post-hatching activities, which included chick brooding, chick feeding, chick guarding, post-fledgling feeding and post-fledgling guarding. We subsequently wanted to calculate average scores for pre- and post-hatching care. This could not be done immediately, as data for some of the eight parental activities were missing for most species (only 32 species had data on all care activities). Just averaging the scores of activities for which data were available would have generated a bias, as the distribution of scores differed markedly between different care forms, and the missing data were strongly related to the care forms. For instance, data on incubation were available for almost all species (n = 1017), with a mean score of 0.90, while data on nest guarding were only accessible for 196 species, with a mean score of 1.44. By averaging over scores, the score for incubation would therefore contribute much more to the final average. To make the scores more comparable, we therefore centralised them by subtracting the average score for this activity (for all species for which data were available on this activity) from the individual scores for each care activity. Subsequently, we determined mean scores for pre- and post-hatching care by averaging the centralised scores for the three pre-hatching activities and the five post-hatching activities (as far as data were available). After score centralization, mean pre-hatching and post-hatching scores ranged from -1.5 (the minimum level of parental cooperation) to +1.5 (the maximum level of parental cooperation).

2.2.3 Ecological and life-history variables

Food type of bird species was classified into three categories: 0: plant materials which included fruits, seeds, leaves, 1: invertebrates (e.g., crustaceans and insects) and 2: vertebrates (e.g., fishes and amphibians). For omnivorous species, their mainly eaten food category was allocated (plant materials vs. invertebrates vs. vertebrates). For species in which parents and nestlings subsist on different food items, data on nestling diet was collected as it is more essential for parental care decisions, especially during chick feeding and post-fledgling feeding.

Nest structure was treated as binary variables (0: open and 1: closed). Open nests, which are exposed to adverse weather conditions and predators, included scrapes (e.g., nests of many shorebirds), cups (e.g., nests of many passerines) and platforms (e.g., nests of raptors) (Hansell, 2000). Closed nests are completely covered by the walls or pliable materials, that is, they can only be accessed by the small entrance. For instance, cavities (e.g., nests of woodpeckers), burrows (e.g., nests of many seabirds), domes and globes (e.g., nests of weavers) are all enclosed structures (Hansell, 2000). We only extracted data on nest structure from studies of natural nests (i.e., nest-box studies were excluded).

Coloniality was categorised into 0: solitary breeding, individuals breed in isolation, 1: semi-colonial breeding, some individuals never breed in groups while others aggregate at specific sites, and 2: colonial breeding, individuals are always aggregated and breed in territories with densely distributed nests (Brown & Brown, 2001; Van Turnhout et al., 2010). We only extracted data on coloniality from studies of natural nests, since the studies of nest-box artificially changed the spatial distribution of nests.

Chick development mode was categorised as follows: 0: altricial species where newly hatched offspring require prolonged parental care as they cannot move or feed themselves, such as most passerines; 1: precocial species where hatchlings are capable of moving and finding their own food, therefore they can leave the nest in a short period, such as many shorebirds. This classification is consistent with other studies (Temrin & Tullberg, 1995; Olson et al., 2008). Adult body mass (in gram) was collected as an index of body size across species in our study. When data on both males and females were available, we calculated the mean value of male and female body mass.

To check the robustness of our dataset, we compared it to previous research that included variables relevant in this study (see Supplementary Fig. S1). Parental care variables were compared to Cockburn (2006), who categorised care patterns into four groups: female-only care, biparental care, male-only care and cooperative breeding. To make data comparable, we scored each care type on a 5-point scale: 0: no male care; 1: 1–33% male care; 2: 34–66% male care; 3: 67–96 99% male care; 4: 100% male care. Moreover, because Cockburn (2006) did not explicitly present the care distribution between the male parent and the female parents in cooperatively breeding species, those species were excluded from consideration when we conducted the comparison. For ecological factors, food type was compared to Wilman et al. (2014), which has, to our knowledge, the largest dataset on diet categories in birds; nest type and coloniality were compared to Varela et al. (2007). In general, our data corresponds very closely to that of previous studies, implying that our data are quite robust.

2.2.4 Phylogenetic comparative analyses

To test whether the extent of parental cooperation in pre-hatching care differs from post-hatching care within each species across the birds in our study, we conducted phylogenetic paired t-tests with maximum likelihood to find the best fitting Pagel's λ as evolutionary history is shared among these species (Pagel, 1999; Freckleton et al., 2002; Lindenfors et al., 2010). λ is estimated to represent the phylogenetic signal and its value varies between 0 and 1. A trait with strong phylogenetic signal is more similar among closely related species, while data points are more independent if phylogenetic signal is weak (Freckleton et al., 2002). For a given λ, the corresponding phylogenetic mean of all of the differences between pre-hatching care and post-hatching care was estimated first, then we compared whether the mean difference was different from zero (Lindenfors et al., 2010). The analyses were implemented using the 'phytools' package (Revell, 2012) in R (3.4.2)

We analysed the correlation between parental care variables and predictor variables by using phylogenetic generalised least squares (PGLS) (Freckleton et al., 2002). This technique controls for the dependence among species traits by incorporating a variance–covariance matrix that expresses their shared evolutionary history. In all analyses, the phylogeny was incorporated by the maximum likelihood of λ ($0 \leq \lambda \leq 1$) (Freckleton et al., 2002). Considering the uncertainty of phylogenetic estimation caused by the absence of empirical support on the prediction of evolutionary relationships among species (Jetz et al., 2012), we randomly extracted 100 phylogenetic trees from the most comprehensive avian phylogenies (Jetz et al., 2012). Each PGLS model was analysed across all of these trees and the mean value of resulting 100 parameter estimates were calculated. Please keep in mind that this approach only allows us to examine correlations, not causal links, between variables.

For each dependent variable (i.e., the extent of parental cooperation in pre-hatching care, the extent of parental cooperation in post-hatching care), we established separate PGLS models to investigate the effect of each ecological and life-history traits. Here, we present (1) the results of bivariate models which only included one of the main predictors, and (2) the results of multi-predictor models. These multi-predictor models contained the following predictors: food type, nest structure, coloniality, chick development mode and body mass (log-transformed). The reason for presenting bivariate models is that data availability across all species for all traits greatly reduced sample sizes when multi-predictor models were conducted, which can result in biased parameter estimates. As a result, multi-predictor models can be complemented by bivariate models, yielding relatively robust analytical results. Since food type, nest structure, coloniality and chick development mode are categorical predictors, they were dummy coded in PGLS models by following previous studies (Olson et al., 2008; Remeš et al., 2015; Cooney et al., 2020). All PGLS analyses were carried out using the R package "caper" (Orme, 2012).

2.3 RESULTS

2.3.1 Phylogenetic patterns in parental cooperation

The extent of parental cooperation varies in avian species ranging from uniparental care to egalitarian biparental care (Fig. 1). First, the level of parental cooperation differs between different clades (Fig. 1a,b). For instance, males and females contribute similarly to their offspring in pigeons, penguins and petrels, whereas one of the sexes invests more in parental care in Galliformes (gamebirds), Anseriformes (ducks, geese and allies) and Strigiformes (owls). Second, the extent of parental cooperation can be diverse even within clades (Fig. 1a,b). For example, in shorebirds, parrots and passerine birds, both biparental care and uniparental care occur within the same clade. Third, the degree of cooperation is different between pre-hatching care and post-hatching care in shorebirds, a greater level of biparental cooperation is exhibited in pre- than in post-hatching care (Fig. 1c, Table 1). In addition, as indicated by the intermediate values of λ (λ ranges from 0.622 to 0.894), parental care strategies are phylogenetically correlated (Pagel, 1999; Freckleton et al., 2002).

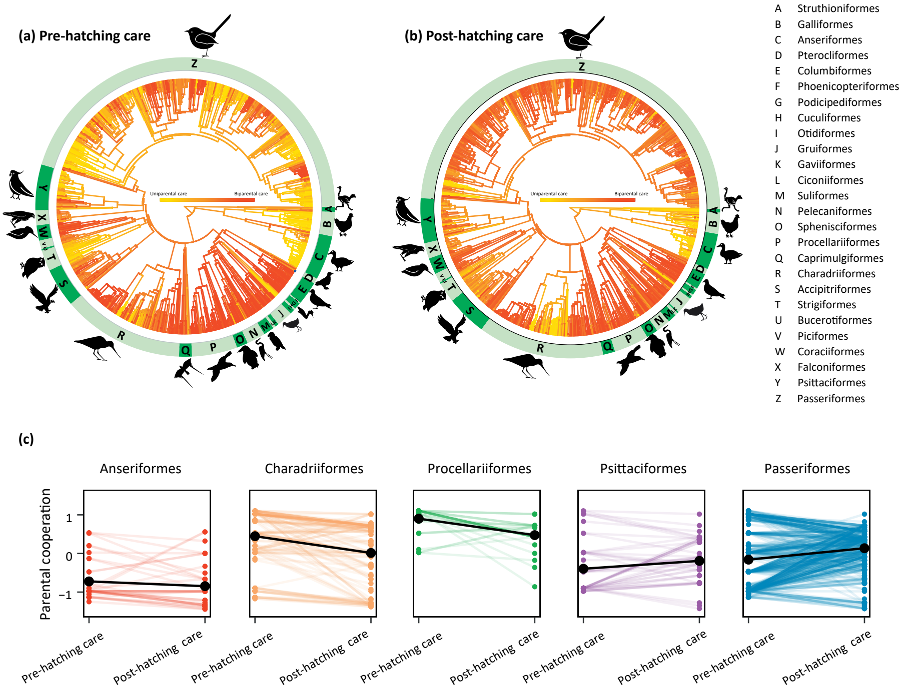

Figure 1. Phylogenetic distribution of parental cooperation in (a) pre-hatching care and (b) post-hatching care (Bayesian maximum credibility tree of 100 phylogenies using 1065 and 991 bird species, respectively). Red = egalitarian biparental care, yellow = uniparental care. (c) The relationship between pre-hatching and post-hatching parental cooperation in five speciose of birds. Each line connecting the degrees of pre- and post-hatching cooperation represents one species. For each avian family, the black points represent the mean levels of pre- and post-hatching parental cooperation. The phylogenetic tree was plotted in R (3.4.2) using the 'phytools' package (Revell 2012).

Table 1. Comparison of pre- and post-hatching parental cooperation. The difference in the levels of pre- and post-hatching parental cooperation was tested using phylogenetic paired t-tests. Tests were applied to all 955 bird species for which data were available and five large avian orders. A positive value indicates that the level of post-hatching biparental cooperation is higher than the level of pre-hatching biparental cooperation. Estimates with standard error (Mean difference ± SE), the corresponding t and p-values, log-likelihood of the fitted model log(L), phylogenetic signal λ and the number of species n are given for each model.

Phylogenetic paired t-test	***Mean difference ± SE***	***t***	***p***	***Log(L)***	***λ***	***n***
All species	-0.248 ± 0.329	-0.991	0.326	-898.17	0.616	955
Anseriformes	-0.181 ± 0.280	-0.758	0.479	-29.368	0.383	38
Charadriiformes	**-0.422 ± 0.124**	**-3.431**	**0.001**	**-114.72**	**0.224**	**130**
Procellariiformes	-0.328 ± 0.220	-1.585	0.147	-25.986	0.519	35
Psittaciformes	0.043 ± 0.326	0.140	0.885	-44.049	0.610	48
Passeriformes	0.066 ± 0.362	0.232	0.818	-444.77	0.642	459

2.3.2 Ecological factors

First, the extent of parental cooperation does not differ between plant-eating, invertebrate-eating and vertebrate-eating species (Table 2). In other words, parental cooperation is not associated with food type. The lack of relationship between food type and parental cooperation is consistent between bivariate and multi-predictor models in which the effects of nest type, coloniality, chick development mode and body mass were controlled for in the analysis.

Second, nest structure does not predict parental cooperation, as the extent of biparental cooperation is not different between species with open and closed nests. Lacking of correlation between nest structure and parental strategies remains in both bivariate model (Table 2a) and multiple regression analyses where all potential confounding variables were included (Table 2b).

Third, parental cooperation is associated with coloniality. In line with our prediction, colonial breeding species presents a higher level of parental cooperation than solitary breeding ones (Table 2, Fig. 2a). Coloniality is significantly related to post-hatching care in both bivariate and full models (Table 2). In contrast, no significant relationship between coloniality and pre-hatching is found in in neither bivariate nor multi-predictor models (Table 2).

Table 2. Parental cooperation in relation to ecology and life history in birds using phylogenetically generalised linear squares models (PGLS). In both bivariate and multi-predictor PGLS models, the extent of parental cooperation in pre-hatching and post-hatching care are the response variables, respectively. Predictors include food type (plants, invertebrates, vertebrates), nest structure (open vs. closed), coloniality (solitary, semi-colonial, colonial), chick development mode (altricial, vs. precocial) and body mass (log-transformed). Parameter estimates with standard error (Slope ± SE), the corresponding t and p-values, R-squared r2, phylogenetic signal λ and sample size n are given for each model. All estimates are means of 100 PGLS analyses using different phylogenies. Significant predictors are highlighted in bold.

(a) Bivariate models	**Parental cooperation in pre- hatching care**						**Parental cooperation in post- hatching care**					
Predictors	***Slope ± SE***	***t***	***p***	***r^2***	**λ**	***n***	***Slope ± SE***	***t***	***p***	***r^2***	**λ**	***n***
Food type	-0.072 ± 0.048	0.406	-1.490	0.002	0.857	1057	-0.046± 0.045	-1.016	0.313	0.001	0.741	985
Nest type	-0.018± 0.069	-0.261	0.785	<0.001	0.862	994	-0.023 ± 0.063	-0.367	0.716	<0.001	0.742	930
Body mass	-0.020± 0.023	-0.855	0.399	0.001	0.854	1060	-0.024± 0.021	-1.135	0.263	0.001	0.743	986
Development	**-0.333± 0.106**	**-3.133**	**0.002**	**0.011**	**0.881**	**881**	**-0.456± 0.106**	**-4.301**	**<0.001**	**0.022**	**0.738**	**828**
Coloniality	0.043 ± 0.028	1.542	0.131	0.003	0.870	835	**0.080 ± 0.028**	**2.845**	**0.005**	**0.010**	**0.671**	**782**

(b) Full model	**Parental cooperation in pre- hatching care**						**Parental cooperation in post- hatching care**					
Predictors	***Slope ± SE***	***t***	***p***	***r^2***	**λ**	**n**	***Slope ± SE***	***t***	***p***	***r^2***	**λ**	**n**
Food type	-0.004 ± 0.054	-0.068	0.894				-0.049 ± 0.056	-0.880	0.381			
Nest type	0.036 ± 0.075	0.480	0.635				-0.019 ± 0.070	-0.276	0.784			
Body mass	-0.001 ± 0.026	-0.018	0.900	0.024	0.894	685	-0.012 ± 0.024	-0.508	0.614	0.053	0.622	645
Development	**-0.404 ± 0.111**	**-3.627**	**<0.001**				**-0.540 ± 0.112**	**-4.819**	**<0.001**			
Coloniality	0.054 ± 0.029	1.843	0.070				**0.104 ± 0.031**	**3.388**	**<0.001**			

2.3.3 Life-history traits

Corresponding to our predictions, parental cooperation is significantly associated with chick development mode (Table 2): a higher level of parental cooperation occurs in altricial species than in precocial species, and this relationship is found in both pre- and post-hatching care (Table 2, Fig. 2b). In addition, the effect of chick development mode is consistent between bivariate and multi-predictor analyses (Table 2). Note that coloniality together with chick development mode only explains a modest proportion of variance in parental cooperation (*R^2* in the PGLS model: 0.01-0.03).

However, we found that the degree of parental cooperation in pre-hatching care and post-hatching care does not correlate with adult body mass (Table 2), which means body size cannot predict parental cooperation. There is no correlation between parental cooperation and body size in either bivariate model or full model (Table 2).

To ensure that the general findings were not an artifact of the methodology used, we conducted the same analysis with the original data on parental care variables (i.e., without centralization). Supplementary Table S2 shows that our findings are still valid when the original data are applied: colonial breeding species are associated with a high degree of parental cooperation in post-hatching care, although this correlation is not found in the bivariate model; altricial species exhibit a higher level of biparental cooperation than precocial species in both pre- and post-hatching care; care patterns are not explained by factors such as food type, nest type, or body size.

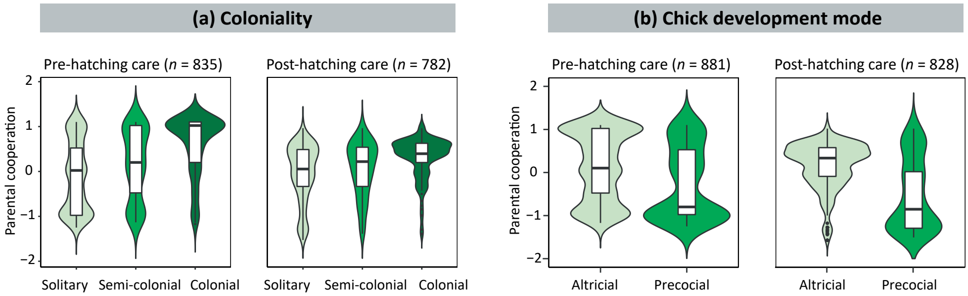

Figure 2. Association of parental cooperation before and after hatching with (a) coloniality and (b) chick development mode. The rectangle of the small box plots inside the violin plots represents the two central quartiles, and the horizontal line indicates the median level of parental cooperation. The kernel density plot of each violin plot shows the distribution of parental care and its probability density. The extent of parental cooperation is cantered at the mean (see Methods), and the number of species n is shown for each plot.

2.4 DISCUSSION

To our knowledge, this is the first study that explicitly investigates whether coloniality predicts parental strategies across a wide range of taxa. Although previous studies explored the correlation between breeding density and care patterns (Owens, 2002; Van Dijk et al., 2010), coloniality of species has not been considered specifically in these studies.

Our study consistently shows that coloniality is related to parental cooperation in birds: colonial breeding species exhibits a higher level of parental cooperation than solitary breeding species in post-hatching care, although this correlation is not found in pre-hatching care. This variation in the correlation between parental strategies and coloniality can be explained by different benefits and costs of various care components. In colonially breeding species, post-hatching care is essential for offspring survival and growth. After hatching, chicks might experience greater conspecific attacks (Ashbrook et al., 2008) and predation risks (Varela et al., 2007), especially in the circumstance where only one parent rears the young, leaving chicks completely exposed to the environment when the single parent is away foraging. Moreover, opportunity of obtaining an additional mate is low for deserting males, since females synchronously produce offspring in colonial species (Gochfeld, 1980, Nelson, 1980, Coulson, 2002). As a consequence, biparental cooperation in post-hatching care may evolve in colonial breeding. On the other hand, biparental cooperation might be the cause rather than the consequence of colonial breeding. By cooperating together, the two parents might reduce potential costs of colonial breeding, such as intense infanticide and mate competition (Danchin & Wagner, 1997, Kiester & Slatkin, 1974), making colonial breeding more likely to arise. Further research is required to investigate the causal relationship between parental care patterns and coloniality. Furthermore, it is not clear whether colonial breeding is associated with parental cooperation as a result of division of parental labour (e.g., one parent protects the broods from predators and conspecifics while the other parent feeds and nurtures the young) or equally dividing care duties (e.g., both parents invest in chick feeding at a similar level). Further studies are needed to explore whether or not males and females specialise in different care tasks in colonial species. In addition, it might be valuable to explore whether coloniality or breeding density is correlated with parental cooperation in other animal taxa, such as in insects, frogs and fishes.

In contrast to our predictions, we found that the extent of parental cooperation is neither related to food type nor to nest structure, two key ecological factors. First, our results suggest that food type cannot explain the considerable variation in parental care patterns, this conclusion is in line with the observations that frugivorous and insectivorous birds exhibit a broad spectrum of parental care patterns (Barve & La Sorte, 2016; Cockle & Bodrati, 2017), and large-scale analyses which indicate diet of species has no effect on care duration that might influence cooperative behavior among breeders (Langen, 2000; Russell et al., 2004). However, note that we used food type to indirectly estimate food availability which is only available from few species (Morton, 1973). This proxy might only capture part of the information in food accessibility and abundance. In further studies, a more direct estimate, such as vegetation growth in the breeding site and the distribution of animal food during the breeding season, will be valuable to justify our conclusions. Furthermore, a recent experimental study on the burying beetle (*Nicrophorus vespilloide*) demonstrates that high abundance of food promotes instead of reducing cooperation between parents (Ratz et al., 2021). It would be worthwhile to test the generality of this finding using large-scale databases on insects.

Second, our study discovered that species with open nests do not show a greater level of biparental care than those with closed nests. The reason for this might be that the presence of both parents (and, in particular, the presence of a brightly coloured father) could make an open nest more conspicuous to predators, hence predation risk may be enhanced rather than reduced if both parents are around (Skutch, 1949; Martin et al., 2000). As a result, species building open nests might take different strategies, with some exhibiting great nest protection by both parents and others displaying low frequency of nest visiting by the less bright parent. It is also possible that nest structure only captures parts of the complexity of nest characters. A recent study showed that nest structure interacts strongly with other nest characters in avian species, such as nest site and nest attachment, and that nest environment is determined by all aspects of the nests (Fang et al., 2018). Thus, birds may make parenting decisions based on multidimensional array of nest characteristics. It will be valid for future studies to take nest structure, nest site, and nest attachment all into account when investigating the relationship between parental strategies and nest characteristics. Furthermore, it is possible that our range-wide analyses overlooked the importance of those two ecological factors operating at smaller scales. We might arrive at different conclusions if we conduct the phylogenetical comparative analysis in specific taxonomic groups. Therefore, investigating the effects of ecological factors on small-scale data sets with more explicit assumptions and high-quality data may be an interesting direction in the future.

Our study also confirms that chick development mode is associated with parental cooperation: parents provide more biparental care in altricial than in precocial species. Our analysis complements earlier studies, which have found that chick development mode plays a crucial role in parental care and mating system in shorebirds (Thomas & Székely, 2005; Thomas et al., 2006), implying that the relationship between parental care patterns and chick development mode is general across bird species. These findings suggest that chick demand can be an important determinant of parental care strategies. However, this relationship between offspring demands and parental care patterns can go the other way around: the willingness of both parents to care for their offspring might increase the care demand of offspring (Kölliker et al., 2005), shifting precocial life-history strategy towards altricial life-history strategy. It will be profoundly valuable to investigate the causal links between parental strategies and chick development in the future.

Our analyses reveal that there is no relationship between body mass and parental cooperation, suggesting that allometric constraints are unlikely to explain variation in parental care patterns in birds. The correlation between body size and parental behaviour was indirectly analysed by some studies but the outcomes are not consistent between studies (Remeš et al., 2015, Liker et al., 2013; Liker et al., 2015). It is possible that various studies are conducted at different spatial scales or using different methodology, more detailed studies are needed to verify our outcome.

Furthermore, our analyses confirm that the extent of parental cooperation is diverse in avian species, with prevalence of egalitarian and partial biparental care in both pre- and post-hatching care (Cockburn, 2006). Intriguingly, we found that in one avian order Charadriiformes (e.g., plovers, sandpipers and allies), the extent of biparental cooperation decreased tremendously after incubation, whereas this pattern was not consistent across birds. Corresponding to our findings, this might be because many shorebirds are precocial (Székely & Reynolds, 1995), the young require little parental care after being hatched (Thomas & Székely, 2005). Therefore, one parent is probably sufficient to raise hatchlings to be independent. Nevertheless, both parents have the chance to desert and search for new mating opportunities. Other factors such as adult sex ratio, sexual selection and certainty of paternity may determine which sex should continually contribute to care (Kokko & Jennions, 2008). The remarkedly diversified care patterns correspond to unusual variations in mating system in shorebirds (Reynolds & Székely, 1997; Eberhart-Phillips et al., 2018), suggesting that shorebirds are an ideal group for testing the theoretical predictions of the evolution of breeding system.

In conclusion, our study provides the most comprehensive analyses investigating the effect of ecology and life history on parental cooperation in birds. We show that parental cooperation is not, as often thought, related to food type, nest structure or body size but rather to coloniality and chick development mode. However, the two recognised factors, coloniality and chick development mode, account for only around 5% of variation in parental care patterns, suggesting that these two factors play a minor role in predicting parental strategies. Experimental studies and field-based observations are needed to unravel the causal relationships between coloniality, chick development mode and parental sex roles in the future. And detailed data from species are needed to advance phylogenetic comparative analyses. For instance, variations in parental strategies among populations and within a single population have been observed in various species (Van Dijk et al., 2010; Bulla et al., 2017; Eberhart-Phillips et al., 2018). Quantifying between- and within-population variations and including these variations might be valuable in future studies.

2.5 ACKNOWLEDGMENTS

We appreciate that Z. Végvári helped with statistical analysis, and we would like to thank the Centre for Information Technology of the University of Groningen for their support and for providing access to the Peregrine high performance computing cluster.

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2.7 SUPPLEMENTARY INFORMATION

This Supplement includes one figure and two tables:

Figure S1. Robustness check of the data.

Table S1. Sample size of each variable.

Table S2. Parental cooperation in relation to ecology and life history in birds

Supplementary References

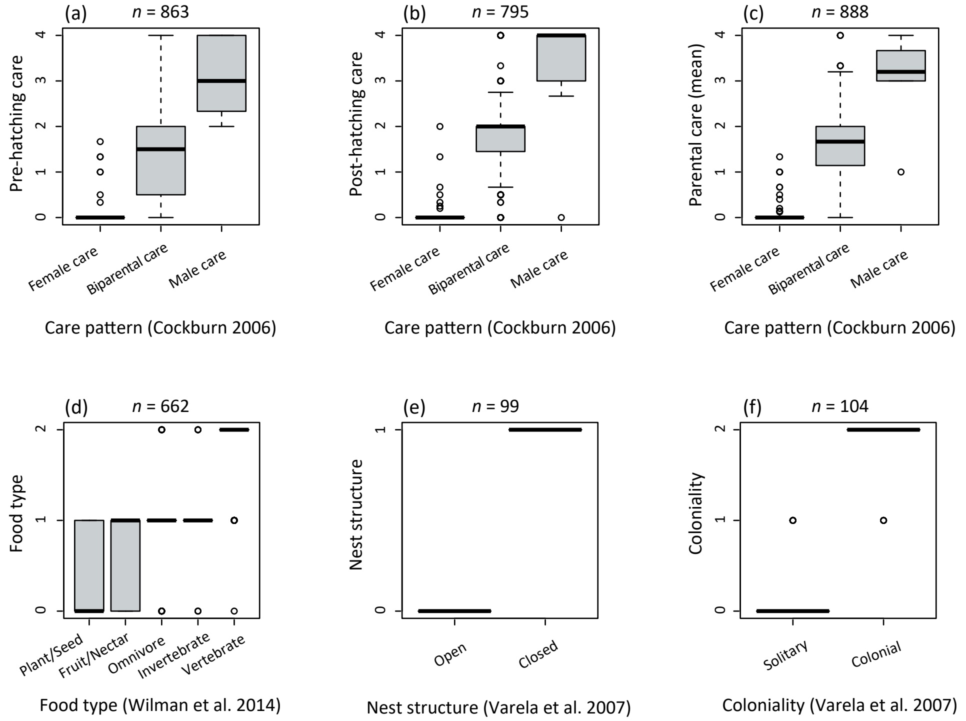

Figure S1. Robustness check of the data. The graphs depict the robustness checks of our data on (**a**) pre-hatching care, (**b**) post-hatching care, (**c**) the mean of pre- and post-hatching care, (**d**) food type, (**e**) nest structure, and (**f**) coloniality. Care patterns were compared to those collected by Cockburn (2006). To make data comparable, here parental care patterns are scored on a 5-point scale in (a-c): 0, no male care; 1, 1–33% male care; 2, 34–66% male care; 3, 67–99% male care; 4, 100% male care. Food type was compared to those collected by Wilman et al. (2014), and it was classified into three categories in our study: 0, plant materials; 1, invertebrates; 2, vertebrates. For omnivorous species, we recorded their mainly eaten food type (plant materials vs. invertebrates vs. vertebrates). Notably, we are mainly concerned with nestling diets, whereas Wilman et al. (2014) focused on diet categories of the adult population. Nest type and coloniality were compared to those collected by Varela et al. (2007). In our study, nest structure was also considered as binary variables: 0, open nests; 1, closed nests. Moreover, coloniality was classified into three categories: 0, solitary breeding; 1, semi-colonial breeding; 2, colonial breeding. Species that are presented in both our study and the previous study were counted (*n*).

Table S1. Sample size of each variable. This table summarises the sample size for parental care variables, which include eight types of parental behaviors in birds, and the sample size for ecological and life-history traits investigated in this study.

<table>
<tr><th colspan="10">Parental care variables</th></tr>
<tr><th colspan="10">Parental cooperation in pre- hatching care</th></tr>
<tr><td colspan="3">Nest building</td><td colspan="3">Nest guarding</td><td colspan="4">Incubation</td></tr>
<tr><td colspan="3">802</td><td colspan="3">196</td><td colspan="4">1017</td></tr>
<tr><th colspan="10">Parental cooperation in post- hatching care</th></tr>
<tr><td colspan="2">Chick brooding</td><td colspan="2">Chick feeding</td><td colspan="2">Chick guarding</td><td colspan="2">Post-fledgling feeding</td><td colspan="2">Post-fledgling guarding</td></tr>
<tr><td colspan="2">742</td><td colspan="2">899</td><td colspan="2">360</td><td colspan="2">435</td><td colspan="2">79</td></tr>
<tr><th colspan="10">Ecological and life-history variables</th></tr>
<tr><td colspan="2">Food type</td><td colspan="2">Nest type</td><td colspan="2">Body mass</td><td colspan="2">Development</td><td colspan="2">Coloniality</td></tr>
<tr><td colspan="2">1092</td><td colspan="2">1026</td><td colspan="2">1096</td><td colspan="2">903</td><td colspan="2">854</td></tr>
</table>

Table S2. Parental cooperation in relation to ecology and life history in birds using phylogenetically generalised linear squares models (PGLS). The table shows the same analysis as Table 2, expect that the parental care variables are not centralised. See the caption of Table 2 for table's conventions.

(a) Bivariate models	Parental cooperation in pre- hatching care						Parental cooperation in post- hatching care					
Predictors	*Slope ± SE*	*t*	*p*	*r^2*	*λ*	*n*	*Slope ± SE*	*t*	*p*	*r^2*	*λ*	*n*
Food type	-0.055 ± 0.049	-1.120	0.269	0.001	0.848	1057	0.058± 0.045	1.317	0.190	0.002	0.737	983
Nest type	-0.036± 0.070	-0.511	0.615	<0.001	0.850	994	-0.009 ± 0.064	-0.137	0.879	<0.001	0.740	930
Body mass	-0.014± 0.024	-0.583	0.565	<0.001	0.845	1060	-0.037± 0.021	-1.710	0.092	0.003	0.745	986
Development	**-0.194± 0.068**	**-2.844**	**0.005**	**0.009**	**0.874**	**881**	**-0.291± 0.069**	**-4.210**	**<0.001**	**0.021**	**0.747**	**828**
Coloniality	0.049 ± 0.028	1.729	0.090	0.004	0.859	835	0.072 ± 0.028	2.540	0.012	0.009	0.681	782

(b) Full model	Parental cooperation in pre- hatching care						Parental cooperation in post- hatching care					
Predictors	*Slope ± SE*	*t*	*p*	*r^2*	*λ*	n	*Slope ± SE*	*t*	*p*	*r^2*	*λ*	n
Food type	0.013 ± 0.055	0.243	0.806	0.020	0.887	685	-0.046 ± 0.056	-0.824	0.412	0.053	0.622	645
Nest type	0.008 ± 0.076	0.101	0.884				0.001 ± 0.072	0.006	0.928			
Body mass	0.003 ± 0.027	0.122	0.878				-0.018 ± 0.024	-0.753	0.455			
Development	**-0.236 ± 0.075**	**-3.167**	**0.002**				**-0.291 ± 0.075**	**-3.877**	**<0.001**			
Coloniality	0.054 ± 0.030	1.808	0.076				**0.095 ± 0.031**	**3.084**	**0.002**			

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Chapter 3

The evolution of parental sex roles: new insights from individual-based simulations

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under review at Proceedings of the National Academy of Sciences

ABSTRACT

The parental roles of males and females differ considerably between and within species. By means of individual-based evolutionary simulations, we strive to explain this diversity. Our findings are in striking contrast to the conclusions of analytical models. When the two parents have an additive effect on offspring survival, our simulations do not predict the evolution of egalitarian care or a line of equilibria, but either strongly female-biased or strongly male-biased care. In longer-term evolution, a population can rapidly switch from one type of equilibrium to the other. This explains the often-reported evolutionary lability of parental sex roles even under constant environmental conditions. If parental investment evolves jointly with sexual selection strategies, evolution results in either the combination of female-biased care and female choosiness or in male-biased care and the absence of female preferences. The simulations suggest that the parental care pattern drives sexual selection, and not *vice versa*. All these results also hold if the parents have a weak synergistic effect on offspring survival; egalitarian biparental care only evolves in case of strong synergy. We also investigated the implications of an asymmetry in pre-mating investment between the parents. If this asymmetry is large, our simulations recover the 'Trivers effect' that the parent with the highest pre-mating investment tends to have the highest post-mating investment. However, complicated evolutionary patterns emerge if the asymmetry in initial investment is small. Throughout, we investigate systematically why the simulation results differ from analytical predictions. It turns out that polymorphisms in care patterns, driven by sexual conflict, play a crucial role. Although these polymorphisms are often transient, they strongly determine the outcome of parental sex role evolution.

3.1 INTRODUCTION

In the animal kingdom, species differ remarkably in the way and degree female and male parents are involved in parental care (Balshine, 2012; Trumbo, 2012). In virtually all mammals, most of the care is provided by females (Clutton-Brock, 1991; Balshine, 2012), while in birds biparental care (with a certain bias towards females) is the most prevalent pattern (Cockburn, 2006; Balshine, 2012). Teleost fishes exhibit a broad variety of care patterns, with male-biased care being the rule rather than the exception (Blumer, 1979; Balshine, 2012). Even within species, parental care patterns can be highly diverse (Webb et al., 1999). For example, in Eurasian penduline tits (*Remiz pendulinus*) female-only care and male-only care co-occur in the same population (Van Dijk et al., 2012), while in Chinese penduline tits (*Remiz consobrinus*) female-only care, male-only care, and biparental care all coexist (Zheng et al., 2018). Moreover, phylogenetic studies suggest that parental care patterns are highly dynamic in that transitions between patterns occur frequently (Székely & Reynolds, 1995; Goodwin et al., 1998; Reynolds et al., 2002).

The explanations that have been proposed for sex differences in parental roles often initiated heated debates in the literature. One debate centres around the role of anisogamy (the difference in gamete size between males and females). Robert Trivers (1972) argued that anisogamy explains the fact that in many taxa females tend to invest more in post-zygotic parental care than males. According to Trivers (1972), the female parent has a strategic disadvantage with respect to the male parent: because the mother has made a large initial investment in the ovum, she has more to lose when deserting the clutch than the father. Some authors pointed out a flaw in Trivers' argument: optimal decision-making should not be based on past investments, but rather on future costs and benefits (Dawkins & Carlisle, 1976). While agreeing with this critique, other authors pointed out that Trivers' prediction can be revived when taking other factors into account, such as female choosiness or uncertainty of paternity (Queller, 1997; Kokko & Jennions, 2003). This viewpoint is, in turn, hotly debated (Gowaty & Hubbell, 2005; 2009; Schärer et al., 2012; Ah-King, 2013). Another debate in the literature is on whether and how the relative abundance of males and females drives parental sex roles (Jennions & Fromhage, 2017). A popular theory predicts that the 'operational sex ratio' (the ratio of males to females among those individuals participating in mating (Emlen & Oring, 1977)) should play a decisive role, because the sex that is overrepresented on the mating market (and hence has fewer mating opportunities) should be predestined for taking on the parental care tasks (Kokko & Jennions, 2008). More recently, attention has shifted to the 'adult sex ratio' (the ratio of males to females in the overall adult population) as a predictor of sex differences in parental sex roles (Kokko & Jennions, 2008; Liker et al., 2013; Székely et al., 2014; Fromhage & Jennions, 2016; Jennions & Fromhage, 2017; Chapter 4). Last, but not least, there is debate in the literature on the role of sexual selection in determining parental sex roles (Trivers, 1972; Queller, 1997;

Kokko & Jennions, 2012). All these debates are intricate in themselves; moreover, they are interwoven, because initial investments, sex ratios, and sexual selection are mutually dependent.

In a situation like this, where the outcome of evolution is determined by the interplay of mutually dependent factors, verbal theories can easily lead astray. As a major step forward, Kokko and Jennions (2008) developed a comprehensive modelling framework, allowing to disentangle the role of the various factors involved in the evolution of parental sex roles. In a first step, male and female fitness functions are calculated, based on a scheme describing the interactions of the sexes in a population. These functions are then analysed mathematically (see Methods), allowing to predict how sex differences in life history parameters, biased sex ratios, multiple mating, and sexual selection affect the evolution of parental sex roles. However, this analytical approach has its limitations. First, the calculations are not trivial and error-prone. Indeed, Fromhage and Jennions (2016) pointed out mistakes and erroneous conclusions in the study of Kokko and Jennions (2008). Second, to keep the model analytically tractable, the factors involved have to be stripped to their bare-bone essentials. For example, the dynamic process of sexual selection is reduced to a set of fixed parameters that cannot coevolve with the parental strategies. Third, the analytical approach focuses on the evolution of population means and thereby neglects intra-population variation around the mean. In other words, populations are considered monomorphic, while it has recently become clear that in natural populations individuals differ systematically in all kinds of behavioural tendencies (Wilson, 1998; Sih et al., 2004; Bell et al., 2009), including parental behaviour (Roulin et al., 2010; Westneat et al., 2011; Stein & Bell, 2012). Various studies have shown that such variation is often shaped by diversifying selection (Wolf et al., 2007; Pelabon et al., 2010), and that it can have important evolutionary implications (Dingemanse & Wolf, 2010; Wolf & Weissing, 2012).

For these reasons, we here consider an extended version of the modelling framework of Kokko and Jennions (2008), and we study the evolution of parental roles by means of individual-based simulations (DeAngelis & Mooij, 2005). This approach has the advantage that more natural assumptions can be made concerning the inclusion of sexual selection or factors such as sex differences in pre-mating investment. Moreover, individual variation emerges in a natural way, making it possible to study its evolutionary implications (DeAngelis & Mooij, 2005).

In a nutshell, our model (see Methods and Fig. 1) follows individual males and females from birth to death. After maturation, adult individuals can be in one of two states: the mating state and the caring state. Individuals seek mating opportunities in the mating state; once mated both members of the mated pair switch to the caring state. Each individual provides care for a time period corresponding to its inherited sex-specific parental care strategy and switches back to the mating state afterwards. The total amount of care provided by both parents determines the survival probability of the offspring in the clutch. The offspring inherit the care strategies from their parents (according to Mendelian inheritance and subject to rare mutations of small effect size). Parental care strategies have to strike a balance between caring as efficiently as possible and mating as often as possible. Both caring and mating are costly, since individuals can die in any state, with a mortality rate that depends on their state and sex. Strategies that perform well are transmitted to a large number of offspring, thereby increasing in relative frequency in the population. Over the generations, an evolutionary equilibrium emerges during the simulation; fitness calculations are not required for this. As explained below, the model can easily be extended to include sexual selection and sex-differences in pre-mating investment.

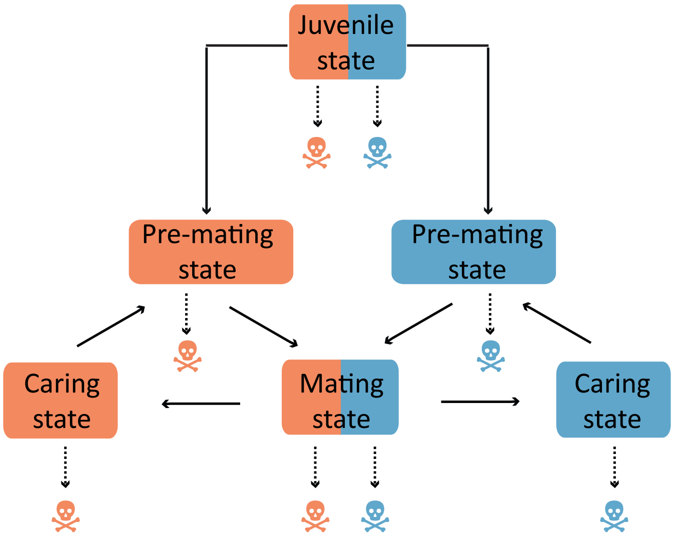

Figure 1. Diagram illustrating the life cycle in our model. Offspring surviving the parental-care period enter the ‘juvenile state’ where they stay for a fixed (and potentially sex-specific) maturation time. Afterwards, they spend a fixed time period (which is zero in the baseline version of the model) in the ‘pre-mating state’. Then they enter the ‘mating state’ where they randomly encounter individuals of the other sex. In case of mate choice, not every encounter results in a mating. If a mating does occur, both mating partners switch to the ‘caring state’, where they stay for a genetically determined time period (T_f or T_m, respectively). The total care duration has a positive effect on the survival of their offspring. Once the care period of a parent has been completed, the individual switches to the pre-mating state, from where the whole cycle repeats itself. In all states, mortality can occur (which potentially is sex-specific). In the baseline version of the model, individual life expectancy is 1000 time units (= ‘days’). For simplicity, we equate this time period with one ‘generation’. Colour conventions: throughout the manuscript females are indicated by the colour red, and males are indicated by the colour blue.

Although the model is very similar in spirit to the analytical models mentioned above, it will turn out that the evolutionary outcome is remarkably different from that reported in the earlier studies of parental sex-role evolution.

3.2 RESULTS

Sex-biased care evolves in the absence of parental sex differences. First, we consider the baseline scenario where mating is at random and the sexes do not differ in their mortality rates or other life-history parameters. Based on their analytical model, Kokko and Jennions (2008) predicted the evolution of egalitarian biparental care for this scenario. Correcting a mistake in the fitness calculations, Fromhage and Jennions (2016) showed that instead the analytical model predicts convergence to a line of equilibria (see Supplementary Fig. S1). If we apply the selection gradient method of Kokko and Jennions (2008) and Fromhage and Jennions (2016) to our slightly modified model, we arrive at the same conclusion (Fig. 2a): the care effort of females and males converges to an equilibrium; there is a continuum of equilibria, which are located on a curve that includes a broad spectrum of parental care patterns. In other words, depending on the initial conditions all types of care strategy, from female-only care via egalitarian biparental care to male-only care, can evolve.

In contrast to these analytical predictions, our individual-based simulations never resulted in egalitarian care or a line (or curve) of equilibria. Instead, all our simulations (>5,000, for different parameter values and different initial conditions) converged to one of two stable equilibria corresponding to either strongly female-biased care or strongly male-biased care. Initial conditions with sex-biased care tended to converge to the corresponding sex-biased equilibrium, while initial conditions without sex-bias converged to each of the two equilibria with equal probability (Fig. 2b). Figs. 2c and 2d show the time trajectories of two replicate simulations starting at a high level of egalitarian care. In a first phase, both populations follow the analytical prediction and converge to a low level of egalitarian care. Then strongly sex-biased care evolves, along the curve of equilibria of the analytical model. Both stable equilibria have the property that the total care provided by the two parents equals $D = 20$, the value maximising the marginal benefit of care in our model (see Methods).

The evolution of sex-biased parental roles is driven by transient polymorphism. Fig. 3 shows in more detail how sex-biased care evolves from egalitarian care. In the simulation shown, the population was initialised at the same care level (20) for males and females. Hence, initially the sum of the parental care levels exceeds the value $D = 20$ that, for the parameters chosen, maximises the marginal benefits of care. Accordingly, there is strong selection in both sexes to reduce the level of care. In the first 800 generations, the care level in males and females rapidly declines until a value of 5 is reached in both sexes (Fig. 3a,b), in line with the predictions of the selection gradient approach (see Fig. 2a). At this care level, the mortality of offspring is very high and additional care would provide a considerable benefit. Yet, the parents are caught in a cooperation dilemma: both are interested in the survival of their offspring, but each parent is better off if most of the care is provided by the other parent (Houston et al., 2005; Lessells, 2012).

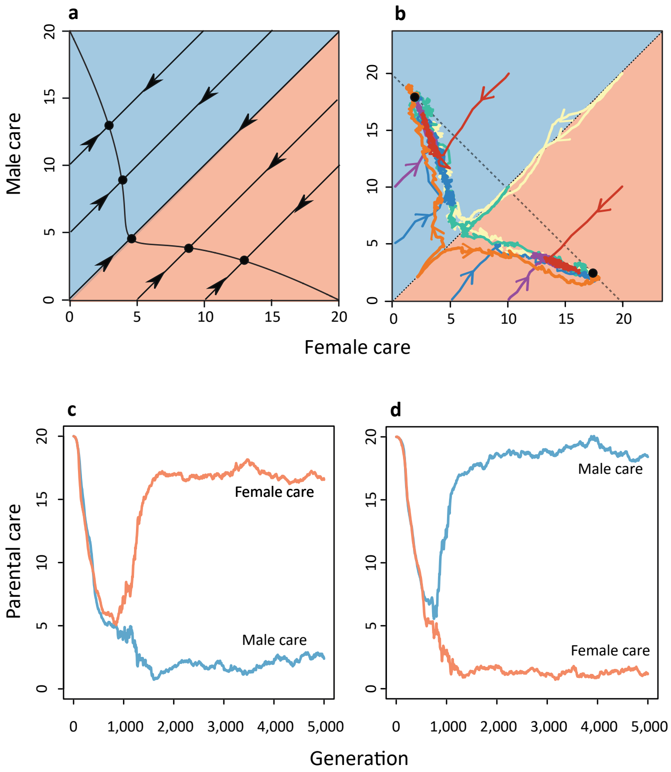

Figure 2. Evolution of sex-biased parental roles in the absence of differences between the sexes. The graphs depict evolutionary trajectories when mating is at random and males and females do not differ in mortality rates or other life-history parameters. **(a)** For this scenario, the selection gradient method predicts convergence to a curve of equilibria (solid black line). **(b)** In contrast, individual-based simulations converge in a characteristic manner to one of two equilibria (black dots) corresponding to either strongly female-biased care or strongly male-biased care. Replicate simulations starting with egalitarian care levels will converge, with equal probability, to **(c)** the female-care equilibrium or **(d)** the male-care equilibrium. Differently coloured lines in (b) indicate different initial conditions. The red and blue lines in (c) and (d) depict the average levels of female care and male care in the evolving population. The dotted line in (b) corresponds to those care levels where the sum of female and male care is equal to , the value of total care maximising the marginal benefits of care in our model (see Methods). Population sizes fluctuated around 2,000 females and 2,000 males. Parents have an additive effect on offspring survival ($\sigma = 0$).

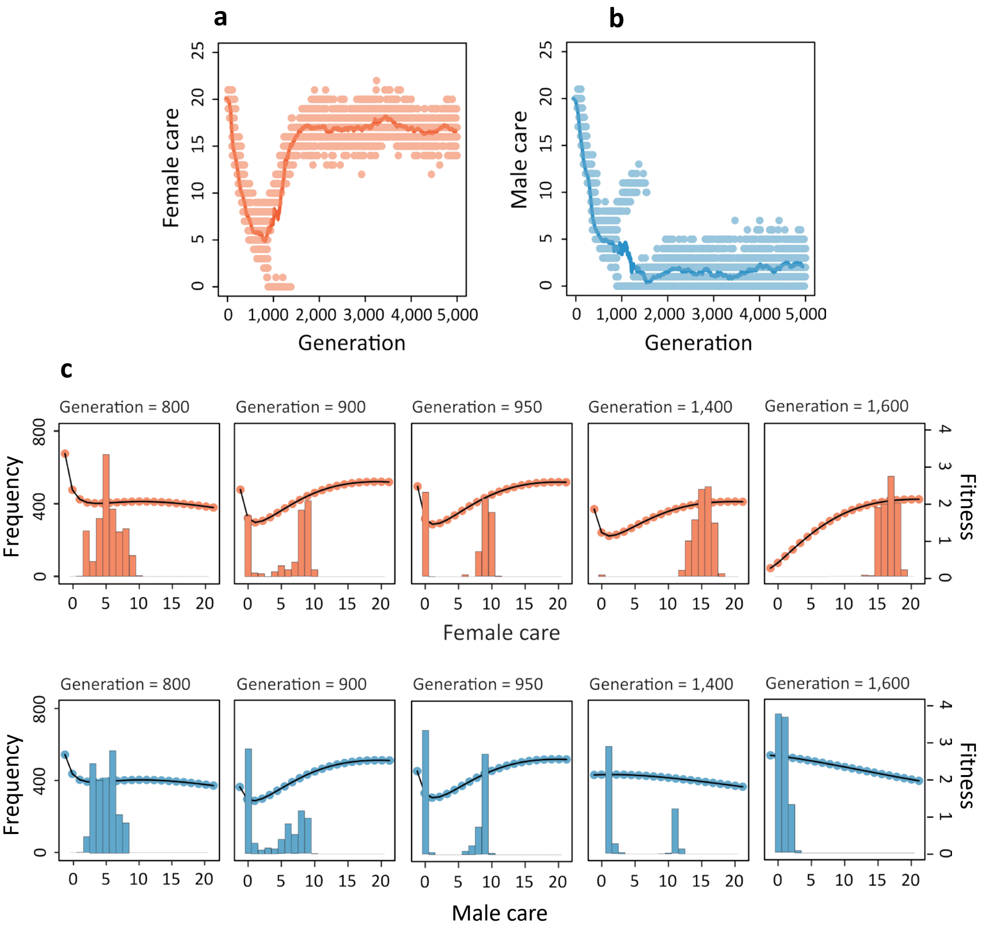

Figure 3. Sex role divergence is driven by transient polymorphism in both sexes. Evolution of **(a)** female and **(b)** male care for the simulation in Fig. 2c. Lines show the average care level of females (red) and males (blue) in the population, while dots represent individual care levels. **(c)** For five different gener¬ations, the histograms (left axis) show the distribution of care levels in females (red) and males (blue). The fitness profiles (dots connected by solid lines; right axis) indicate in each case the expected lifetime reproductive success of females and males with care strategies ranging from 0 to 20 in the corresponding population.

To understand the further course of evolution, we first considered the simplified version of the model where parental care is constrained to be egalitarian (i.e., individuals cannot determine their care duration dependent on their sex). In this egalitarian model, a care level of 5 for both parents corresponds to an 'evolutionary branching point' (Geritz et al., 1998) (see Fig. S3): at such a point, directional selection changes into disruptive selection, where extreme strategies have the highest fitness. This is confirmed by the U-shaped fitness profile and the emerging bimodal distribution of care levels in both sexes in generation 900 (see Fig. 3c). The process continues, and in generation 950 there are two types of females and two types of males: one type not caring at all and the other type caring at a level around 10. In the egalitarian version of the model, the process would continue until part of the population would not care at all while the other part would care at level $D = 20$. Such a population is not very efficient, because many matings would result in either no care at all or a very high care level of 40. When individuals can make their care strategy dependent on their sex (or any other phenotypic marker), there is an escape route (Rueffler et al., 2006): one of the two 'branches' becomes associated with the female sex, while the other becomes associated with the male sex. In the simulation in Fig. 3, the high-care strategy becomes associated with the female sex and the no-care strategy becomes associated with the male (the opposite happened in 50% of the simulations). In generation 1400, the no-care strategy has almost disappeared in females and selection is directional in males (in favour of the no-care strategy). In the end (generation 1600), directional selection keeps the care level low in males, while stabilising selection keeps the care level just below 20 in females. Without exception, the same sequence of events (with similar timing) was observed in hundreds of simulations starting with similar care levels in the two sexes.

Biparental synergy can lead to fluctuating polymorphism or inefficient biparental care. In contrast to the simulations reported above, egalitarian biparental care occurs in many bird and fish species, and in other animal taxa (Clutton-Brock, 1991; Cockburn, 2006; Balshine, 2012; Trumbo, 2012). A potential reason is that in natural populations the parents complement each other, thereby providing more benefits to their offspring than the sum of their individual contributions (Maynard Smith, 1977; Grafen & Sibly, 1978; Yamamura & Tsuji, 1993). Division of labour or other sources of synergy among the parents could reduce sexual conflict about who should do the caring and strongly select for biparental care (Lessells, 2012; Pilakouta et al., 2018). Here we introduce parental synergy in our model in line with earlier modelling studies (Kokko & Johnstone, 2002; Fromhage & Jennions, 2016): we assume that the care levels T_f and T_m of the two parents provide a benefit $T_f + T_m + \sigma\, T_f\, T_m$ to their offspring, where the degree of synergy σ is a positive parameter (in the additive model considered until now, $\sigma = 0$.) In the analytical model of Fromhage and Jennions (2016), the introduction of a small degree of synergy transformed their curve of equilibria (Fig. S1) into a single stable equilibrium corresponding to egalitarian biparental care.

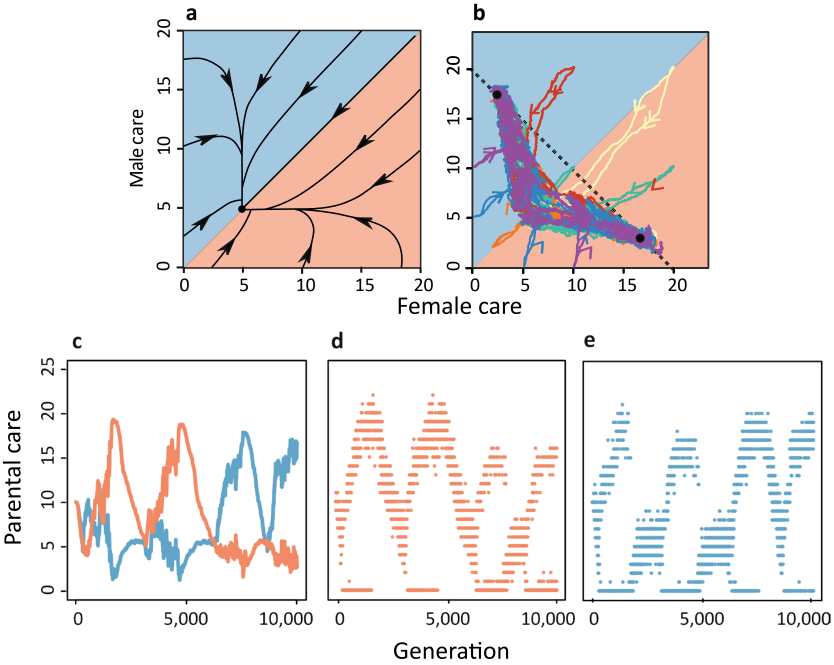

Figure 4. Evolution of parental roles when biparental care has a synergistic effect. In contrast to Fig. 2, where the two parents have an additive effect on offspring survival (σ = 0), we here consider the case of biparental synergy (σ = 0.05). **(a)** Now the analytical selection gradient approach predicts the evolution of egalitarian biparental care (black dot). **(b)** Individual-based simulations again spend most of the time close to the two black dots, representing strongly male-biased care and strongly female-biased care. However, the evolutionary trajectories repeatedly switch between these two care patterns. **(c)** This representative simulation shows the relatively rapid (in evolutionary time) succession of strongly male-biased and strongly female-biased care. Throughout, there is considerable variation in **(d)** female and **(e)** male care strategies. Notice that changes in the 'direction' of evolution are always associated with extreme transient poly¬morphisms in both sexes, where the no-care strategy coexists with a high-care strategy.

Fig. 4 considers the case of relatively weak synergy ($\sigma = 0.05$). As shown in Fig. 4a, the selection gradient approach predicts indeed the evolution of egalitarian biparental care, irrespective of the initial conditions. Again, the individual-based simulations (Fig. 4b) differ strikingly from this prediction. As in Fig. 2b, all simulations converged to either strongly female-biased care of strongly male-biased care. However, as illustrated by a representative simulation in Fig. 4c, the average care level in both sexes exhibits large fluctuations, corresponding to rapid transitions between female-biased and male-biased care. Moreover, most of the time there is considerable variation in care level in both sexes (Fig. 4d,e), and once in a while there are brief periods of egalitarian care (where the average care levels of both parents are very similar). Whenever such a situation arises, a similar phenomenon occurs as in Fig. 3. First, both sexes become strongly polymorphic for the no-care strategy and a high-care strategy, but this polymorphism is transient and breaks down, giving way to the re-establishment of strongly female-biased or strongly male-biased care.

Supplementary Fig. S5a-c shows what happens in case of an intermediate level of synergy ($\sigma = 0.20$). Now, all simulations converge to egalitarian care. However, the care level in both females and males is highly variable. Moreover, the average care level in both sexes is about $T_f = T_m = 5$ and, hence, very low. Taking synergy into account, this investment results in a total care level of about $5 + 5 + 0.2 \cdot 25 = 15$. This is considerably less than in the additive model without synergy ($\sigma = 0$: Fig. 2b), where in both non-egalitarian equilibria the total care level is equal to $D = 20$, the value maximising the marginal benefits of parental care. Apparently, an intermediate level of synergy does not allow the parents to escape from the cooperation dilemma by the evolution of either male-biased or female- biased care. Instead, the conflict between the sexes continues, resulting in a broad spectrum of care strategies and an outcome that is, regarding offspring survival, quite inefficient. This conclusion only changes for a high degree of synergy ($\sigma = 2.0$, Fig. S5d-f): now the population converges to an egalitarian care level satisfying $T_f + T_m + \sigma\, T_f\, T_m = D$.

Evolutionary lability of parental sex roles. The switches between two alternative equilibria that we observed in Fig. 4b is not restricted to the case of (weak) parental synergy. They also occur regularly in the absence of synergy ($\sigma = 0$), but on a much longer time scale. This is demonstrated in Fig. 5, which shows that, on a long-term perspective, rapid switches from one equilibrium to the other occur regularly. In fact, we *always* observed such switches in situations with alternative stable equilibria, provided that the simulations were run for a sufficiently long time period. Accordingly, our simulations suggest that parental roles can be evolutionarily labile. This is in line with phylogenetic studies, which also conclude that parental care patterns are highly dynamic and that, on a long-term perspective, transitions between different care patterns have occurred frequently in many animal taxa (Székely & Reynolds, 1995; Goodwin et al., 1998; Reynolds et al., 2002).

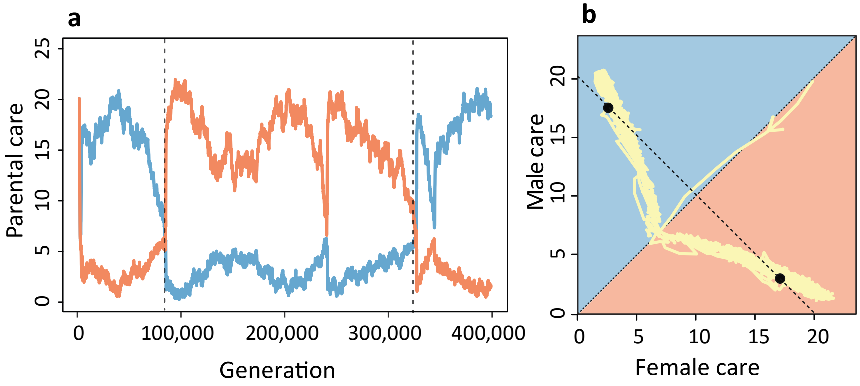

Figure 5. Evolutionary lability of parental sex roles. Whenever simulations were run for extended periods of time, transitions occurred between the two stable equilibria. In other words, long periods of male- or female-biased care were followed by rapid switches to a situation where most of the care was provided by the other sex. Here, this is shown for a long-term simulation of the scenario in Fig. 2, but with a one-day pre-mating period in both sexes.

In a stochastic dynamical system with alternative stable states, spontaneous transitions from one state to the other are not really surprising (Scheffer et al., 2009). They occur, for example, in ecological systems (Scheffer et al., 2001; Hirota et al., 2011), in the climate system (Livina et al., 2010), and in physical systems (Mel'nikov, 1991) (think of the spontaneous reversal of polarity in magnets (Ren et al., 1998)). The average time between switches depends on the degree of stochasticity and the strength of attraction, which in our case corresponds to population size and the steepness of the selection gradients. Decreasing the population size by relaxing density dependence or by increasing the mortality rate for both sexes did indeed lead to much faster transitions between states (see Figs. S6 and S7). The same happened when we weakened selection by prolonging the pre-mating period in one or both sexes (as in Fig. 5).

Joint evolution of mating and parental strategies. Mating and parental care strategies are closely interrelated, but the causal relationships between the two types of strategy are difficult to disentangle. Mathematical models incorporating both factors tend to be analytically intractable and can only be solved by iteration methods (Kokko & Johnstone, 2002). Many models on the evolution of parental roles therefore represent mating patterns by a parameter that cannot change in time (e.g., Kokko & Jennions, 2008). It is a clear advantage of individual-based simulation models that various scenarios for the joint evolution of mating and parental care strategies can be implemented in a natural way. To demonstrate this, we extended the baseline version of the model by allowing female preferences and male ornaments to evolve alongside with the parental strategies. We restrict ourselves to a simple model of sexual selection, leaving the analysis of more complicated scenarios (e.g., mutual mate choice, differences in parental ability, condition-dependent mating and parental strategies) to a future attempt. In the Fisherian model (Iwasa & Pomiankowski, 1995), female preferences and male ornaments are characterised by heritable parameters p and s, respectively. When female preferences are zero, all males have the same probability of being chosen and mating occurs at random. When female preferences are above zero, males with large ornaments are preferred. Male ornamentation is costly in that it negatively affects male survival. Female choosiness is costly, because choosy females may take a longer time before they find a mate. Fig. 6 shows some representative simulations, all starting with random mating ($p = s = 0$) but with different initial levels of parental care. All simulations converge to one of two equilibria (with equal probability) that are characterised by either male-biased care or female-biased care. Whenever male-biased care evolved (Fig. 6b), female preferences stayed at a very low level, corresponding to random mating. Whenever female-biased care evolved (Fig. 6c), female preferences for male ornaments evolved as well, together with elaborate male ornamentation. In all simulations leading to female-biased care, female choosiness only got off the ground after female care levels had reached relatively high levels.

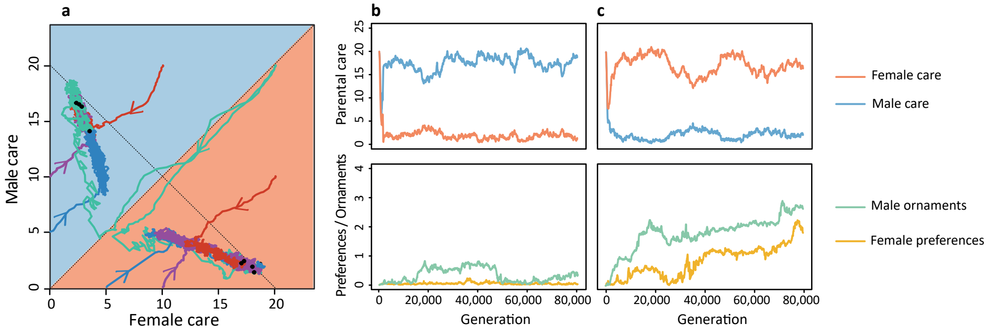

Figure 6. Joint evolution of mating and parental strategies. **(a)** If parental care strategies evolve alongside with the evolution of female preferences for a costly male ornament, all simulations resulted in one of two alternative equilibria. **(b)** One equilibrium is characterised by male-biased care, the absence of female preferences, and a small degree of male ornamentation. **(c)** The other equilibrium is characterised by female-biased care, strong female preferences, and a high degree of male ornamentation. In this simulation, there was no pre-mating period and no parental synergy.

Also these two types of equilibrium do not persist forever. As shown in Fig. S8, each equilibrium defines the dominant sex role pattern for long periods of time (many thousands of generations), followed by a rapid switch to the other type of equilibrium. These transitions proceed in both directions. We investigated many of these transitions, and in all cases the parental strategy changed first (either from male-biased care to female-biased care, or *vice versa*), followed by the emergence or disappearance of female choosiness and male ornamentation. From this we tacitly conclude that, at least for the mating strategies considered in our simple model, the causal relationship goes from parental sex roles to mating roles, and not the other way around.

Asymmetry in pre-mating investment affects the evolution of parental sex roles. In most taxa females tend to invest more in post-zygotic parental care than males (Balshine, 2012; Trumbo, 2012; Kokko & Jennions, 2012). Since females are, by definition, the sex producing larger gametes, it has been suggested that anisogamy plays an important role in the evolution of parental sex roles (Trivers, 1972). Trivers' argument that the sex with the highest pre-mating investment is predestined to invest more in post-zygotic care because it has 'more to lose' is generally considered to be flawed (Dawkins & Carlisle, 1976), but various authors pointed out other causal links from anisogamy to female-biased care, via secondary effects of anisogamy, such as higher competition among males or a lower certainty of parentage in males (Queller, 1997; Kokko & Jennions, 2003). To investigate the role of pre-mating investment, we extended our model by introducing a pre-mating period for one of the sexes. Before entering the mating phase, an individual of that sex has to spend a fixed number of days with other activities (like growing a new clutch of eggs in females or building a new nest in males). Mating is assumed to be at random, there is no parental synergy, and the sexes only differ with respect to their pre-mating investment.

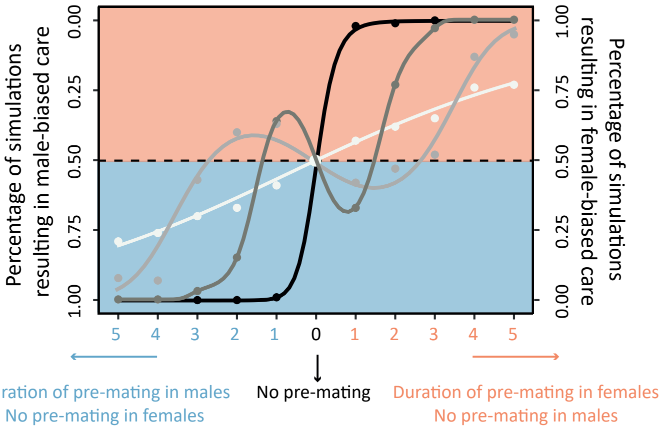

Figure 7. A pre-mating investment bias selects for an associated bias in parental sex roles. Percentage of simulations resulting in male-biased care (left axis) or female-based care (right axis) depending on the duration of the pre-mating period in either males (blue) or females (red). Mortality in the pre-mating period was (1) zero (**white** dots and white line fitted by logistic regression); (2) the same as in the mating phase (**light grey** dots and line); (3) twice as high as in the mating phase (**dark** grey dots and line); (4) five times as high as in the mating phase (**black** dots and line). 100 replicate simulations were run for 100,000,000 generations per parameter setting, all starting from egalitarian care ($T_f = T_m = 20$). All of these 4,400 simulations resulted either in female-biased care or male-biased care.

Fig. 7 shows, for four mortality levels in the pre-mating period, that the sex with the higher pre-mating investment tends to evolve a higher degree of post-zygotic parental care in most of cases. This trend is very pronounced (black curve) if the mortality in the pre-mating period is five times as high as in the mating period. This is not too surprising: the sex with higher mortality has a shorter life expectancy; this in turn makes every mating very valuable, shifting the balance between current and future reproduction toward a higher investment in the current clutch (Stearns, 1976; Klug et al., 2013; Chapter 4). However, this cannot be the whole story, as the 'Trivers effect' is also noticeable when the pre-mating period does not affect life expectancy (white curve: zero mortality in the pre-mating state). We originally thought (Long & Weissing, 2020) that this outcome results from the fact that the sex with shorter pre-mating period has a higher variance in mating success, which selects for higher mating effort and reduced parental care (Sutherland, 1985). But our simulation data and mathematical analyses did not support this explanation. We also extrapolated our findings for extremely high (black curve) and extremely low (white curve) mortality to conclude that "Trivers was right, be it for the wrong reason" (Long & Weissing, 2020). Fig. 7 shows that, actually, the situation is more complicated: if the pre-mating period is short and the mortality costs are at an intermediate level (light grey and dark grey curves), it is the sex with the *lower* pre-mating investment that evolves more frequently a high post-zygotic care level. This is investigated in more detail in Fig. S9. We do not have a convincing explanation for this and have to conclude that the casual link between pre-mating investment and post-zygotic parental care is more complex than Trivers and others (including ourselves) envisaged.

3.3 DISCUSSION

Here we investigated an individual-based simulation implementation of a modelling framework (Kokko & Jennions, 2008) that may be viewed as the cornerstone of sex-role evolution theory. Although we made very similar assumptions as the analytical models, we arrived at remarkably different conclusions than the earlier mathematical analyses. First, the populations in our 'null model' (random mating, no sex differences in life-history parameters, no parental synergy) do not evolve to egalitarian care (Kokko & Jennions, 2008) or to a line (or curve) of equilibria (Fromhage & Jennions, 2016) but rather to one of two stable equilibria corresponding to either strongly male-biased care or strongly female-biased care. Second, parental synergy does not necessarily lead to egalitarian care. Even if it does, the evolutionary outcome is not necessarily efficient: in the presence of synergy the parents can be kept in a parental cooperation dilemma that in the absence of synergy is resolved by parental specialisation. Third, our simulations reveal that, as in the analytical models (Kokko & Jennions, 2008; Fromhage & Jennions, 2016), sexual selection can lead to a situation where males are highly competitive on the mating market, while females provide most of the parental care. However, this is not the only outcome:

there is a second equilibrium (that is equally likely) where males do most of the caring while the evolution of female choosiness is suppressed. Our simulations provide evidence that, in our model, the parental care pattern drives sexual selection and not the other way around. Fourth, our simulations suggest that (parental and mating) sex roles are evolutionarily labile. For most of the parameters considered, the model has two 'stable' equilibria. Whenever this is the case, a simulation attains one of these equilibria for a long but limited period of time, followed by a rapid transition to the other equilibrium. Hence, male-biased care can switch to female-biased care, and *vice versa*. Similarly, a population can rapidly switch from a state of female choosiness, male competitiveness, and female-biased care to a state of male-biased care in the absence of choosiness and competitiveness. These transitions occur for the same parameter settings; in contrast to other models (e.g., Klug et al., 2013) they are not necessarily induced by a change in environmental conditions. Finally, our simulations shed new light on the Trivers effect (Trivers, 1972) that the sex with the highest pre-mating investment is predestined for doing most of the post-mating parental care. Although we do not agree with Trivers' line of argumentation, most of our simulations recover this effect even under random-mating conditions, demonstrating that it does not depend on factors as sexual selection or uncertainty of paternity. Intriguingly, under some conditions (see Fig. 7) we observed the opposite effect (that the sex with lower pre-mating investment is predestined for shouldering most of the post-mating care). This exemplifies how difficult it is to disentangle the web of causal factors underlying the evolution of parental sex roles.

Why do our simulations lead to contrasting conclusions from earlier analyses of very similar models? We think that our results highlight two limitations of analytical approaches that are mainly based on fitness considerations. As shown by Kokko & Jennions (2008) and Fromhage & Jennions (2016) the analysis of selection differentials and selection gradients can be very informative: they clearly indicate the effects of strategic parameters (like parental effort) on life history parameters (like own survival and offspring survival), thus quantifying the trade-offs between fitness components. However, selection-gradient based plots like Fig. 2a or 4a should not be over-interpreted, because it is not self-evident that evolution by natural selection proceeds in the direction of the selection gradient (the direction of steepest ascent of the fitness landscape). This only happens under restrictive assumptions, such as weak selection (McElreath & Boyd, 2008), simple interactions across loci (Nagylaki, 1992), uncorrelated mutations of similar effect sizes (Arnold et al., 2008), and a simple structure of the genetic variance-covariance matrix (Roff, 1997). A comparison of Figs. 2a and 2b shows that the gradient method predicts the simulation trajectories reasonably well when the fitness gradient is steep, but that it fails to detect directional selection away from egalitarian care when the curve of equilibria is approached (where the fitness gradient is close to zero). One might argue that the discrepancy between Figs. 2a and 2b is not too surprising, because a curve of equilibria, as predicted by the analytical model, is 'structurally unstable'

(Bulmer, 1994), meaning that it will disappear if the model is slightly changed. However, this cannot be the sole explanation, as we observed similar discrepancies in the parental synergy scenario (Fig. 4a,b) where the gradient method predicts a structurally stable pattern of egalitarian care while the simulation model predicts the coexistence of two stable equilibria corresponding to either strongly male-biased or strongly female-biased care.

A second limitation of selection gradient methods is their focus on population averages. Averages have only a clear biological meaning if variation around them is small and symmetrically distributed (Kokko et al., 2017). In recent years, it is becoming increasingly clear that in the behavioural domain this assumption is not satisfied: in virtually all animals studied, individuals differ strongly and systematically in all kinds of behavioural tendencies (Wilson, 1998; Sih et al., 2004; Bell et al., 2009) (including parental (Roulin et al., 2010; Westneat et al., 2011; Stein & Bell, 2012) and mating behaviour (Jennions & Petrie, 1997; Schuett et al., 2010), exhibiting so-called 'animal personalities' (Stamps & Groothuis, 2010). Figs. 3 and 4 show that such individual variation in parental strategies, within and between the sexes, is also to be expected in the evolution of sex roles; in fact, it is shaped by natural selection (Figs. 2 and S3). It has been argued before (Dingemanse & Wolf, 2010; Wolf & Weissing, 2012) that such 'patterned' variation can strongly affect the course and outcome of evolution. This is clearly exemplified by our model, where the emergence of a bimodal distribution of care strategies is, in virtually all our simulations, the first step toward the evolution of sex role specialisation. The take-home message is that 'selection gradient dynamics' have to be interpreted with care if the emergence of individual variation is to be expected. Our simulations reveal that even transient polymorphisms can have a lasting effect on the course and outcome of evolution. Hence, individual differences can even be relevant if they persist for only brief periods of time.

At present, individual-based simulations are not yet very popular in evolutionary studies, presumably because of the belief that they do not add much to the evolutionary theory toolbox. Our study demonstrates that such simulations can be a useful check of analytical results, in particular in cases where the complexity of the evolutionary dynamics necessitates the usage of 'short-cut' methods (such as the selection-gradient method). On top of this, individual-based simulations have other advantages. They are easy to implement, without the necessity of performing complicated fitness calculations. For example, the fact that in the simulations each offspring has one mother and one father automatically guarantees that the 'Fisher condition' (that total reproductive success of all females is equal to the total reproductive success of all males) is satisfied, while the incorporation of this constraint in analytical models is not obvious (Queller, 1997; Houston & McNamara, 2002; Kokko & Jennions, 2008; Houston et al., 2013). Stochasticity, spatial structure, and environmental variation can easily be included in simulation models, in a variety of ways. The life cycle of the individuals can be much more intricate (and realistic) than in analytical models. Perhaps most importantly, individual interactions can be implemented in a natural way (DeAngelis & Mooij, 2005). We have demonstrated how the evolution of mate choice can be included in the model, instead of representing sexual selection by constant parameters. This is relevant, because mating strategies and parental strategies must be allowed to evolve side by side in order to study evolutionary feedbacks between them. We are aware that our model of sexual selection is quite simple, but it is straightforward to include 'good genes' and 'direct benefits' variants (Hoelzer, 1989; Andersson, 1994), as well as condition-dependent preferences (Cotton et al., 2006) and ornaments (Warren et al., 2013).

We do not plead for replacing analytical methods by simulations. Simulations have the big disadvantage that their outcome can easily be 'as complicated as reality', thereby not furthering our understanding and sharpening our intuition. Instead, we recommend a pluralistic approach (Kuijper et al., 2012) where analytical insights are checked and expanded by individual-based simulations, while the simulation outcomes are scrutinized with the help of analytical tools (such as the pairwise invasibility plots in Figs. S3 and S4). The hope is to achieve a deeper understanding by a combination of diverse methods, in the spirit of Richard Levins' insight (Levins, 1966) (in our own wording): every model is a lie – all we can hope for is to approach truth by the intersection of independent lies.

3.4 METHODS

Model structure. In line with the models of Kokko and Jennions (2008) and Fromhage and Jennions (2016), we consider a population with overlapping generations and discrete time structure. To be concrete, we assume that a time unit corresponds to one day. The population consist of females and males that, on each day, can be in one of the following states: juvenile, pre-mating, mating, or caring. In each of the four states, there is a fixed mortality rate, which can be sex-specific. Unless stated otherwise, all mortalities were set to 0.001 day^{-1}. Therefore, the expected lifespan of an individual is 1000 days, a value that we consider a proxy for generation time. Offspring mortality is density dependent, thus ensuring a limited population size. In our baseline scenario, population size fluctuates around 2000 females and 2000 males.

The life cycle of our model organisms is illustrated in Fig. 1. Offspring that survive the period of parental care spend a fixed number of days (the maturation time) in the juvenile state. In all simulations reported, the maturation time of both sexes was equal to 20 days. After maturation, the surviving individuals enter the pre-mating state, corresponding to a condition where they prepare for mating (e.g., territory establishment; nest building; replenishment of gametes). After a fixed sex-specific number of days, the pre-mating state changes into the mating state. Unless stated otherwise, the pre-mating period was set to zero, meaning that individuals move to the mating state without delay. Once in the mating state, individuals seek for mating opportunities. In our baseline scenario, females and males mate at random, but we also consider a mate-choice scenario where females have a preference for certain male ornaments. On a given day, mating is modelled as follows: one by one, a female in the mating state is selected at random. As long as there are still males in the mating state, the female encounters one of these males at random. In the random mating scenario, such an encounter always results in mating; in the mate-choice scenario, the male can be rejected if its ornamentation does not fit to the preference of the female (see below). When mating does occur, both the male and the female immediately leave the mating state and both enter the caring state. When a female-male encounter does not result in mating, both individuals stay in the mating state, but they are no longer available for mating on that day. Hence each individual in the mating state can only have one encounter per day, and a female and a male both lose one day if their encounter does not result in mating. Mating will stop for the day when no more males in mating state are available and/or when all females in mating state have made their mating decisions. All remaining individuals stay in the mating state, but they will only have a new mating opportunity on the following day.

Once a mating has occurred, the mated couple produces a clutch of offspring. Offspring survival strongly depends on the amount of parental care received. The female care duration T_f and the male care duration T_m are heritable traits that may differ between individuals. The evolution of T_f and T_m is the core subject of our study. We interpret T_f and T_m as the 'intended' cared duration: if one of the parents dies during the care period, this intended care duration is replaced by the actual care duration (the time from mating to death). To consider the possibility of synergy between the two parents, we assume that their total parental effort is given by $T_{tot} = T_f + T_m + \sigma\ T_f\ T_m$ where the 'synergy' parameter σ is non-negative. Unless stated otherwise, we assume that $\sigma = 0$, meaning that each parent has an independent additive effect on total care. Offspring survival is proportional to $S(T_{tot}) = T^2_{tot}/(T^2_{tot}+D^2)$, an increasing sigmoidal function of total parental care. The parameter D may be viewed as a measure of the care demand of offspring: the function S has a turning point at $T_{tot} = D$, implying that the marginal benefits of care are maximal when the total parental effort matches D. Throughout, we consider the case $D = 20$, i.e., the offspring demand the equivalent of 20 days of care. When the care period T_f (resp. T_m) has passed, the corresponding parent changes into the pre-mating state. When the longest-caring parent stops caring, the surviving offspring enter the juvenile state. As mentioned above, population size is regulated in our model by assuming that offspring survival is density dependent: it is given by $S(T_{tot}) / (1+\gamma N)$, where N is the current population size and the parameter γ quantifies the degree of density dependence. This form of density regulation ensures that expected lifetime reproductive success (the fitness measure used by analytical approaches; see below) does indeed predict the course and outcome of evolution (Mylius & Diekmann, 1995). Our choice $\gamma = 0.003$ ensured relatively large populations (about 2000 females and 2000 males) with limited genetic drift and demographic stochasticity.

At the start of a new day, the survival of each individual was checked according to the individual's sex- and state-specific mortality. Non-survivors were removed from the population.

Sexual selection. In part of our study, we consider a mate-choice scenario where females can evolve a preference p for a male trait of size s, where p and s are both heritable traits. In line with Kokko and Johnstone (2002), we assume that the probability that a female with preference p that encounters a male with trait size s will actually mate with this male is given by the logistic $(1 + \kappa \exp(\alpha(p\text{-}s)))^{-1}$. For all non-negative values of p, this expression increases with s (hence all females have a preference for males with larger ornament sizes), and the rate of increase is positively related to p (hence females with a large value of p discriminate more strongly against males with a small trait size). The parameters κ and α are scaling factors that affect the intensity of sexual selection. The mate-choice simulations shown are all based on the parameter values $\kappa = 0.02$ and $\alpha = 2$. For these parameters, an 'unattractive' male with $s = 0$ is accepted for mating with probability 0.98 by a female with a preference value $p = 0$ (hence, $p = 0$ is almost undistinguishable from random mating) and with probability 0.48 by a female with preference value $p = 2$. We assume that male ornamentation is costly: each time step, the survival probability of a male with trait size s is reduced by a percentage βs^2, where we chose $\beta = 10^{-6}$.

Reproduction and inheritance. For simplicity, we consider a population of haploid individuals that may differ in their alleles at four gene loci. The T_f-locus and the p-locus are only expressed in females, and the T_m-locus and the s-locus are only expressed in males. The alleles at the T_f-locus and the T_m-locus determine the duration of maternal and paternal care, respectively. The allele at the p-locus determines the degree of female preference, while the allele at the s-locus determines the size of the male trait. In our baseline scenario (random mating), the p-allele and the s-allele are not expressed. Offspring inherit their alleles from their parents' subject to mutation. In a first step, the allele at each locus is drawn at random from one of its parents. Moreover, offspring sex is determined at random, with equal probability. In a second step, mutations could occur with probability μ= 0.005 per locus. If a mutation occurs at the T_f-locus or the T_m-locus, the current allele is either increased or decreased by 1, with equal probability. This ensures that the parental care times T_f and T_m are natural numbers. If a mutation occurs at one of the other two loci, a small mutational step of size ε was drawn from a Cauchy distribution (with location parameter 0 and scale parameter 0.01) and added to the current value of p or s, respectively. We used the Cauchy distribution (rather than a normal distribution) because it allows for occasional larger step sizes. However, we limited mutational step sizes to a maximum value of max $\varepsilon = 0.05$.

Initialisation and replication. In all simulations, the p- and the s-locus were initialised at $p = s = 0$. The T_f-locus and the T_m-locus were initialised at different values (leading to the different trajectories in Figs. 2b, 4b, and 6a). Each time, we started with a monomorphic population. For each parameter combination, we ran at least 100 replicate simulations. In all cases, the outcome was highly repeatable, allowing us to focus on one or two replicates. As partly documented in the Supplement, we also ran numerous simulations for model variants that differed from the baseline model in its parameter values (state- and sex-specific mortalities; offspring demand D; cost of ornamentation β; density dependence γ; mutation rate μ), the survival function $S(T_{tot})$, the mate choice function, or the distribution of mutational step sizes. In all cases, we arrived at the same conclusions as reported in the manuscript. We therefore conclude that our results and conclusions are quite robust.

Mathematical analysis. As a standard of comparison for our individual-based simulations, Figs. 2a and 4a show the trajectories of the corresponding deterministic model, making use of the fitness gradient method described in Kokko and Jennions (2008) and Fromhage and Jennions (2016). In a nutshell, this method calculates the selection gradient (indicating the strength and direction of selection) in males and females for each combination of parental care parameters (T_f, T_m). This gradient points into the direction of steepest ascend of the fitness landscape, where fitness is defined by expected lifetime reproductive success. Under the assumption that evolution will proceed in the direction of the selection gradient, evolutionary trajectories as in Figs. 2a and 4a are obtained. Our model is inspired by the model of Kokko and Jennions (2008) and Fromhage and Jennions (2016), but it differs from the former models in various respects. In the Supplement (Figs. S1 to S4), we discuss these differences and demonstrate that our main results are also recovered for the earlier models, again indicating the robustness of our results and conclusions.

3.5 CODE AVAILABILITY

The C++ simulation code and a Mathematica file with an implementation of the fitness gradient method are available for download from https://github.com/xiaoyanlong/evolution-of-sex-roles.

3.6 ACKNOWLEDGEMENTS

We are grateful to L. Fromhage for sharing technical details of the fitness gradient method and some computational resources with us and to H. Hildenbrandt and M. Mosna for writing a first version of the simulation programme. We thank J. Komdeur, T. Székely, G. S. Van Doorn, R. Scherrer and the MARM group at the University of Groningen for valuable discussion, comments, and suggestions. We also thank the Centre for Information Technology of the University of Groningen for their support and for providing access to the Peregrine high performance computing cluster. X.L. is supported by a PhD fellowship of the Chinese Scholarship Council (NO. 201606380125). F.J.W. acknowledges funding from the European Research Council (ERC Advanced Grant No. 789240).

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3.8 SUPPLEMENTARY INFORMATION

This Supplement includes nine supplementary figures:

Figure S1. Rescaled version of the Fromhage & Jennions (2016) model.

Figure S2. Evolution of sex-biased care in the model of Fromhage & Jennions (2016).

Figure S3. Evolutionary branching of parental care strategies.

Figure S4. Pairwise Invasibility Plot of the Fromhage & Jennions (2016) model.

Figure S5. Evolution of egalitarian care in case of substantial parental synergy.

Figure S6. Effect of population size on the timing of evolutionary transitions.

Figure S7. Effect of mortality rates on the timing of evolutionary transitions.

Figure S8. Transitions between alternative mating and caring strategies.

Figure S9. Evolution of parental roles in the presence of pre-mating investment.

Supplementary References

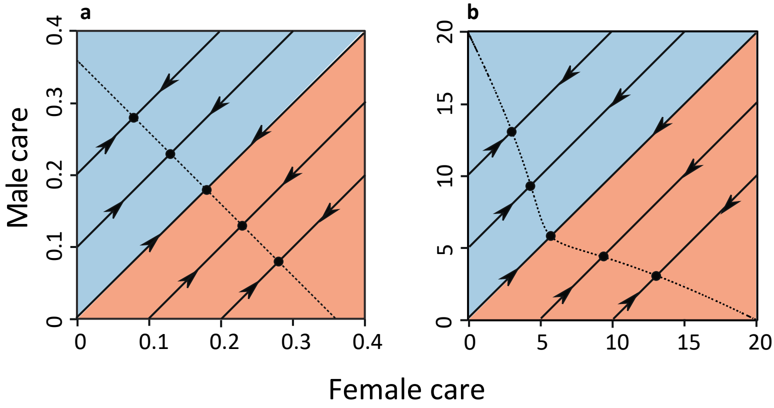

Figure S1. Rescaled version of the Fromhage & Jennions (2016) model. The simulation model investigated in this manuscript was inspired by the analytical model of Fromhage and Jennions (2016). However, we replaced their offspring survival function $S(T_{tot}) = \exp(-D/T_{tot})$ by the more symmetric function $S(T_{tot}) = T^2_{tot}/(T^2_{tot} + D^2)$. **(a)** For their parameter setting $D = 20$ and $\mu = 0.01$ (where μ denotes the mortality rate per day), Fromhage and Jennions concluded that the selection gradient method predicts convergence to a line of neutrally stable equilibria (Fig. 1a of their article). **(b)** For the parameters used in our model ($D = 20$ and $\mu = 0.001$), the model of Fromhage and Jennions produces an almost identical pattern as our variant of the model (see our Fig. 2a). This shows that, also in the model of Fromhage and Jennions, the 'curve of equilibria' is not necessarily a straight line.

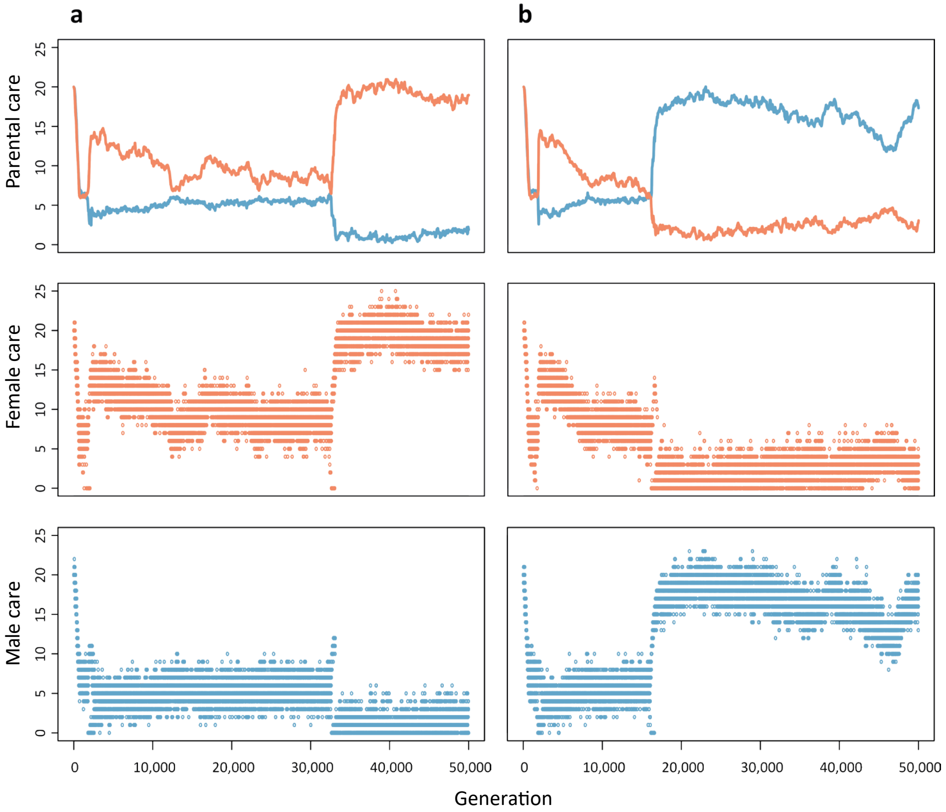

Figure S2. Evolution of sex-biased care in the model of Fromhage & Jennions (2016). This figure demonstrates that individual-based simulations based on the model of Fromhage and Jennions (2016) (rescaled version: D = 20 and μ = 0.001, see Figure S1(b)) exhibits a very similar behaviour as our model (which uses a different function for offspring survival). Two representative simulations show **(a)** the evolution of female-biased care; and **(b)** the evolution of male-biased care. On a long-term perspective, transitions between the two types of equilibria also occurred. Notice that a longer period of low-level egalitarian care precedes the first switch to sex-biased care. This is explained by the Pairwise Invasibility Plot in Fig. S4.

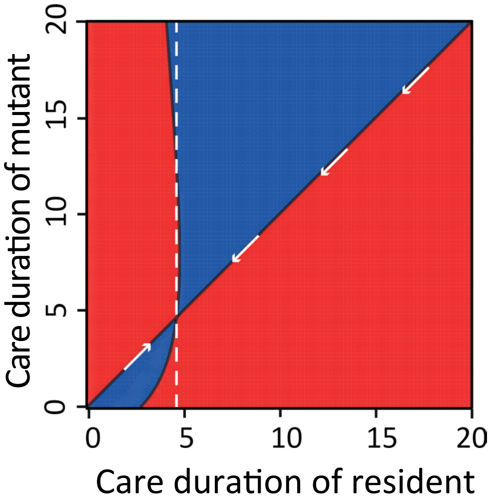

Figure S3. Evolutionary branching of parental care strategies. The graph shows a Pairwise Invasibility Plot (PIP) of the baseline version of our model (random mating, no differences between the sexes, no parental synergy). We restrict attention to egalitarian care ($T_f = T_m$), allowing us to conduct a one-dimensional analysis. A PIP illustrates which mutant strategies can invade when rare in a given resident population. As explained in detail in Geritz et al. (1998), the x-axis depicts all possible care durations of a resident population, while the care durations of mutants are represent¬ted on the y-axis. The red area of the plot corresponds to mutant-resident combinations where the mutant has a higher fitness than the resident and, hence, can invade the resident population. Here, fitness is calculated as in Fromhage and Jennions (2016). The blue area indicates those mutant-resident combinations where the mutant has a lower fitness than the resident and is selected against. The separating black lines corresponds to situations where mutants and residents have the same fitness. The two equal-fitness lines intersect at the value $T^* = 4.67$, which is a so-called Evolutionarily Singular Strategy. The white arrows indicate that this strategy is convergence stable: in the course of evolution, the resident population is shifted toward T^*. The dashed vertical line lies in the red region (at least for mutants close to T^*), implying that there are mutants that can invade the resident T^*. This means that T^* is not evolutionarily stable. A configuration like this (convergence to an evolutionarily unstable strategy) is called a 'branching point', because it indicates that directional selection (toward T^*) switches to disruptive selection (once T^* is reached) indicates that directional selection (toward T^*) switches to disruptive selection (once T^* is reached). When the population would remain constrained to egalitarian care, a dimorphic population would result, where part of the population would care less than $T^* = 4.67$ while another part would care more than this value. If sex differentiation in care is possible, it is to be expected that each of the 'branches' gets associated with one of the two sexes (e.g. low-care might get associated with the female sex and high-care with the male sex) (see Rueffler et al., 2006). A *Mathematica* file with the implementation of the PIP is available via the link in the main text.

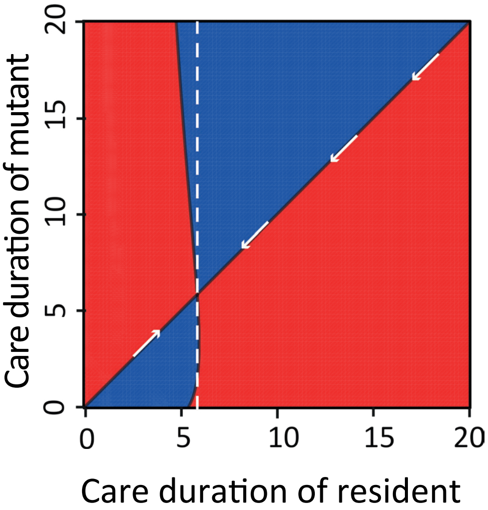

Figure S4. Pairwise Invasibility Plot of the Fromhage & Jennions (2016) model. With the same method as in Fig. S3, we constructed a PIP for the model of Fromhage and Jennions (2016) (rescaled version: D = 20 and μ = 0.001, see Fig. S1(b)). Now there is a convergence stable singular strategy at T^* = 5.87. In contrast to our version of the model (Fig. S3), this singular strategy is not a branching point but evolutionarily stable (mutants close to T^* cannot invade, as the dashed vertical line lies in the blue for mutants close to T^*). Standard adaptive dynamics theory (Geritz et al., 1998) would therefore predict that egalitarian care at level T^* is an evolutionary attractor, and, hence, and endpoint of evolution. In contrast, all 100 simulations resulted in the evolution of sex-biased care (see Fig. S2). Similar observations were made in other simulation studies (Wolf et al., 2007; Berngruber et al., 2010; Baldauf et al., 2014), where diversification occurred at an evolutionary attractor. In all these cases, T^* is locally but not globally evolutionarily stable, as the dashed vertical line transverses the red region as well (mutants with a very short care duration can invade the population of T^* residents. If one waits long enough, such mutants will invariably appear in individual-based simulations (and in the real world). As argued in Wolf et al. (2008), the analytical conditions for evolutionary branching are based on the assumption of infinitesimally small mutational step sizes and therefore correspond to a 'worst-case scenario for evolutionary diversification'. In simulations, diversification (or, as in our case, sex differentiation) can predictably occur under much milder conditions.

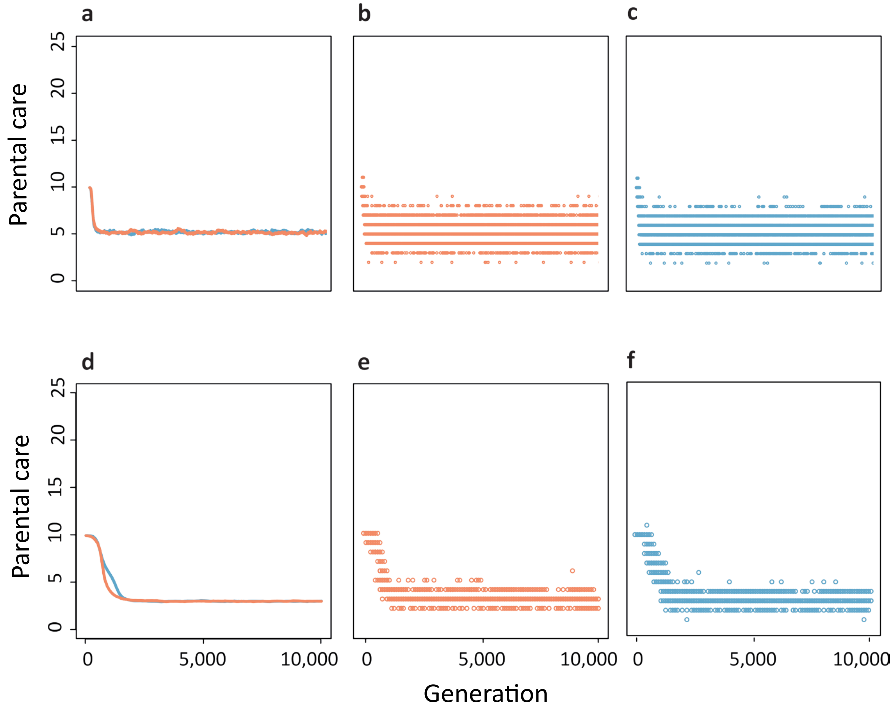

Figure S5. Evolution of egalitarian care in case of substantial parental synergy. Fig. 4 shows that the sex bias in parental care observed in the absence of parental synergy ($\sigma = 0$) also evolves in case of weak synergy ($\sigma = 0.05$). Here we illustrate by two representative simulations that pronounced parental sex roles do no longer evolve if the synergistic effects of the parents on offspring survival are relatively large. **(a)** In case of intermediate synergy ($\sigma = 0.20$), evolution leads to an equilibrium where both parents provide, on average, the same level of care. However, both in **(b)** females and **(c)** males there is considerable variation in care strategies. Total care $T_f + T_m + \sigma T_f T_m$ is considerably smaller than $D = 20$, the value maximising the marginal benefit of care in our model. **(d)** In case of strong synergy ($\sigma = 2.0$), the evolving egalitarian-care equilibrium exhibits relatively little variation in **(e)** females and **(f)** males, and total care now matches $D = 20$.

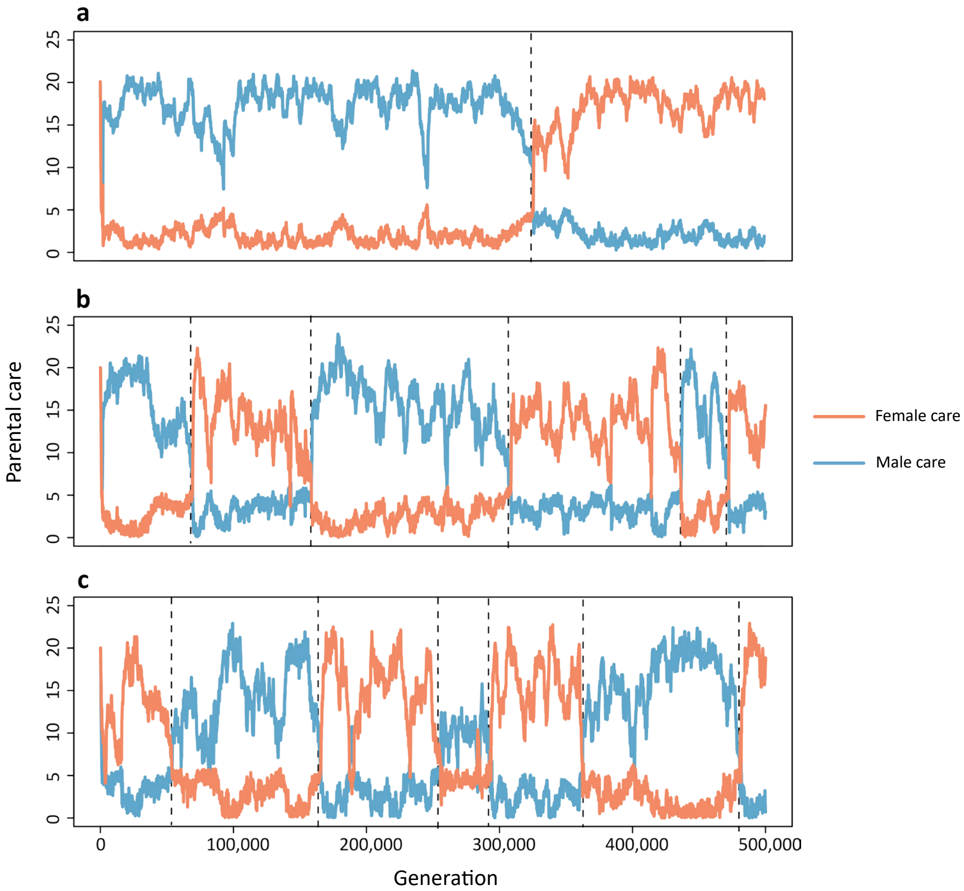

Figure S6. Effect of population size on the timing of evolutionary transitions. As shown in Fig. 5, parental roles are evolutionarily labile in that spontaneous transitions occur from one parental-care equilibrium to the other. As explained in the main text, the mean time between transitions depends on the duration of the pre-mating period (affecting the strength of selection) and on population size (affecting genetic drift). The three panels illustrate, for simulations without pre-mating period, how the number of transitions within a fixed period of 500,000 generations increases with a decrease of population size. **(a)** 2,000 females and 2,000 males: one transition; **(b)** 650 males and 650 males: five transitions; **(c)** 300 females and 300 males: six transitions. Population sizes fluctuated and were regulated by changing model parameter γ (see Methods).

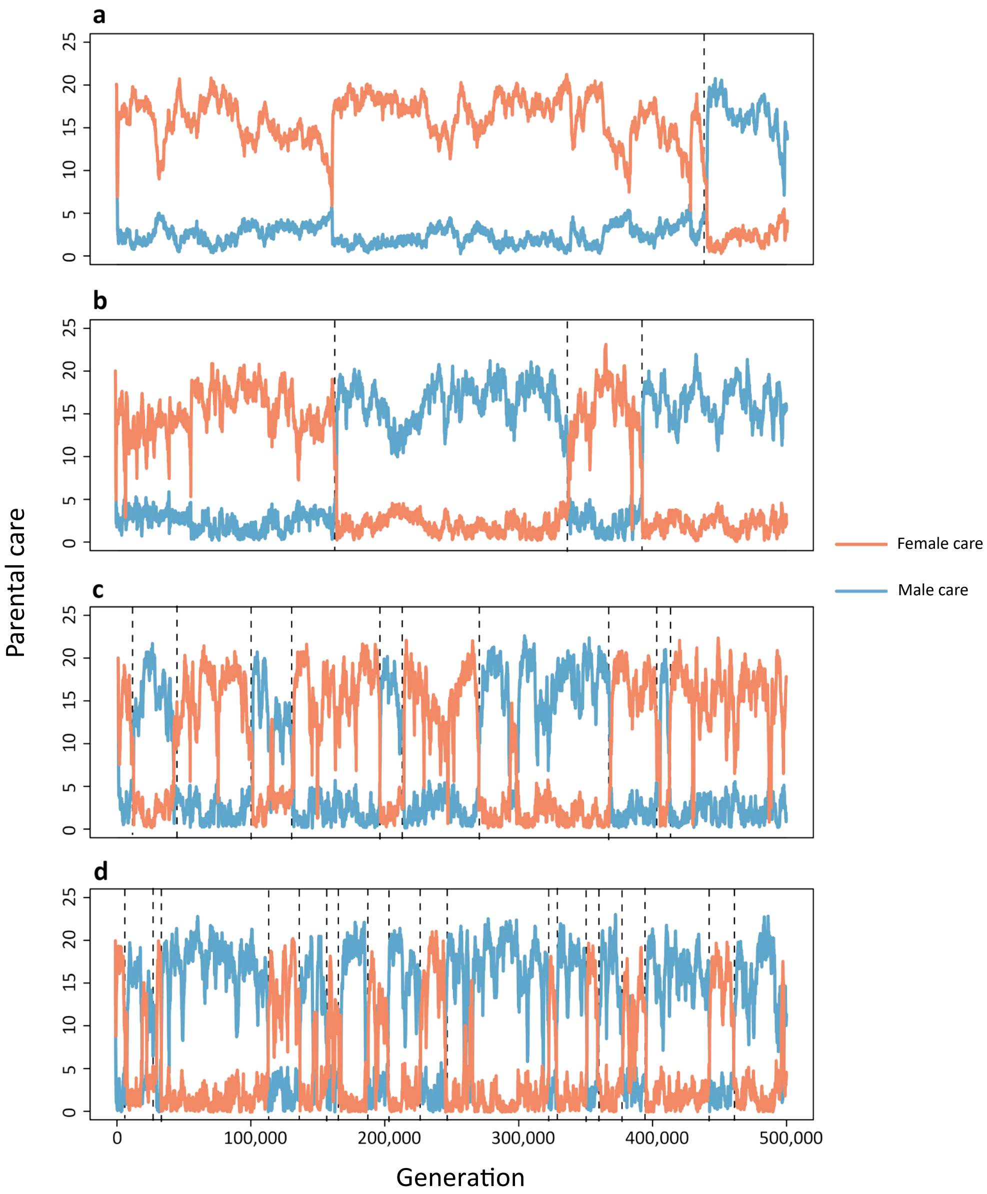

Figure S7. Effect of mortality rates on the timing of evolutionary transitions. Mortality rates affect the average time between transitions via influencing genetic drift. The graphs show that the number of transitions increases as mortality rates of males and females in the caring state increase. In each simulation, mortality rates of each sex in the juvenile, pre-mating and mating were set to 0.001 day^{-1}, while the mortality rate in the caring state was **(a)** 0.001 day^{-1}: one transition; **(b)** 0.002 day^{-1}: three transitions; **(c)** 0.003 day^{-1}: ten transitions; **(d)** 0.004 day^{-1}: nineteen transitions.

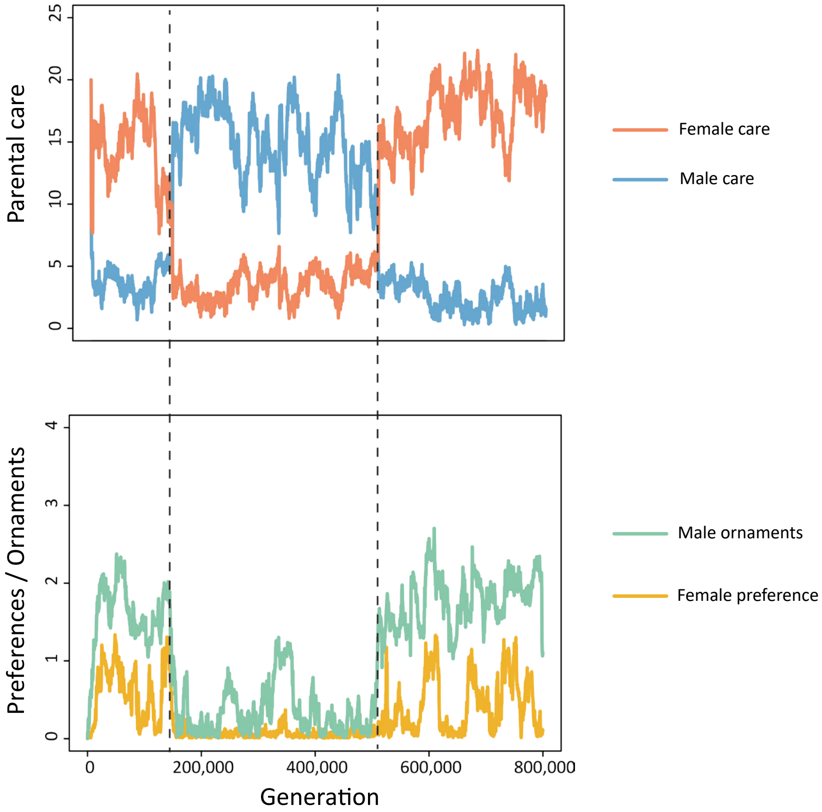

Figure S8. Transitions between alternative mating and caring strategies. As shown in Fig. 6, the joint evolution of mating and parental care strategies leads to one of two equilibria: strongly male-biased care in the absence of female choosiness, and strongly female-biased care associated with a female preference for ornamented males and costly male ornamentation. The simulation demonstrates that also these combined mating and parental roles are evolutionarily labile in that spontaneous transitions occur from one equilibrium to the other. Epochs with female choosiness and female-biased care (here: first 180,000 generations, last 300,000 generations) alternate with epochs with random mating (= no female preference) and male-biased care (here: generations 180,000 till 500,000). A more detailed analysis revealed that the change in female preferences was always preceded by a change in the parental care strategies of the two sexes.

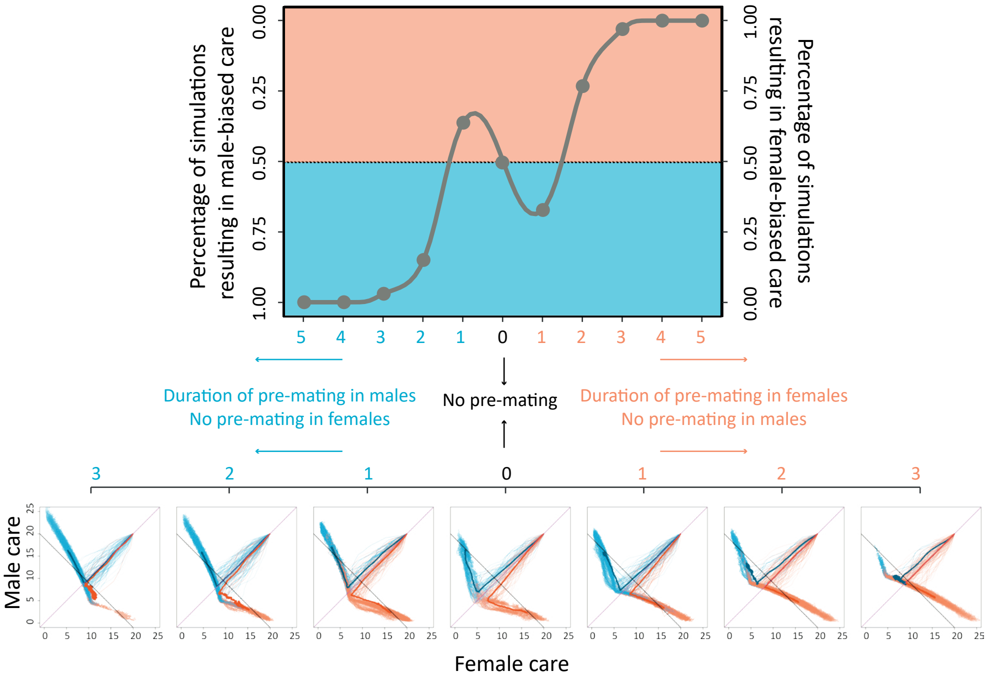

Figure S9. Evolution of parental roles in the presence of pre-mating investment. As shown in Fig. 7, sex differences in pre-mating investment have a predictable but complicated effect on the evolution of parental sex roles. Here we analyse one of the four scenarios shown in Fig. 7 in more detail: the mortality rate in the pre-mating phase was 0.002 day^{-1} and hence twice as high as in all other phases. **(a)** Sex differences in the duration of the pre-mating period influence the percentage of simulations resulting in male-biased care (left axis) or female-based care (right axis) in a non-monotonic way. **(b)** Phase plots for the simulations underlying the summary graph (a). Dark-coloured lines show the average care level of simulations resulting in male-biased care (blue) and female-biased care (red), respectively. Light-coloured lines represent 100 replicate simulations for each parameter setting. When there is no pre-mating investment, either male-biased care or female-biased care evolves, with equal probability. When the bias in the duration of the pre-mating period is very strong (2 days or more), the sex with the longer pre-mating duration (i.e., the sex with the higher pre-mating investment) is selected to provide more post-zygotic care; the care level provided in this case exceeds the offspring demand (D = 20). Interestingly, the pattern is reversed if the bias in the duration of the pre-mating period is small (here: 1 day). Now the sex with the smallest pre-mating investment tends to provide more post-mating care.

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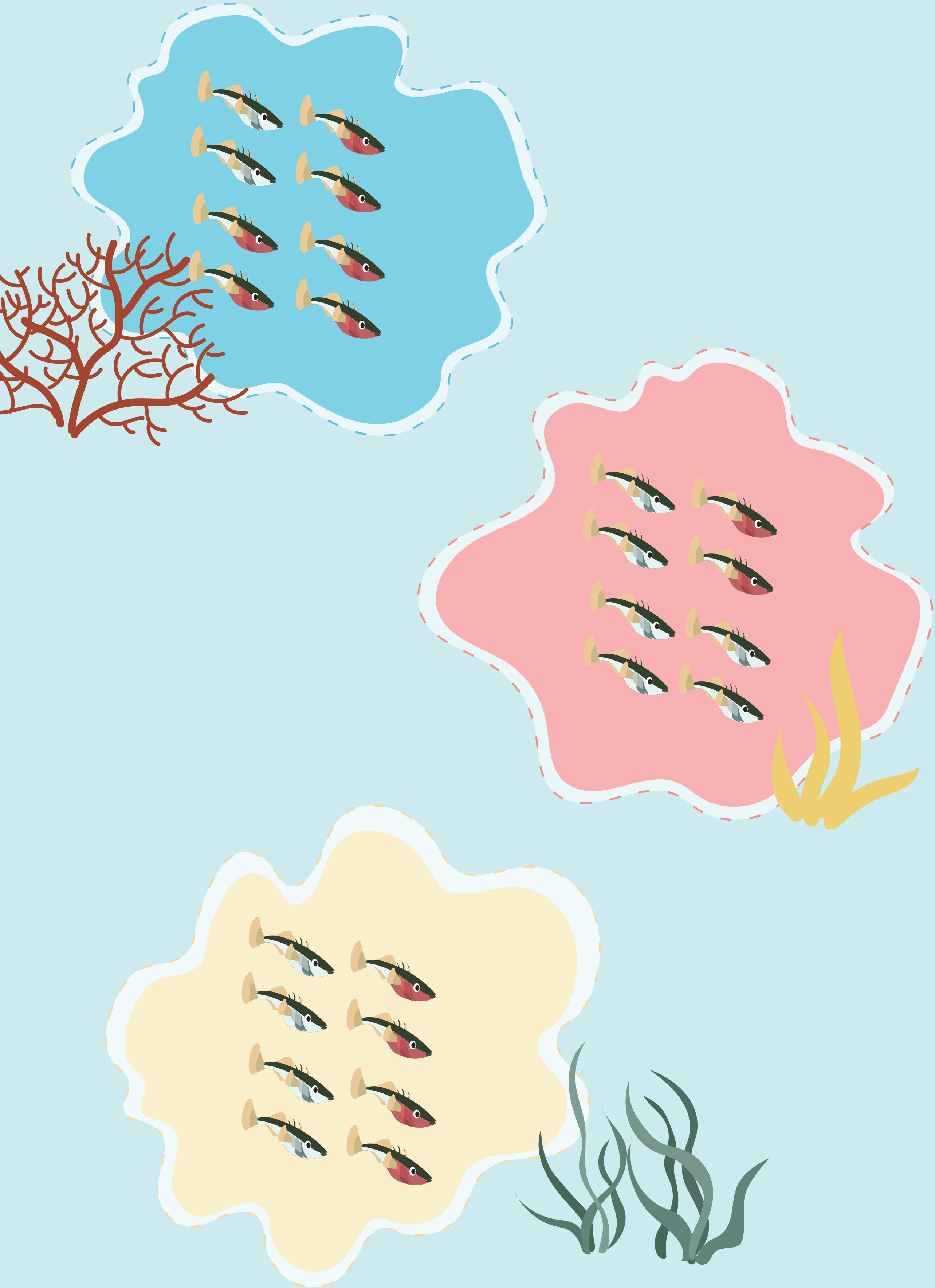

Chapter 4

A life-history perspective on the evolutionary interplay of sex ratios and parental sex roles

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in preparation

ABSTRACT

Parental care is one of the most diverse social behaviours, and caring by the male, female or both parents is essential for successful reproduction of many organisms. Theoretical and empirical studies suggest that parental sex roles are associated with biased sex ratios. However, there is considerable debate on the causal relationship between parental sex roles and sex ratio biases and on the relative importance of the operational sex ratio (OSR), the adult sex ratio (ASR), and the maturation sex ratio (MSR). Here we use individual-based evolutionary simulations to investigate the joint evolution of sex-specific parental behaviour and the various sex ratios in several life history scenarios. We show that sex differences in maturation time or mortality rates at various life-history stages predict the evolution of parental sex roles relatively well: typically, but not always, parental care is biased toward the sex with the lower mortality or the faster maturation. The association of parental sex roles with the various sex ratios is more intricate. In our simulations, the operational sex ratio at evolutionary equilibrium was typically biased toward the less-caring sex. However, the direction and strength of OSR biases often changed drastically in the course of evolution, implying that, rather than being a driver of parental sex roles, OSR biases emerge as a consequence of sex-biases in parental care. When the MSR or the ASR is biased, this bias is generally associated with a bias in parental care: the overrepresented sex does most of the caring. However, the opposite pattern (that the underrepresented sex did most of the caring) also occurs in some scenarios. Moreover, pronounced parental sex roles may also evolve in the absence of an MSR or ASR bias. Taken together, we conclude that none of the sex ratios can be viewed as drivers of a parental care bias; they rather co-evolve with parental care bias in a subtle manner.

4.1 INTRODUCTION

When animal species provide post-zygotic parental care, the degree to which each sex contributes varies strongly across taxa (Clutton-Brock, 1991; Balshine, 2012; Trumbo, 2012). Females provide most of the care in mammals and invertebrates (Balshine, 2012; Trumbo, 2012), both sexes are involved in parental duties in the majority of avian species (Cockburn, 2006; Balshine, 2012), and male-biased or male-only care is common in fishes with parental care (Blumer, 1979; Mank et al., 2005). In amphibians, either males or females care for the offspring (Reynolds et al., 2002; Furness & Capellini, 2019; Vági et al., 2019), whereas in reptiles, female-only care is widespread, but biparental care also occurs (Reynolds et al., 2002; Balshine, 2012; Halliwell et al., 2017).

Sex ratios have been suggested to play a crucial role in explaining the diversity of parental care patterns (Emlen & Oring, 1977; Kokko & Jennions, 2008; 2012; Liker et al., 2013; Székely et al., 2014). Traditionally, the operational sex ratio (OSR, hereafter defined as the proportion of males among those individuals in the population that are ready to mate) was considered a prime determinant of parental roles (Emlen & Oring, 1977). The underlying idea is that there is a trade-off between parental efficiency and competitive ability on the mating market (Magrath & Komdeur, 2003). As the members of the majority sex on the mating market have to compete more intensely for matings, these members should, so the argument goes, invest relatively more in their competitiveness than in parental care (Clutton-Brock & Parker, 1992; Kvarnemo & Ahnesjo, 1996; Simmons & Kvarnemo, 2006; Janicke & Morrow, 2018). This, in turn, induces the members of the limiting sex to be choosy and to provide more parental care. However, this argument has been criticized for three reasons. First, the existence of a universal trade-off between parental efficiency and competitive ability on the mating market is debatable (Stiver & Alonzo, 2009). In some organisms, it is likely that armament and ornamentation increasing success on the mating market are a handicap when it comes to parental care (e.g., Duckworth et al., 2003; Mitchell et al., 2007). Conspicuous colouration, for example, may attract predators to the nest (Huhta et al., 2003; Morehouse & Rutowski, 2010). However, many structures and signals that are relevant for mating do not necessarily interfere with parenting (e.g., because they are only expressed during the mating period). Second, selection on competitiveness does not necessarily lead to a high investment in competitive structures in all members of the competing sex (Baldauf et al., 2014). Mating competition may become prohibitively costly, to the point where it becomes advantageous to focus on other reproductive activities (e.g., parental care) (Kokko & Jennions, 2008; Baldauf et al., 2014). This can result in a self-reinforcing process: individuals that are less competitive on the mating market cannot expect many future matings; accordingly, they should invest a lot into each of the few matings (and the resulting brood) that they can realise. In other words, one would expect considerable variation in the level of parental care in the majority sex, and it is not self-evident that this sex should care less on average. Third, the parental care pattern has immediate repercussions on the OSR (Székely et al., 2000; Kokko & Jennions, 2008; Jennions & Fromhage, 2017). If one sex does all the caring, the availability of this sex on the mating market will typically be reduced. In other words, the causal relationship between OSR and the pattern of parental care is reciprocal (Székely et al., 2000; Kokko & Jennions, 2008): the OSR may be a “driver” of parental sex roles, but at the same time it is also “driven” by the parental care pattern. Therefore, the role of OSR as a driver of parental sex roles is, at best, ambiguous.

Recently, the adult sex ratio (ASR, defined as the proportion of males among the adult individuals in the population) has garnered considerable attention from both empiricists and theorists (Kokko & Jennions, 2008; Liker et al., 2013; Székely et al., 2014; Fromhage & Jennions, 2016; Schacht et al., 2017). Their work suggests that a male-biased ASR promotes males to provide more parental care, while a female-biased ASR leads to female-biased care. For two reasons ASR variation is considered a better predictor of parental patterns than OSR variation. First, the “Fisher condition” is applicable to the ASR, rather than the OSR. According to Fisher (1930), in diploid sexually reproducing organisms each offspring has one father and one mother. As a result, the total number of offspring produced by each sex must be equal. Any bias in the ASR has therefore a straightforward implication: the minority sex, on average, produces more offspring than the majority sex (Queller, 1997; Houston & McNamara, 2002). Thus, the more abundant sex receives less fitness revenue from mating than the rarer sex and, all other things being equal, the members of the majority sex benefit more from devoting time and energy to parental care. Second, the ASR is determined by a variety of factors (e.g., sex differences in maturation, survival, dispersal, and migration (Székely et al., 2014; Ancona et al., 2020) that are often only loosely related to parental behaviour. Accordingly, the causality between the sex ratio and the parental care pattern is expected to be reciprocal to a smaller extent in case of the ASR than in case of the OSR. However, it is important to realise that also the ASR is affected by reproduction-related feedbacks. Such feedbacks easily arise when mortality rates differ between the mating and the caring stage and/or between the sexes (Fromhage & Jennions, 2016; Jennions & Fromhage, 2017). Accordingly, it may be difficult for both, the ASR and the OSR, to disentangle cause and effect when discussing the relationship between parental care and the sex ratio.

In view of these intricacies, it is difficult, if not impossible, to predict evolutionary outcomes by using only verbal arguments. Therefore, mathematical models have been built in an attempt to understand in what way sex ratios influence parental care patterns. To be mathematically tractable, early models (e.g., Clutton-Brock & Parker, 1992; Yamamura & Tsuji, 1993; Queller, 1997; Houston & McNamara, 2002) incorporated sex ratios as a fixed parameter; accordingly, they could not address the feedbacks mentioned above. This changed with the landmark paper of Hanna Kokko and Mike Jennions (2008), who developed a simple and elegant framework to address the joint evolution of parental roles and sex ratios. Based on this framework, Kokko and Jennions (2008) drew some interesting conclusions, but as pointed out later by Lutz Fromhage and Mike Jennions (2016), their analysis is flawed due to a mistake in their fitness function. For example, Kokko and Jennions (2008) had argued that the sex that is overrepresented in the OSR should provide more care, and egalitarian biparental care should evolve in the limiting case of no differences between the sexes. In contrast, Fromhage and Jennions (2016) concluded that an OSR bias does not select for a care bias; in the limiting case of no sex differences their fitness gradient method does not predict the evolution of egalitarian care, but rather evolution to a neutral line of equilibria, ranging from male-only care via egalitarian care to female-only care. Kokko and Jennions (2008) also made the prediction that the ASR has a direct role in driving parental sex roles: according to their analysis, the more common sex in the adult population is selected to provide more care. Based on their improved fitness function, Fromhage and Jennions (2016; see also Jennions & Fromhage, 2017) showed that this conclusion is incorrect, because the route by which the ASR becomes biased may play a crucial role for the outcome of parental care evolution. In other words, parental sex roles are not driven by an ASR bias, but by the factors (e.g., sex-differential mortalities) underlying this bias. According to Jennions and Fromhage (2017), one of these factors is the maturation sex ratio (MSR, defined as the proportion of males among those individuals that are at the start of their adult life). They argue that the more common sex at maturation is selected to provide more care, and that, accordingly, MSR has the property ascribed by Kokko and Jennions (2008) to the ASR.

In the present study, we complement the mathematical analysis of Fromhage and Jennions (2016) by individual-based evolutionary simulations that make use of a very similar model structure. Such a simulation approach is important for at least three reasons (Chapter 3). First, the fitness considerations underlying the mathematical analysis of sex role evolution are intricate and therefore error-prone. This is illustrated by the fact that the analysis of some foundational studies on the evolution of parental care is fundamentally flawed (see Houston & McNamara, 2005; Fromhage & Jennions, 2016). It is therefore useful to check the analytical predictions by means of an independent approach, which is, as our simulations, not based on the analysis of a fitness function. Second, mathematical analyses are restricted to highly simplified scenarios, as the limitations of analytical tractability are soon reached in models of sex role evolution. These limitations do not apply to simulation models. For example, sexual selection can be incorporated in a more natural way than in the framework of Kokko and Jennions (2008). Third, and most importantly, the mathematical analysis is often based on (hidden) assumptions that are not always justified. For example, the selection gradient approach used by Kokko and Jennions (2008) and Fromhage and Jennions (2016) implicitly assumes that the male and female parts of the population are monomorphic. As shown in Chapter 3, this assumption is not justified: when the sexes have conflicting interests (as in sex role evolution), the population undergoes periods of divergent selection, leading to polymorphism. Even if polymorphism is transient, it can be decisive for the evolutionary outcome. This is illustrated by the baseline model of Fromhage and Jennions (2016) (no sex differences in mortality, no parental synergism): while the selection gradient approach predicts a selectively neutral line of equilibria, the simulations reveal that there are actually two stable outcomes, either male- or female-biased care. Simulations are therefore an important check of whether the analytical methods predict the evolutionary outcome correctly.

Here, we use the simulation model of Chapter 3 to systematically study the joint evolution of parental behaviour and sex ratios (MSR, ASR, OSR) for various types of sex difference in life history parameters (maturation rate, juvenile mortality, mortality in the mating phase, mortality in the caring phase). First, we consider the case that the parents have an additive effect on offspring survival. As the mathematical model is degenerate in this case (exhibiting a neutral line of equilibria), no analytical predictions are available for this case. Second, we extend the analysis to parental synergy. By rescaling the model of Fromhage and Jennions (2016), we can systematically compare the simulation outcomes with their analytical predictions.

Throughout, we address the following questions: Do sex differences in life history characteristics have a predictable outcome on the evolution of parental care biases? How do sex ratios co-evolve with parental care patterns? Is there a consistent relationship between the bias in one of the sex ratios (MSR, ASR, OSR) and the parental care bias? In addition, we will touch upon questions as: Is, for a given parameter combination, the evolutionary outcome unique or are there alternative stable states? Does parental synergy lead to strongly different outcomes than scenarios where parental effects on offspring survival are additive? To what extent do the simulation outcomes confirm the analytical predictions of analogous mathematical models.

4.2 METHODS

The individual-based simulations were based on (a slightly simplified version of) the model in Chapter 3. We consider a randomly mating population with overlapping generations. The time structure of the model is discrete; a time unit is thought to represent one day. The model considers the evolution of two strategic parameters: T_f and T_m, the number of days invested in the care of the current brood when being the female or male parent, respectively. T_f and T_m are natural numbers that are encoded on two unlinked gene loci that are expressed in a sex-specific manner. They evolve via mutation and selection, and the evolutionary outcome determines the parental sex roles in the population. For simplicity, the individuals in our model are haploid.

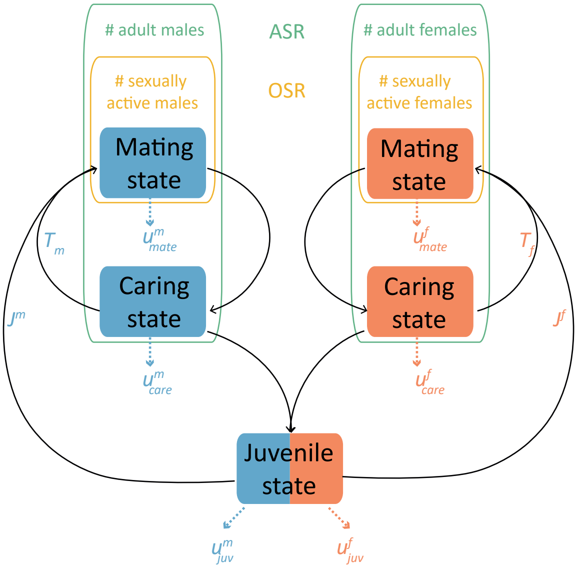


Figure 1. A schematic representation of the life cycle in our model. Individual males (blue) and females (red) can be in three states. Surviving offspring first spend some time in the juvenile state. After a sex-specific maturation time (J^m or J^f) they enter adulthood, where they switch between the mating state and the caring state. Unless stated otherwise, the maturation time is 20 time unites for both sexes ($J^m = J^f = 20$). The time in the mating state depends on the availability of mates and hence on the operational sex ratio (OSR), the proportion of males among the individuals in the mating state. In contrast, the adult sex ratio (ASR) refers to the proportion of males among all adult individuals. After mating, the mates spend T_m and T_f time units in the caring state; afterwards they return to the mating state. T_m and T_f are heritable traits that evolve subject to mutation and selection. A longer care time increases the survival probability of the offspring. In all states, (sex-specific) mortality occurs with probability $u^m_{\cdot}$ and $u^f_{\cdot}$ per time unit (juvenile state: u^m_{juv} , u^f_{juv}, mating state: u^m_{mate}, u^f_{mate}, caring state: u^m_{care}, u^f_{care}). Unless stated otherwise, the mortality rates are $u^m_{\cdot} = u^f_{\cdot} = 0.001$, corresponding to a life expectancy of 1,000 time units.

Life cycle. Each day, the individuals in our model are in one of three states (see Fig. 1): the juvenile state, in which newly born offspring stay until maturation; the mating state, in which males and females seek for mating partners; and the caring state, in which individuals provide parental care to their offspring. Offspring surviving the parental care period enter the juvenile state, where they experience the sex-specific mortality rate (i.e., the probability to die per day) u^f_{juv} or u^m_{juv}, respectively. Surviving juveniles mature after J^f or J^m days; after this time, they begin their adult life in the mating state. While in the mating state, the individuals are exposed to the sex-specific mortality rates u^f_{mate} and u^m_{mate}. Each individual in the mating state has one mating opportunity per day: pairs are formed at random, until only one sex is left in the mating state. Unmated individuals stay in the mating state for another day. The mated individuals switch to the caring state, where they stay for T_f or T_m days, depending on their inherited parental-care strategy. The mortality rates in the caring state are u^f_{care} and u^m_{care}, respectively. After leaving the caring state, surviving parents enter the mating state again. Each mated pair gives birth to one offspring, whose survival depends on the amount of care provided by the two parents (see below). Surviving offspring enter the juvenile state.

As our main focus, we investigate the effects of sex differences in the mortality rates in each of the three states and in maturation time. In all cases, we take the following baseline scenario as our point of departure: the maturation time of both sexes is $J^f = J^m = 20$ days, and the mortality rate is 0.001 day^{-1} in each state for both sexes. This means that the life expectancy of an individual in the baseline scenario is 1000 days, which, for simplicity, we regard as a proxy for generation time. In the sex-specific life-history scenarios, males and females may die at different rates or may have different maturation times. We consider one life-history parameter at a time. When we consider mortality differences in one of the states, the sex with the lowest mortality dies at the default rate of 0.001 day^{-1}, while the mortality rate of the vulnerable sex ranges from 0.001 day^{-1} to 0.1 day^{-1}. The mortality rate in the two other rates has the default value 0.001 day^{-1} for both sexes. In the case where juvenile females and males mature at different rates, one of the two sexes only requires 5 days to mature, while the maturation time of the other sex ranges from 5 to 50 days (with the exception of Figure S2(b)). In this scenario, all mortality rates are fixed at the default value 0.001 day^{-1}.

In our model, the sex ratios at any given day can easily be calculated by counting the number of males and females in the mating state (for the OSR), the number of adult males and females (for the ASR), and the number of juveniles that are maturating on that day (for the MSR). Sex ratios are expressed as the proportion of males among all individuals in the corresponding category.

Reproduction. Whenever a mating pair is formed, it produces a single offspring. The sex of the offspring is assigned at random, both sexes having the same probability. Offspring survival strongly depends on the total care effort provided by the parents. This is given by $T_{tot} = T_f + T_m + \sigma T_f T_m$, where T_f and T_m are the inherited care strategies of the two parents, while the term $\sigma T_f T_m$ (which for a given sum $T_f + T_m$ is largest when $T_f = T_m$) quantifies the synergistic benefits of egalitarian care. We first consider the case $\sigma = 0$ (no synergy), where the parents have an additive effect on offspring survival. In addition, we consider the case $\sigma = 0.2$, where egalitarian care provides a relatively strong benefit. As shown in Chapter 3, egalitarian biparental care evolves if $\sigma = 0.2$ and the life history parameters are the same for both sexes. The care-dependent survival probability of the offspring is given by $S_0\ (T_{tot}) = T^2_{tot}/(T^2_{tot} + D^2)$, where D can be interpreted as the care demand of the offspring (see Chapter 3). We chose $D = 20$ in all simulations. In addition, offspring survival is density dependent: $S(T_{tot}, N) = S_0\ (T_{tot})/(1 + \gamma N)$, where N is the current total population size and γ is a scaling parameter. This ensures that the population size remains constant. In all simulations, we set γ = 0.003; as a result, the total population size stabilised at approximately 4000 individuals.

The offspring inherit the traits T_f and T_m from their parents. For each of the two loci, either the paternal or the maternal allele was transmitted, with equal probability. Immediately after inheritance, a mutation could occur, with probability μ = 0.005 per locus. In case of a mutation, the inherited allele value was either increased or decreased by 1, with equal probability. Mutations from zero to a negative allele value were neglected.

Initialisation and replication. All simulations were started with a monomorphic population of 1000 adult males and 1000 adult females. The T_f-locus and T_m-locus were initialised at different values (see Fig. 2 and 3), The mortality rates and maturation times were varied across a wide range of parameter values, as stated above. For most parameter combinations, equilibrium was reached within 1,000 generations. In these cases, we ran 100 replicate simulations for 5,000 (or, in some cases, 50,000) generations to ensure that the results were representative. In some scenarios, there were two alternative stable outcomes. In these cases, attaining equilibrium may take a substantially longer period; therefore, we conducted 20 replicate simulations for 500,000 generations. All simulations were executed in C++.

4.3 RESULTS

We first discuss the joint evolution of parental care patterns and sex ratios for the case that the parents have an additive effect on offspring survival (σ = 0). Later we discuss the effects of parental synergy.

4.3.1 Sex differences in juvenile mortality or juvenile maturation time

Figure 2 illustrates how sex differences in juvenile mortality affect the evolution of sex-specific parental care patterns and the associated evolution of the OSR and the ASR (in this scenario, where adult mortalities are the same in both sexes, the ASR is identical to the MSR). When juvenile mortality differs between the sexes (and all other life-history parameters are the same for both sexes), uniparental care evolves, irrespective of the initial conditions (Fig. 2(a_1,c_1)). As illustrated in the time plots in Fig. 2(a_2,c_2), in evolutionary equilibrium all the care is provided by the sex with the lower juvenile mortality. In these example simulations, which started at a high degree of egalitarian biparental care (T_f = T_m = 20), the care level in both sexes first declines, as long as the total care provided ($T_f + T_m$) exceeds the care demand of the offspring (D = 20). The decline in care level continues in the sex with higher juvenile mortality, until the members of this sex do not care anymore. When the total care level $T_f + T_m$ has dropped below the care demand D, the sex with lower juvenile mortality increases its parental effort again, until this sex satisfies the care demands of the offspring on its own. Not surprisingly, the ASR is biased toward the sex with lower juvenile mortality (Fig. 2(a_3,c_3)) throughout the whole evolutionary trajectory. In contrast, the OSR changes quite dramatically in the course of evolution. In the initial period (the first 500 generations), when both sexes provide similar levels of care, the OSR is strongly skewed in the same direction as the ASR (toward the sex with lower juvenile mortality), but once uniparental care evolves, it becomes extremely skewed in the opposite direction, toward the non-caring sex. Fig. 2(b) shows the border case where *all* mortality rates are the same for both sexes. In line with our earlier study (Chapter 3), all simulations converged to one of two evolutionary equilibria, corresponding to either strongly female-biased care and strongly male-biased care (Fig. 2(b_1,b_2)). The ASR (= MSR) remains unbiased, and the OSR is strongly biased toward the non-caring sex (Fig. 2(b_3)). Figure 2 shows the evolutionary outcome for three particular combinations of mortality parameters. We will show later (see Fig. 5(a)) that these simulations are representative for a more general pattern.

In the Supplement (Figs. S1 and S2(a)), we show how the evolutionary outcome is affected by a sex difference in juvenile maturation times. Again, uniparental care or biparental care with a strong care bias evolved in all simulations. Typically, the faster maturating sex is the one that provides all or most of the care at evolutionary equilibrium (Fig. S1). However, even in case of a strong asymmetry in maturation rates there are two stable equilibria, and the opposite pattern of parental sex roles (where the more slowly maturating sex does most of the caring) evolves in a considerable percentage of the simulations (see Fig. S2(a_1)). The ASR (which is equal to the MSR in this scenario) remains even, unless the asymmetry in maturation rates is very strong (Fig. S2(a_2)). The OSR is, as before, strongly biased to the non-caring sex (Fig. S2(a_3)).

We can conclude that sex differences in the juvenile state have a predictable effect on the evolution of parental care: they lead to pronounced parental sex roles, where the sex that matures faster or is exposed to lower mortality is typically, but not always, does (most of) the caring. Notice, however, that the ASR (= MSR) tends to be unbiased in case of sex differences in maturation, while it is biased in case of sex differences in mortality. Accordingly, ASR and MSR are, on their own, not sufficient to predict the outcome of parental sex role evolution.

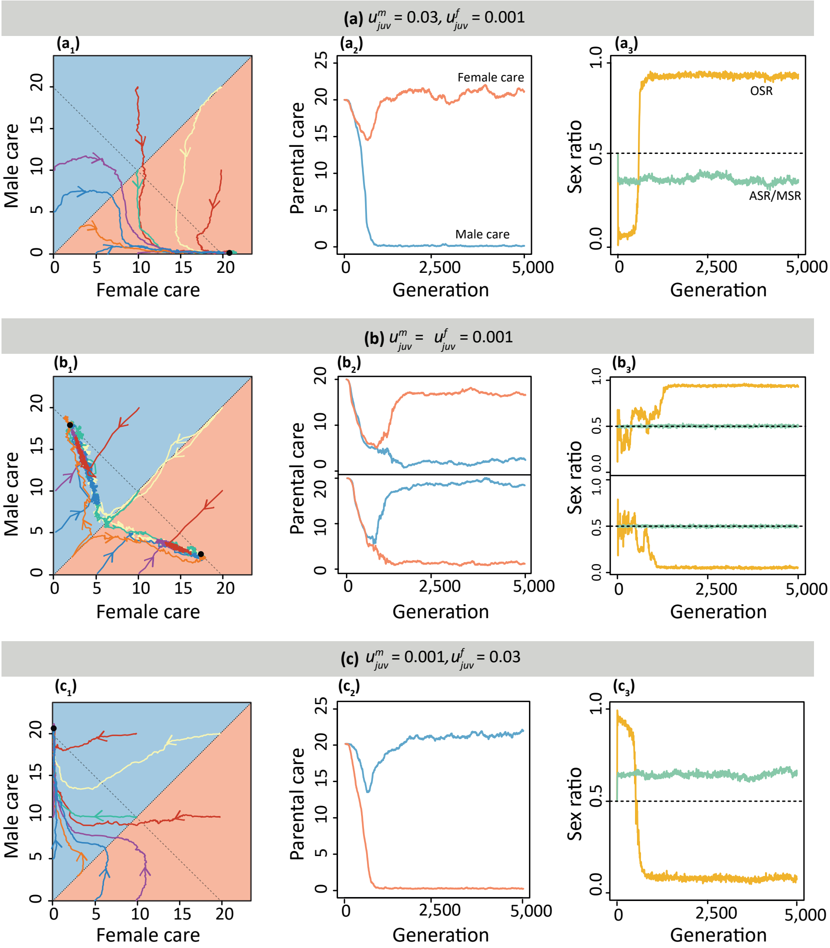


Figure 2. Sex differences in juvenile mortality drive sex role divergence. The graphs consider three scenarios where males and females differ only in their juvenile mortality rates (u^m_{juv} and u^f_{juv}). Since all adult mortality rates are the same, the ASR is identical to the MSR. **(a)** If male juvenile mortality is higher than female juvenile mortality (here: u^m_{juv} = 0.03, u^f_{juv} = 0.001), female-only care evolves, as is illustrated in (a_1) by the coloured trajectories that, starting from different initial conditions, all converge to the point (T_m, T_f) = (0,20) (indicated by a black dot). The yellow trajectory, starting at high-level egalitarian care (T_m, T_f) = (20,20), is shown as a time plot in (a_2). Panel (a_3) shows that the ASR (=MSR) (green line) stays approximately constant at 0.35. The OSR (yellow line) is first strongly female-biased and later, when evolutionary equilibrium is attained, strongly male-biased. **(b)** In the absence of sex differences (u^m_{juv} = u^f_{juv} = 0.001), either female-biased care (upper panels in b_2 and b_3) or male-biased care (lower panels in b_2 and b_3) evolves, with equal probability. In this case, the ASR (=MSR) is unbiased and the OSR is biased toward the less-caring sex. (c) If female juvenile mortality is higher than male juvenile mortality (here: u^m_{juv} = 0.001, u^f_{juv} = 0.03), male-only care evolves, with an ASR (=MSR) and an OSR pattern that is the mirror image of the pattern in (a). In all panels, male and female mortality rates in the mating and caring state were equal to 0.001. In all simulations parents had an additive effect on offspring survival (no synergy, $\sigma = 0$).

4.3.2 Sex differences in caring mortality

When the sexes differ in their mortality rates during parental-care periods, pronounced parental sex roles evolve in all simulations (Fig. 3). Irrespective of the initial conditions, the sex with the lower caring mortality tends to do the caring (Fig. 3(a_1,b_1)). The evolutionary trajectories of sex-specific care levels (Fig. 3(a_2,b_2)) show a very similar pattern as in Fig. 2. The same holds for the OSR (Fig. 3(a_3,b_3)), which again is strongly biased to the sex with lower mortality in the initial period (first 500 generations), where both parents are caring, and later switches to a strong bias toward the higher-mortality sex that, once evolutionary equilibrium is reached, refrains from caring.

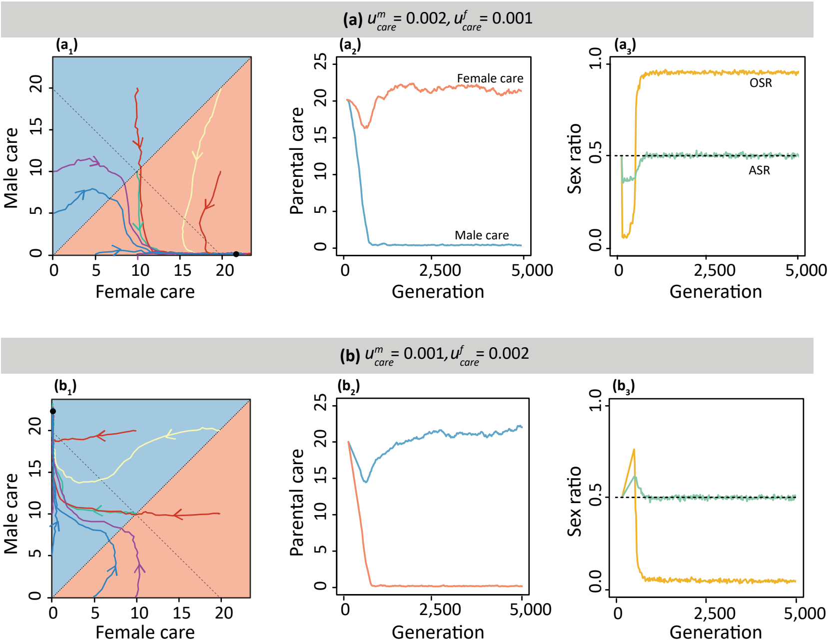


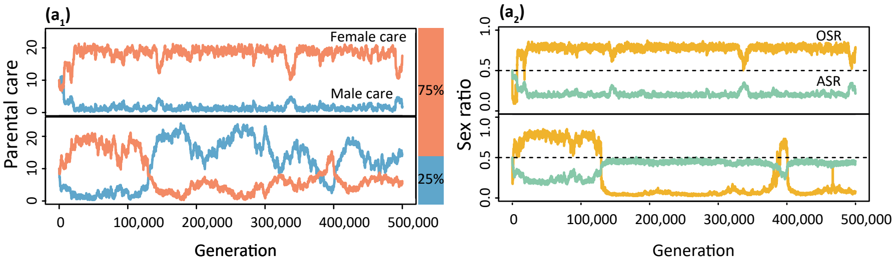
Figure 3. Sex differences in mortality while caring drive sex role divergence. The graphs consider two scenarios where males and females differ only in their caring mortality rates (u^m_{care} and u^f_{care}). As juvenile life-history parameters are identical in this scenario, the MSR is unbiased. **(a)** If caring for offspring is more dangerous for male than for female parents (here: $u^m_{care} = 0.002$, $u^f_{care} = 0.001$), female-only care evolves, resulting in an unbiased ASR and a strongly male-biased OSR. **(b)** Male-only care evolves if females die at a higher rate during the caring stage ($u^m_{care} = 0.001$, $u^f_{care} = 0.002$), leading to an unbiased ASR and strongly female-biased OSR. Graphical conventions as in Fig. 2. Male and female mortality rates in the juvenile and mating state were all equal to 0.001. In all simulations parents had an additive effect on offspring survival (no synergy, $\sigma = 0$).

In contrast to Fig. 2, the ASR is biased toward the sex with lower caring mortality in the initial period; at evolutionary equilibrium it becomes unbiased again, because the vulnerable sex avoids the risky task of caring for the offspring (Fig. 3(a_3,b_3)). Figure 3 shows the evolutionary outcome for two particular mortality scenarios. We will show later (see Fig. 5(b)) that these simulations are representative for a more general pattern. However, when the sex difference in caring mortality is small, an appreciable percentage of the simulations converged to the opposite equilibrium, where parental care is provided by the sex with the *higher* caring mortality. In these cases, both ASR and OSR are biased toward the low-mortality and low-caring sex throughout the whole evolutionary trajectory (see Fig. 5(b)).

4.3.3 Sex differences in mating mortality

Pronounced parental sex roles also evolve when the sexes differ in their mortality rates during the mating state (Fig. 4). Again, the sex with the lower mortality from mating typically most or all of the caring at evolutionary equilibrium (top panels in Fig. 4(a_1,b_1)). In this case, the ASR is biased to the caring sex (which has a lower mortality), while the OSR is biased toward the non-caring sex (top panels in Fig. 4(a_2,b_2)). However, even in case of considerable differences in mating mortality, two alternative evolutionary outcomes exist and a considerable percentage of all simulations end up in parental sex roles where most of the caring is done by the sex with the higher mortality during the mating state (bottom panels in Fig. 4(a,b)). When this happens, the ASR tends to be unbiased, while the OSR is strongly biased toward the non-caring sex (bottom panels in Fig 4(a_2,b_2)). As shown in Fig. 5(c), the outcome of the simulations in Fig. 4 is quite representative. The middle panel in Fig. 5(c) seems to indicate a considerable bias in the ASR in those cases where the high-mortality sex does the caring. However, this is most likely reflects the fact that non-equilibrium periods are included in Fig. 5(c), due to the lower stability of this sex role pattern (as indicated by the bottom panels of Fig. 4(a,b)).

(a) $u^m_{mate} = 0.005$, $u^f_{mate} = 0.001$



(b) $u^m_{mate} = 0.001$, $u^f_{mate} = 0.005$

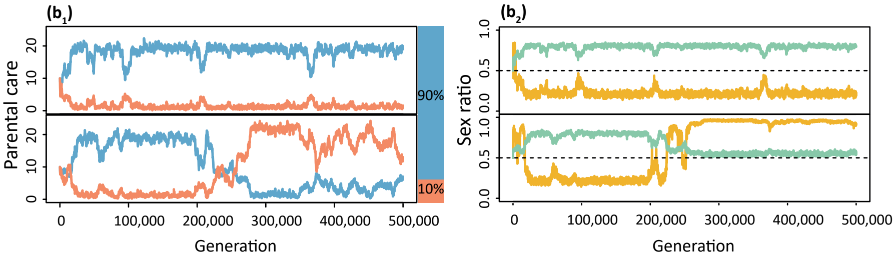


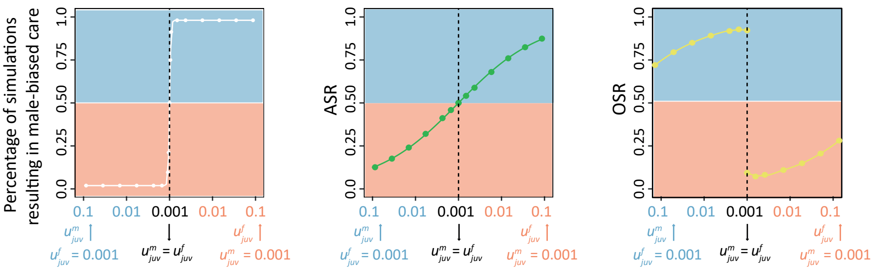
Figure 4. Sex differences in mortality while competing for mates drive the evolution of parental roles. The graphs consider two scenarios where males and females differ only in mortality when they are in the mating state (u^m_{mate} and u^f_{mate}). As juvenile life-history parameters are identical in this scenario, the MSR is unbiased. **(a)** When males face greater risk when competing for mates ($u^m_{mate} = 0.005$, $u^f_{mate} = 0.001$), female-biased care evolved in 15 out of 20 replicate simulations (75%; upper panels in (a_1) and (a_2)), corresponding to a strongly female-biased ASR and a strongly male-biased OSR. In the other 25% of the simulations there are extended periods of male-biased care (lower panels); in these periods, the ASR is slightly female-biased, while the OSR is strongly female-biased. **(b)** When females face a higher mortality risk when in the mating state ($u^m_{mate} = 0.001$, $u^f_{mate} = 0.005$), male-biased care evolved in 18 out of 20 replicate simulations (90%; upper panels in (b_1) and (b_2)), associated with a male-biased ASR and a female-biased OSR. In the other 10% of the simulations there are extended periods of female-biased care, associated with an ASR that is slightly male-biased and a strongly male-biased OSR. Male and female mortality rates in the juvenile and caring state were all equal to 0.001. 20 replicate simulations were run for 500,000 generations per parameter setting. In all simulations parents had an additive effect on offspring survival (no synergy, $\sigma = 0$).

4.3.4 Overview of evolutionary outcomes in the absence of parental synergy

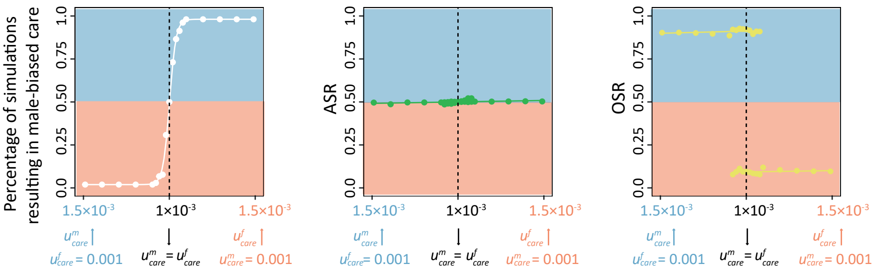
As shown in the overview figures (Fig. 5 and Fig. S2(a)) and in Table 1, a clear pattern arises in the no-synergy scenario ($\sigma = 0$) considered thus far, where the parents have an additive effect on offspring survival. Pronounced parental sex roles evolved in all simulations, in a predictable manner. Generally, the sex with the faster maturation or the lower mortality tends to become the caring sex, unless the sex difference in maturation times or mortalities is very small. In the latter case, two alternative stable outcomes, corresponding to either strongly male-biased care or strongly female-biased care do exist, as analysed in detail in our earlier study (Chapter 3). However, there are two scenarios where alternative outcomes also occur in case of considerable asymmetry between the sexes: when the sexes differ in maturation time (Fig. S2(a)), and when they differ in mortality during the mating phase (Fig. 5(c)). In these two scenarios, the opposite outcome (that parental care is strongly biased toward the sex with slow maturation or with high mortality) also evolves in a considerable percentage of the simulations.

In many of the scenarios considered, the evolved sex roles were associated with a bias in the ASR: the sex that does the caring is overrepresented in the population. This, however, is not always the case. When parental sex roles evolve in response to sex differences in maturation time (Fig. S2(a_2)) or in caring mortality (Fig. 5(b), middle panel), the ASR remains unbiased, despite pronounced sex differences in parental care. When the sexes differ in mating mortality (Fig. 5(c), middle panel), female-only care can also evolve in case of a male-biased ASR, while male-only care can evolve in case of a female-biased sex ratio. In other words, a bias in the adult sex ratio is not a reliable indicator for the outcome of parental sex role evolution. In all simulations considered thus far, the OSR is always biased toward the non-caring sex. Contrary to predictions in the literature (Kokko & Jennions, 2008; Fromhage & Jennions, 2016), however, the ASR and the OSR are often not biased in the same direction and not always responding in a similar way to changes in a parameter (e.g., Fig. 5(a)).

(a) Sex differences in juvenile mortality



(b) Sex differences in caring mortality



(c) Sex differences in mating mortality

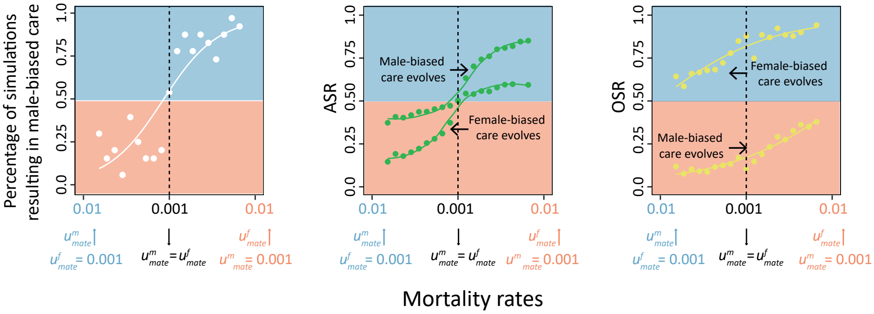


Figure 5. Implications of sex differences in mortality on the joint evolution of parental roles and sex ratios in the absence of parental synergy. Outcome of a large number of simulations considering sex differences in **(a)** juvenile mortality (u^m_{juv} and u^f_{juv}), **(b)** mortality while caring for the offspring (u^m_{care} and u^f_{care}), and **(c)** mortality while competing for mates (u^m_{mate} and u^f_{mate}). In (a) and (b), each dot represents 100 replicate simulations run for 5,000 generations for the mortality parameters indicated on the horizontal axis of each panel; in (c), each dot represents 20 replicate simulations run for 500,000 generations. All simulation started from egalitarian care ($T_m = T_f = 10$). The left panels show the percentage of simulations resulting in male-biased care. In all simulations, pronounced parental sex roles evolved, where one sex does most of the caring. In all three mortality scenarios, the sex with the lowest mortality tended to do most of the caring. The alternative outcome (that the sex with highest mortality does most of the caring) did occur in scenarios (a) and (b), but only when sex disparities in mortality rates were very small. In contrast, this alternative outcome arose more frequently in scenario (c). The middle and right panels show the ASR and OSR averaged over the simulations; in scenario (c) ASR and OSR are shown separately for the cases where male-biased care evolved and the cases where female-biased care evolved. In all cases, the OSR is biased toward the non-caring sex. In (a) and (c), the ASR is biased toward the low-mortality sex, while an even ASR evolves in scenario (b). In all simulations parents had an additive effect on offspring survival (no synergy, $\sigma = 0$).

4.3.5 Overview of evolutionary outcomes in the presence of parental synergy

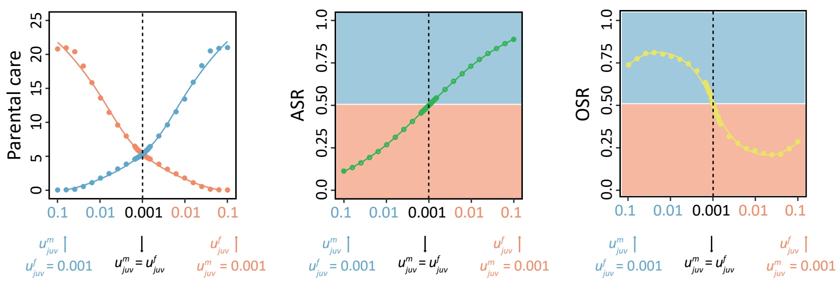
For all the scenarios considered above, we also ran replicate simulations for the case that parents have a synergistic effect on offspring survival ($\sigma = 0.2$). The results are summarised in Fig. 6, Fig. S2(b), and in Table 1. In contrast to the case of additive parental effects reported above ($\sigma = 0$), now biparental care evolved, unless the sex differences in mortality rates or maturation times were very large. The figures therefore do not show the percentage of simulations resulting in male-only or female-only care, but the average evolved care level in males and females. For all parameter combinations considered, all 100 replicate simulations converged to the same equilibrium outcome, and equilibrium was typically reached within a few hundred generations.

When juvenile mortality differs between the sexes (Fig. 6(a)), both parents care, but the level of parental care is inversely related to juvenile mortality. In other words, the sex with lower juvenile mortality cares more than the sex with higher juvenile mortality. The ASR (which is identical with the MSR in this scenario) is biased toward the sex with lower juvenile mortality, which is also the sex doing most of the caring. Interestingly, the OSR shows the opposite bias than the ASR: it is biased toward the non-caring sex. Moreover, the relationship of the OSR with the degree of juvenile mortality is non-monotonic. A very similar picture arises when juvenile maturation times differ between the sexes (Fig. S2(b)): both parents care, but the level of care is positively related to maturation time. Hence, the faster maturating sex cares more than the sex with a longer maturation time. The ASR is biased toward the non-caring sex, while the OSR is biased toward the caring sex.

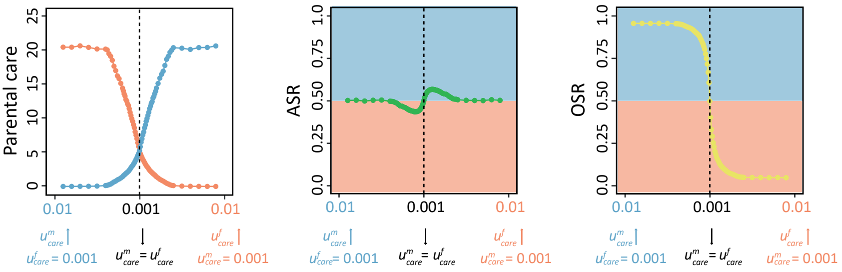
When the mortality rate during the period of parental care differs between the sexes (Fig. 6(b)), parental sex roles are more pronounced than in the other scenarios – already a relatively small sex difference in caring mortality leads to a strong sex bias or even to uniparental care. Again, the sex with lower caring mortality does most of the caring. For parameter combinations leading to uniparental care, the ASR is unbiased. When biparental care occurs, the ASR is biased toward the sex doing more of the caring. The opposite is the case for the OSR, which is strongly biased toward the non-caring sex.

When the mortality rate in the mating phase differs between the sexes (Fig. 6(c)), egalitarian biparental care evolves for all parameters considered. ASR and OSR are both biased toward the sex with lower mating mortality.

(a) Sex differences in juvenile mortality



(b) Sex differences in caring mortality



(c) Sex differences in mating mortality

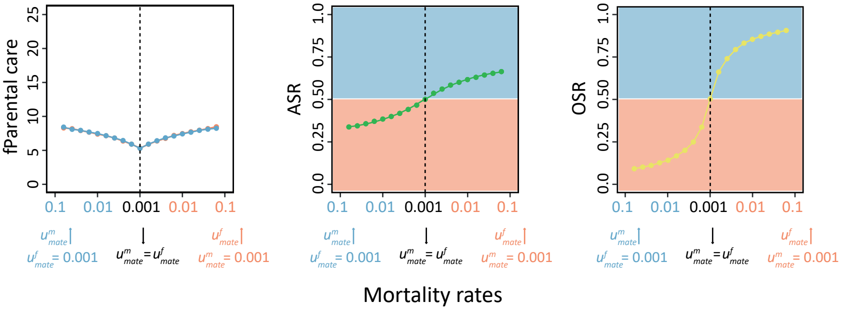


Figure 6. Implications of sex differences in mortality when biparental care has a synergistic effect. Outcome of a large number of simulations considering sex differences in **(a)** juvenile mortality, **(b)** mortality while caring for the offspring, and **(c)** mortality while competing for mates. In all panels, each dot represents 100 replicate simulations run for 5,000 generations (starting from egalitarian care: $T_m = T_f = 10$) for the mortality parameters indicated on the horizontal axis. In contrast to Fig. 5, biparental care has a synergistic effect on offspring survival (here: $\sigma = 0.2$). In this case, biparental care evolves when sex-specific mortalities are not too different. Therefore, the left panels now show the average level of male and female care (averaged over the 100 replicates). Notice that in scenario (c) egalitarian care evolved in all cases, even if mortality in the mating state differed strongly between the sexes.

In case of parental synergy, our simulations can be compared with analytical predictions that make use of the selection gradient method of Fromhage and Jennions (2016). The results are shown in Fig. S3. A comparison of this figure with Fig. 6

reveals that the simulations agree very well with the predictions of the Fromhage-Jennions model (see the caption of Fig. S3 for details). This is in contrast to the model variant without parental synergy, where the two approaches led to very different conclusions (see Chapter 3). We also run the Fromhage-Jennions model for another parametrization (Fig. S4). A comparison of Figs. S3 and S4 reveals that some of the patterns described above are not general, in that they depend on the parametrization of the model. For example, ASR and OSR show the opposite bias in Fig. S3(a), while they are biased in the same direction in Fig. S4(a) (see the caption of Fig. S4 for more details).

4.4 DISCUSSION

Using individual-based evolutionary simulations, we investigated the implications of sex differences in several life-history parameters on the joint evolution of parental sex roles and various sex ratios. Our conclusions are summarised in Table 1. Throughout, we considered two cases: one in which the parents have an additive effect on offspring survival and one in which they have a synergistic effect. In the first case, we consistently observed the evolution of pronounced parental sex roles (typically uniparental care), while in the second case biparental care (with a certain care bias) evolved in most simulations. Our study reveals that sex differences in life history characteristics have a systematic and predictable effect on parental care patterns. As a general rule, the sex with the lower mortality or the faster maturation is selected to provide most (or all) of the care (Figs. 5 and 6). However, in the case of additive parental effects, the opposite outcome (the sex with the highest mortality or the slowest maturation does most of the caring) evolved in a substantial proportion of the simulations (Fig. 5).

Two similar lines of reasoning, leading to opposing conclusions, can explain the different outcomes. The first line is based on biased sex ratios and explains why a lower mortality (or a faster maturation) is associated with a higher level of parental care. The argument goes like this: the sex with the lower mortality (or the faster maturation) is overrepresented in the population. In view of the Fisher condition, the members of the majority sex (here: the sex with lower mortality) have a lower *per capita* reproductive success. In our model, this means that the expected number of future matings is lower for a member of the majority sex than for a member of the minority sex. In the trade-off between current and future reproduction, the members of the majority sex should therefore place (relatively) more emphasis on the current brood than the members of the minority sex. The majority sex is therefore more strongly selected to provide care. Eventually, this asymmetry may result in parental care roles where the parent belonging to the majority sex (here: the sex with lower mortality) does most of the caring. The second line of reasoning makes use of similar life-history considerations, but arrives at the opposite conclusion.

Here, the argument goes like this: the sex with the higher mortality has a shorter life expectancy and consequently a lower potential for future reproduction (Stearns, 1976; Klug et al., 2013). Using the same argument as before, this sex should be more strongly selected to invest in the current brood, leading to a parental sex bias toward the sex with higher mortality. In a situation like this, where two similar lines of reasoning lead to opposite conclusions, verbal reasoning alone is not sufficient to predict the evolutionary outcome.

Table 1. Overview of the effects of sex differences in life-history characteristics on the joint evolution of parental roles and sex ratios. The table summarises the conclusions of our simulation study for two scenarios: **(a)** the parents have an additive effect on offspring survival (no synergy, $\sigma = 0$); **(b)** the parents have a synergistic effect on offspring survival ($\sigma = 0.2$). When the sexes differ in mortality in one of the life history states, the sex with a lower mortality dies at a rate of 0.001 day^{-1}, while the other sex dies at a higher rate. The mortality rates in the other states were set to 0.001 day^{-1} for both sexes. When the sexes mature at different rates, the faster-maturing sex takes 5 days to mature, while the slower-maturing sex takes longer. In this care, all mortality rates were fixed at 0.001 day^{-1}.

(a) Parents have an additive effect on offspring survival				
Sex differences in:	**Parental care pattern**	**MSR**	**ASR**	**OSR**
Juvenile mortality	The low-mortality sex does most of the caring	Biased toward the high-care sex	Biased toward the high-care sex	Biased toward the low-care sex
Maturation rate	The fast-maturating sex typically, but not always, does most of the caring	Unbiased	Unbiased	Biased toward the low-care sex
Caring mortality	The low-mortality sex does all of the caring	Unbiased	Unbiased	Biased toward the non-caring sex
Mating mortality	The low-mortality sex typically, but not always, does most of the caring	Unbiased	Biased toward the low-mortality sex	Biased toward the low-care sex
(b) Parents have a synergistic effect on offspring survival				
Sex differences in:	**Parental care pattern**	**MSR**	**ASR**	**OSR**
Juvenile mortality	Both parents care, with the low-mortality sex doing most of the caring	Biased toward the high-care sex	Biased toward the high-care sex	Biased toward the low-care sex
Maturation rate	Both parents care, with the fast-maturating sex doing most of the caring	Unbiased	Unbiased	Biased toward the low-care sex
Caring mortality	A small sex difference in caring mortality leads to a strongly sex-biased or even to uniparental care, with the low-mortality sex doing most/all of the caring	Unbiased	Unbiased	Biased toward the non-caring sex
Mating mortality	Egalitarian biparental care	Unbiased	Biased toward the low-mortality sex	Biased toward the low-mortality sex

What role, then, do sex ratios play in the evolution of parental care? A given sex ratio bias (be it in the OSR or the ASR) does of course affect the selection pressure on sex-specific parental care patterns. When, for example, the OSR is sex-biased (and the sexes do not differ in adult life-history traits), the members of the majority sex have a lower expected number of matings over lifetime, favouring a greater investment in parental care over mating competition (Kokko & Jennions, 2008). However, the OSR is not fixed and may change in the course of evolution (see Figs. 2 to 4). The reason is that the causality between OSR and parental sex roles is not unidirectional but reciprocal (Székely et al., 2000; Jennions & Fromhage, 2017): if one of the sexes provides most (or all) of the care, the members of that sex will typically be less available for mating, shifting the OSR toward the less-caring sex. In all scenarios explored in this study (with the exception of Fig. S4(b)), the OSR is, at evolutionary equilibrium, skewed toward the sex that provides less care. Yet, this should not lead to the conclusion that parental sex roles evolve in response to an OSR bias. The opposite seems to be the case. As revealed by the evolutionary trajectories (e.g., Figs. 2 and 4), the OSR can change strongly in the course of evolution, switching from a strong male-bias to a strong female-bias or *vice versa*. A close inspection of the trajectories reveals that changes in the parental care patterns tends to precede the change in OSR. From this we conclude that, at least for the random-mating scenarios considered in this study, parental sex roles drive the OSR, and not the other way around.

If we consider an ASR bias in isolation, the overrepresented sex in the adult population is most strongly selected to do the caring. This is because the Fisher condition applies to the ASR (as long as it is relatively constant over individual lifetime): at any given point in time, the offspring produced at that time have one adult mother and one adult father, implying that the more common sex in the adult population has a lower *per capita* reproductive output. As argued above, this tips the balance between current and future reproduction toward a higher investment in the current offspring. Thus, individuals of the overrepresented sex in the ASR are expected to do most of the caring. In a large number of simulations, we indeed found that female-biased care evolves under a female-biased ASR, whereas male-biased care evolves under a male-biased ASR (Figs. 5(a) and 6(a)). However, we also observed that under some circumstances (e.g., sex-specific caring mortality), strongly sex-biased care can evolve in the absence of ASR bias (Figs. 5(b) and 6(b)), and that under other conditions (e.g., sex-specific mating mortality), the underrepresented sex can even be associated with a much higher level of care (Figs. 5(c) and 7). This indicates that, as in the case of the OSR, there is feedback from parental care roles to the ASR, leading to a change in the ASR over evolutionary time (see the lower panels in Fig. 5).

To illustrate the reciprocal causation between ASR and parental care, we take the most noticeable case where the sexes differ in the mortality rate while caring. In this scenario, the members of the sex with the higher mortality bear a higher 'burden'; as a consequence, the members of the other sex are more strongly selected to care. In our model, this leads to extreme parental sex roles, where the members of the high-mortality sex abstain entirely from caring. This way, they avoid the high-mortality life-history state altogether, eventually leading to an unbiased ASR. Thus, selection on the ASR and sex roles interact in a dynamic manner, making it challenging to attribute a driving role to the ASR in the evolution of parental care. From our simulations, we arrive at the same conclusion as the analytical study of Fromhage and Jennions (2016): the processes by which the ASR becomes biased, rather than the ASR itself, causes sex role divergence.

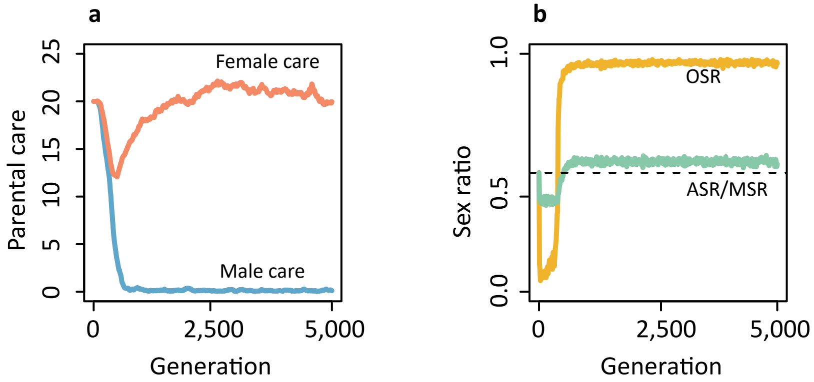


Figure 7. Parental sex roles are not necessarily predicted by the maturation sex ratio (MSR) or the adult sex ratio (ASR). When female juvenile mortality is higher than male juvenile mortality (here: $u^f_{juv} = 0.01$, $u^m_{juv} = 0.001$), the maturation sex ratio is male-biased. In the absence of sex differences in adult mortality, this would select for male care (see Fig. 5(a)). In the simulation shown here, there is an additional mortality bias in the adult stage: males die at a higher rate than females in the caring state (here: $u^f_{care} = 0.001$, $u^m_{care} = 0.002$). **(a)** Females are selected to care for their offspring, despite of the fact that **(b)** the MSR and the ASR are both biased in favour of males. Male and female mortality rates in the mating state were set to 0.001. Since males escape from the hazardous caring activity, adult males and adult females die at the same rate in the end, the ASR is then entirely determined by the MSR. In this simulation parents had an additive effect on offspring survival (no synergy, $\sigma = 0$).

To what extent, then, can MSR predict parental sex roles? According to the studies of Fromhage and Jennions (2016) and Jennions and Fromhage (2017), the MSR may be more relevant for the evolution of parental care than the ASR. In our simulations, we observed a clear-cut relationship between the MSR and care patterns when the MSR was biased due to sex-differential juvenile mortality: male-biased care evolved whenever the MSR was male-biased, while female-biased care evolved when the MSR was female-biased (Figs. 2 and 5(a)). This, however, is not a universal pattern, because other processes, different from juvenile mortality, also play a role (see also Chapter 5). For example, when the sexes mature at different rates, uniparental male or female care evolves, despite of an unbiased MSR (Figs. S1 and S2(a)). Moreover, even strong biases in the juvenile state can be 'overruled' by weak biases in an adult state. This is illustrated in Fig. 7, which considers a scenario where female juveniles die at a much higher rate than male juveniles ($u^f_{juv} = 0.01$, $u^m_{juv} = 0.001$), while males have a higher mortality than females while caring ($u^f_{care} = 0.001$, $u^m_{care} = 0.002$). In this scenario, female-only care evolves, despite of the fact that the MSR (and the ASR, which is identical to the MSR at evolutionary equilibrium) becomes biased in favour of males. Again, we conclude that also the MSR is affected by reciprocal causality, implying that an MSR bias can change in the course of evolution (as shown in Fig. 7).

Summarising all our findings, we arrive at the conclusion: none of the sex ratios should be viewed as a 'driver' of the evolution of parental sex roles; instead, sex disparities in life-history characteristics drive the joint evolution of sex ratios and parental sex roles. An important reason is that the sex ratios in our model are not fixed but dynamic in evolutionary time: they jointly evolve with the parental care patterns, and both the strength and the direction of the sex ratio biases often changes in the course of evolution. Having said this, we would like to qualify our above conclusion that sex differences in life history characteristics are *the* drivers of parental sex roles. This holds in our model, where the life history characteristics are fixed by assumption. In reality, mortality rates and maturation times are also evolvable properties. For example, female preferences can induce males to develop 'handicapping' traits compromising their survival (Zahavi, 1975; Maynard Smith, 1991; Kuijper et al., 2012). It would therefore be interesting to consider models where the life history parameters are not externally given but at least partly 'internalised'. In such a case, even more feedback can arise, potentially leading to different conclusions regarding the causality underlying the evolution of parental sex roles.

In our current work, we examine fairly straightforward scenarios. Most of the time, we simply look at one aspect of life history at a time. In natural systems, the sexes differ at various life stages (Orzack et al., 2015; Storchová & Hořák, 2017). The systematic investigation of the interplay of various sex differences is beyond the scope of this study. Here, we only show by means of an example (Fig. 7) that a sex difference in one mortality component (here: at the time of caring) seems to be more important than a difference in another component (here: juvenile mortality). Is this a special feature or does it reflect a general principle? What if other factors, such as sex-specific mating mortality, are introduced? Studying the interplay of such factors may seem a plausible next step, but such an endeavour may soon become unrealistic, as it would require a huge number of simulations.

For simplicity, we have focussed on random mating, thus neglecting sexual selection, which most likely will play an important role in the evolution of parental sex roles. The evolutionary interplay between sexual selection and parental care patterns may be more intricate than verbal or simple mathematical models suggest. This is exemplified in Chapter 3, where this interplay led to two alternative outcomes: one with strongly female-biased care associated with choosy females and bright males, and another with strongly-male biased care associated with non-choosy females and dull males. Will this interesting pattern (including long-term switches between the outcomes) remain when sex differences in life history characteristics are incorporated in the model? How will males allocate their resources to mating competition (ornamentation) on the one hand, and to parental care on the other, if ornamentation does not only affect mating success, but also mortality in the mating and the caring state? Addressing such questions seems interesting and important, but we have to leave this to a future attempt.

Last but not least, although we have explored the roles of OSR, ASR and MSR in the evolution of parental care, the role of the most fundamental sex ratio, namely the primary sex ratio (PSR), has not yet been studied. Sex ratio theory predicts that the PSR should be biased under certain circumstances (e.g., when sons and daughters require different amounts of resources; Fisher, 1930; West, 2009), with obvious implications for the sex ratios at later stages of the life history. Therefore, the question arises whether a bias in the PSR has a long-lasting effect on parental sex roles, and how parental care patterns, in turn, affect the evolution of the PSR. This topic will be the subject of Chapter 5.

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4.6 SUPPLEMENTARY INFORMATION

This Supplement includes four supplementary figures:

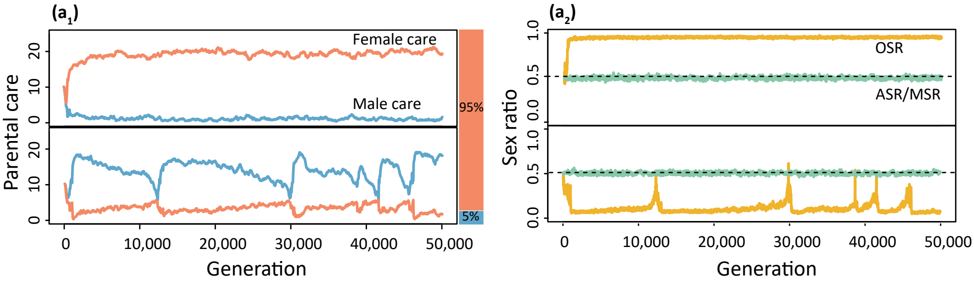
Figure S1. Sex differences in maturation time select for parental roles.

Figure S2. Overview of the effects of sex differences in maturation time.

Figure S3. Analytical predictions of the Fromhage-Jennions model.

Figure S4. Analytical predictions of the Fromhage-Jennions model (original parametrization).

(a) $J^m = 30, J^f = 5$



(b) $J^m = 5, J^f = 30$

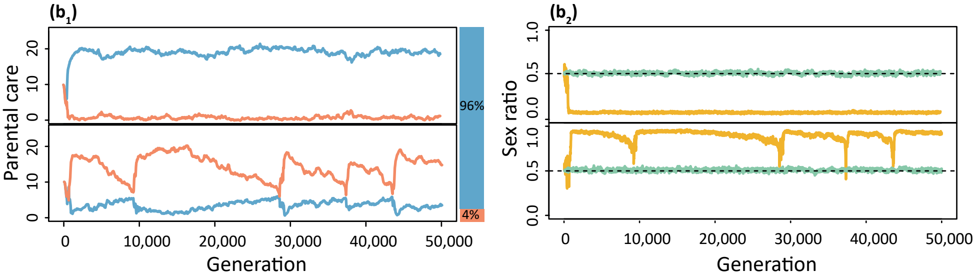
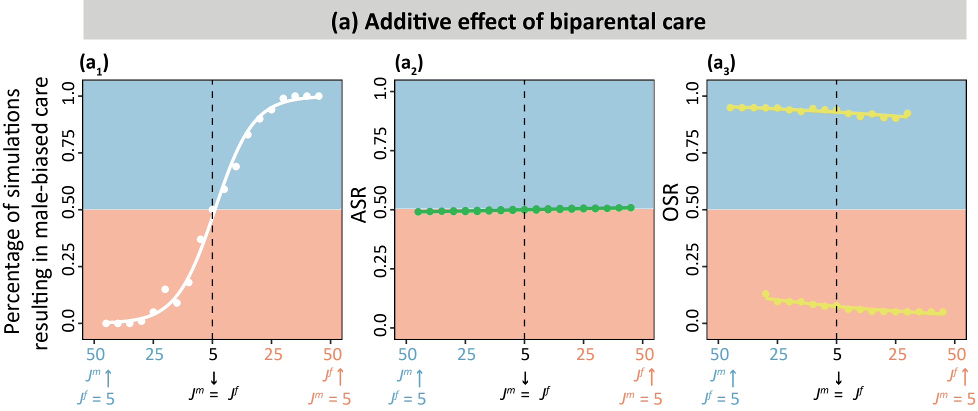
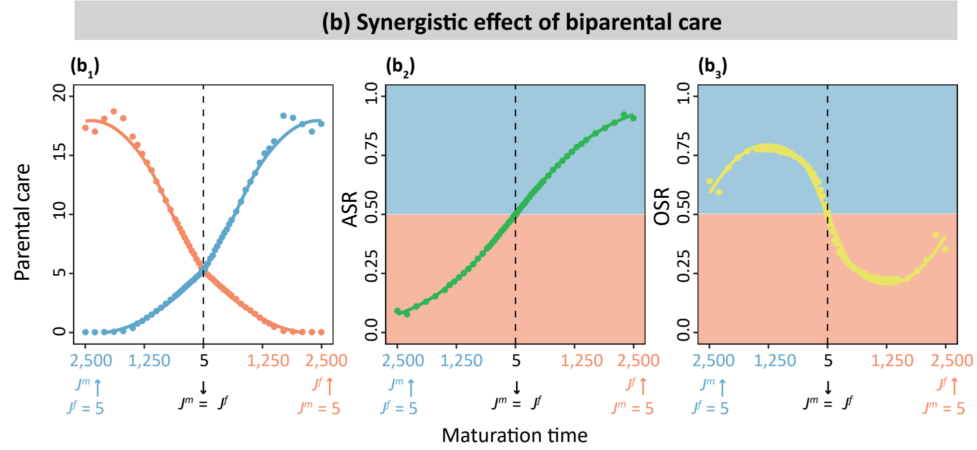


Figure S1. Sex differences in maturation time select for parental sex roles. The graphs depict a situation in which males and females mature at different rates (J^m and J^f). Since all adult mortality rates are the same, the ASR is identical to the MSR. **(a)** When males mature relatively slowly (J^m =30, J^f = 5), female-biased care evolved in 95 of 100 simulations, together with a nearly unbiased ASR and a strongly male-biased OSR (the upper panels in (a_1) and (a_2) show a representative example). In 5 simulations (lower panels), male-biased care evolved, together with an almost unbiased ASR and a strongly female-biased OSR. **(b)** When females take a longer period to mature ($J^m = 5$, $J^f = 30$), male-biased care evolved in 96 of the 100 simulations (upper panels in (b_1) and (b_2)), together with a nearly unbiased ASR and a strongly female-biased OSR. In 4 simulations (lower panels), female-biased care evolved, together with an unbiased ASR and strongly male-biased OSR. Mortality rates are 0.001 for both sexes in all stages, and 100 replicate simulations with 50,000 generations were run per parameter setting. In all simulations parents had an additive effect on offspring survival (no synergy, $\sigma = 0$).



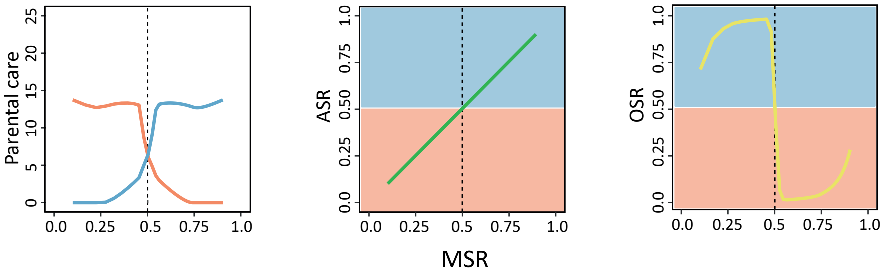
(a) Additive effect of biparental care



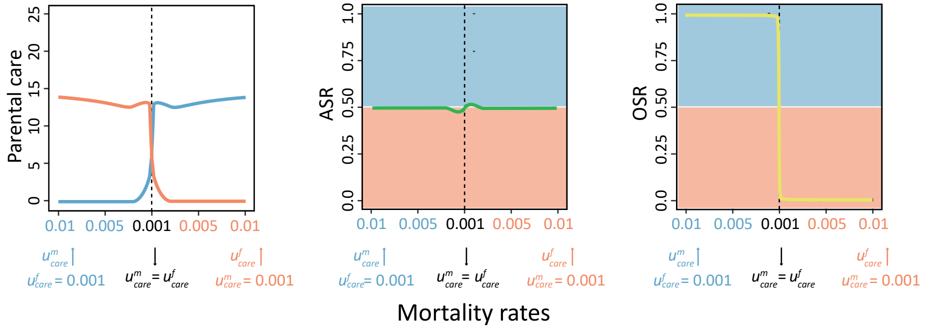
(b) Synergistic effect of biparental care

Figure S2. Overview of the effects of sex differences in maturation time. Outcome of a large number of simulations considering sex differences in maturation time. **(a)** In the absence of parental synergy ($\sigma = 0$), when parents have an additive affect of offspring survival, all simulations resulted in either strongly male-biased or strongly female-biased care. The percentage of simulations resulting in either outcome depends on the direction and degree of the asymmetry in maturation times as shown in (a_1): when males mature slowly, female-biased care is more likely to evolve, while male-biased care occurs more often when female juveniles spend a longer period to mature. The panel (a_2) shows ASR is unbiased, unless the asymmetry in maturation times is very strong. The OSR is shown separately for the simulations resulting in male- and female-biased care in the panel (a_3), in all cases, the OSR is skewed towards the less-caring sex. **(b)** In the presence of parental synergy ($\sigma = 0.2$), biparental care evolves when sex-specific mortalities are not too different. Therefore, the panel (b_1) now shows the average level of male and female care (averaged over 100 replicates). The sex that maturates faster tends to provide more care, and uniparental care evolves if the maturation time of the sexes is very different. In case of an extreme (more than 10-fold) asymmetry in maturation rates, the sex that maturates at a very slow pace has a larger chance of dying before reaching adulthood, resulting in an ASR bias in favour of the faster maturating sex. The OSR is biased toward the less-caring sex, and the relationship between the OSR and the degree of sexual asymmetry in maturation times is non-monotonic. 100 replicate simulations were run for (a) 50,000 generations and (b) 5,000 generation for each parameter setting. All simulations started from egalitarian care ($T_f = T_m = 10$), each dot of the ASR, OSR (in a and b), male care level and female care level (in b) shown in the graph is the mean of 100 equilibrium outcomes. Notice that the horizontal scales of (a) and (b) are very different, we here show a considerably large range of asymmetry in maturation rate in (b) to make it comparable to Fig. 6.

(a) Maturation sex ratio



(b) Sex differences in caring mortality



(c) Sex differences in mating mortality

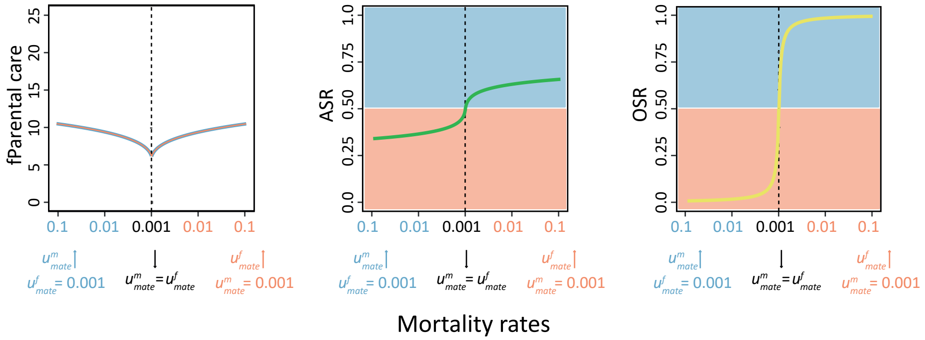


Figure S3. Analytical predictions of the Fromhage-Jennions model. By making use of the selection gradient method (evolution is supposed to proceed in the direction of steepest fitness ascent), Fromhage and Jennions (2016) were able to derive predictions on stable parental care levels and the corresponding ASR and OSR for various life-history scenarios. The analytical predictions could only be derived for the case of parental synergy. Although the Fromhage-Jennions model deviates from our model in several ways (see Chapter 3 and below), all their conclusions concur with ours for the case of parental synergy (which are summarised in Fig. 6). **(a)** Fromhage and Jennions did not directly consider sex differences in juvenile mortality or maturation rate; instead, they used the maturation sex ratio (MSR), which is identical to the ASR in this scenario, as an indirect measure summarising these differences. In line with Fig. 6(a) and Fig. S2(b), Fromhage and Jennions predict biparental care with a care bias toward the overrepresented sex under mild deviations from an even MSR, and uniparental care in case of large deviations. The predicted relationship between OSR and MSR also agrees well with the outcome of our simulations. When the sexes differ in **(b)** mating mortality rates or **(c)** caring mortality rates, the analytical predictions also agree very well with our simulations (see Fig. 6(b,c)). In the Fromhage-Jennions model, the offspring survival function is given by $S(T_{tot}) = \exp(-D/T_{tot})$, where T_{tot} is defined in a more complicated way than in our model: $T_{tot} = (T_m + T_f)(1+ \sigma T_m T_f/((T_m + T_f)/2)^2)$. Accordingly, the parental synergy parameter σ has a slightly different meaning in our model. For the figure panels, we used the parametrization $D = 20$ and $\sigma = 0.1$; moreover, all mortalities were, unless stated otherwise (along the horizontal axes), set to our default value 0.001. This choice aligns the two models relatively well (see Chapter 3). For comparison, Figure S4 shows the predictions of the Fromhage-Jennions model for their original parametrization.

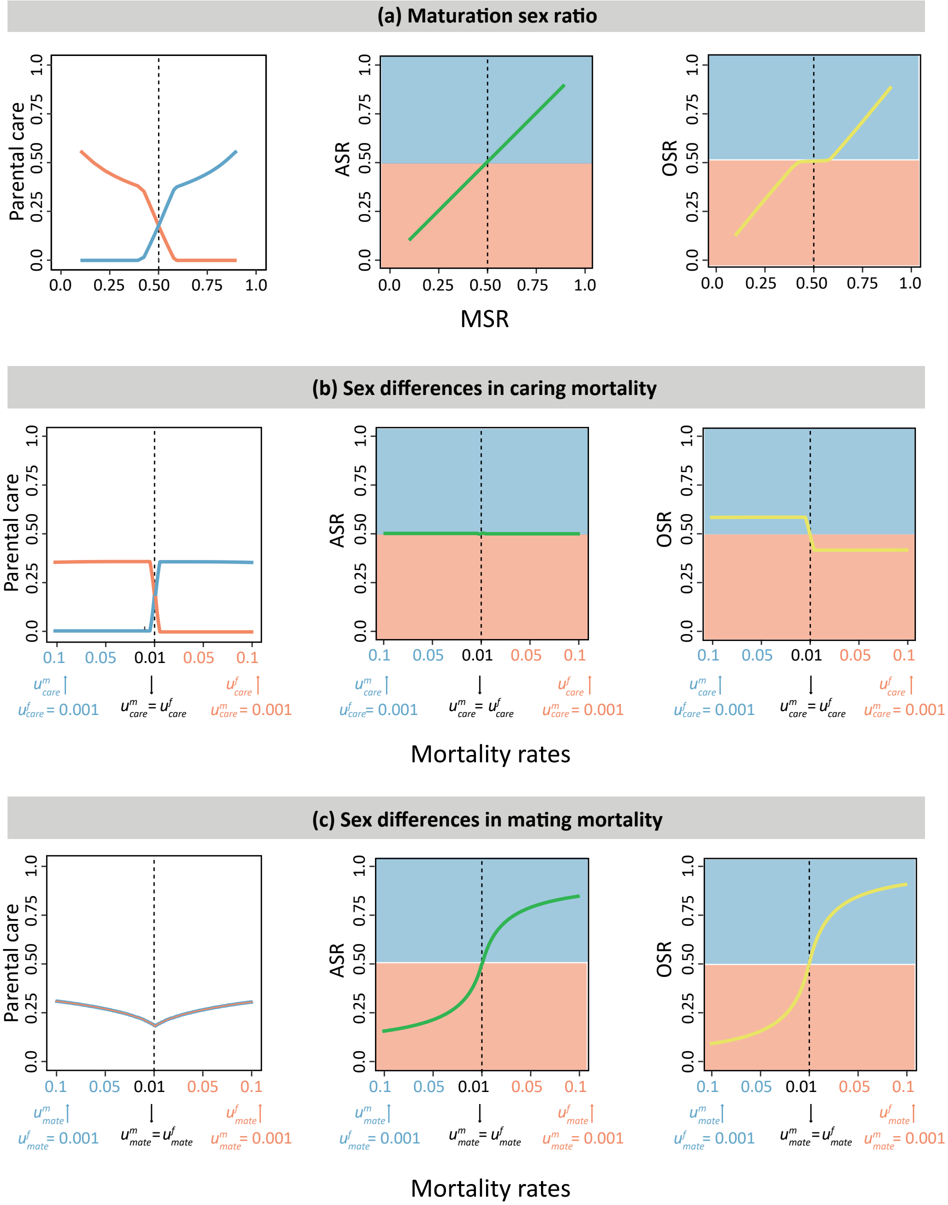


Figure S4. Analytical predictions of the Fromhage-Jennions model (original parametrization). Here we show the predictions of Fromhage and Jennions (2016) for the parametrization used in their article: $D = 0.1$, $\sigma = 0.1$, and baseline mortality 0.01 (instead of our default value 0.001). Apart from some rescaling effects, the predictions concur well with those of Fig. S3, with two notable exceptions. First, the relationship between OSR and ASR (= MSR) is completely different in Figs. S3(a) and S4(a). This shows that same parental care pattern can be associated with very different OSR patterns. Second, the original parametrization predicts an even ASR in scenario (b) (sex differences in caring mortality), whereas Figs. S3(b) and Fig. 6(b) predict a small but systematic deviation from an even adult sex ratio. Fig. S4(b) shows that the evolution of pronounced parental sex roles is not necessarily associated with a bias in ASR (or MSR).

Chapter 5

Joint evolution of parental effort and the primary sex ratio

Xiaoyan Long, Jan Komdeur, Tamás Székely, Franz J. Weissing

In preparation

ABSTRACT

According to Fisher's equal allocation principle, parents should invest equal amounts of their parental resources in the production of sons and daughters, implying that the 'cheaper' sex should be overproduced in the population. In most models investigating Fisher's principle, the investment per son and per daughter is viewed as an externally given parameter. Here, we consider an individual-based evolutionary model where the parental investment in sons and daughters is an evolvable trait that coevolves with the primary sex ratio (PSR). We consider various scenarios and show that the evolutionary outcomes deviate strongly from Fisher's principle. (1) When the parental care level coevolves with the PSR in the absence of linkage between the gene loci determining care and the loci determining the PSR, the evolved PSR is more strongly biased than Fisher's equal allocation principle predicts. (2) In the presence of linkage, polymorphism in care strategies and sex ratios evolves; the average PSR in the population is even more strongly biased than before. (3) If biparental care can evolve and females control the PSR (without linkage), male-only care and an unbiased PSR evolve if daughters are more costly to raise than sons; female-only care with a strongly biased PSR evolves if sons are more costly. (4) In the presence of linkage, uniparental care evolves as before, but in case of female care polymorphism evolves with an even more strongly biased PSR. (5) In some scenarios biparental care can evolve, with a PSR that is biased towards the more expensive sex. We conclude that details matter when predicting the joint evolution of parental effort and the primary sex ratio. However, deviations from Fisherian sex ratios are to be expected under a broad range of conditions. Moreover, selection on the PSR can have important implications for the evolution of parental sex roles.

5.1 INTRODUCTION

Sex-allocation theory is one of the most successful branches of evolutionary biology (Charnov, 1982; West, 2009). It attempts to explain how sexually reproducing organisms allocate their resources to male versus female reproduction. In dioecious species, it seeks to explain the observation that male and female offspring are produced in roughly equal numbers in most organisms, and also deviations from this general principle. Arguably, Fisher's (1930) equal allocation principle is the cornerstone of sex allocation theory. Fisher (1930) argued that in sexually reproducing organisms each offspring has one father and one mother; accordingly, the reproductive value (the genetic contribution to future generations) of all males must equal the reproductive value of all females. As a consequence, the *per capita* reproductive value of males is inversely proportional to the number of males in the population, while the *per capita* reproductive value of females is inversely proportional to the number of females. If there were an excess of one of the two sexes, the rare sex would thus have a greater *per capita* reproductive value, favouring parents to produce the rare sex until a balanced primary sex ratio (PSR; the ratio of male to female offspring at conception) is achieved. Fisher generalised this argument to situations where one sex is more costly to produce than the other sex. He showed that, at evolutionary equilibrium, parents should divide their reproductive resources equally between the production of sons and the production of daughters ('equal allocation principle'). Therefore, the 'cheaper' sex should be overproduced when sons and daughters are not equally costly to produce (Fisher, 1930).

Fisher's pioneering verbal argument laid the groundwork for many theoretical studies that formalised and clarified the equal allocation principle. Shaw and Mohler (1953) were the first to translate Fisher's reasoning into a mathematical formula (the 'Shaw-Mohler equation'). In essence, they derived a fitness function that describes how the offspring sex ratio influences an individual's relative genetic contribution to future generations, allowing for a systematic calculation of the evolutionarily stable sex ratio (see Pen and Weissing (2002) for a derivation and extensions of the Shaw-Mohler equation). Bodmer and Edwards (1960) used the Shaw-Mohler approach to formalise Fisher's (1930) argument that sex-differential mortality of the offspring during the period of parental care is relevant for the evolutionarily stable PSR, as early-dying offspring will need fewer parental resources (and therefore are 'cheaper'). They argued that, in the presence of sex-differential offspring mortality, Fisher's equal allocation principle does not apply to the primary sex ratio, but rather to the fledging sex ration (FSR; the ratio of male to female offspring at the end of parental care). In other words, the FSR, instead of the PSR, will evolve to such a value that at the end of parental care the total investment in *surviving* sons equals the total investment in *surviving* daughters. Kolman (1960) extended Fisher's original model to a situation in which individuals differ in the PSR they produce. He observed that a given PSR at the population level can be achieved in a multitude of ways.

For example, a 1:1 sex ratio can be achieved by a monomorphic population where all individuals produce a 1:1 sex ratio, or by a dimorphic population where half of the population only produces sons, while the other half only produces daughters. Accordingly, Kolman argued that Fisher's equal allocation principle applies to the PSR at the population level, and that the predicted equilibrium can be realised in a variety of ways. Since these early contributions many theoretical studies, using a variety of approaches, have further formalised and specified Fisher's verbal argument (e.g., MacArthur, 1965; Leigh, 1970; Charnov, 1982; Karlin & Lessard, 1986; Seger & Stubblefield, 2002; Pen & Weissing, 2002).

Before proceeding, we would like to stress that there are numerous situations where Fisherian sex ratios are not to be expected (see Charnov, 1982; Karlin & Lessard, 1986; West, 2009). For example, resources may not be allocated equally between sons and daughters when there is selection on adjusting the PSR in response to factors such as local mate competition (Hamilton, 1967), parental conditions (Trivers & Willard, 1973), and parent-offspring conflict (Trivers, 1974; Trivers & Hare, 1976). In particular, Frank and Swingland (1988) showed that the equal allocation principle is systematically violated at evolutionary equilibrium if the offspring sex ratio is made dependent on environmental conditions: in such a case, the sex that is produced under unfavourable conditions (which will often be the 'cheaper' sex) will be more abundant than the Fisher's principle predicts.

Here, we will stay close to the conditions under which Fisherian equal allocation can be expected to hold. However, our model will deviate in one important respect from the classical models briefly discussed above. All these models assumed (explicitly or implicitly) that the costs of producing sons and daughters are externally given; accordingly, these costs are treated as constant parameters (e.g., Shaw & Mohler, 1953; Bodmer & Edwards, 1960; Kolman, 1960; MacArthur, 1965; Leigh, 1970; Seger & Stubblefield, 2002). In contrast to this assumption, reproduction costs will typically be at least partly dependent on the investment decisions of the parents, which makes them evolvable properties. If this is the case, evolutionary feedbacks may arise between the PSR and the production costs of sons and daughters (see the Discussion in Chapter 4 on similar feedbacks between sex ratios and parental investment decisions). It is conceivable that such feedbacks can lead to substantial deviations from the equal allocation principle.

To investigate this, we consider a model where the PSR evolves in parallel with parental investment decisions. To our knowledge, such a situation has until now only been considered by Pen (2000) and Pen and Weissing (2002). Both studies point out various situations where deviations from Fisherian sex ratios are to be expected. These include a cost of sex ratio control, trade-offs between current and future reproduction, the inability to fine-tune clutch size, and parent-parent conflict over the PSR. The present simulation study complements the analytical approach of Pen and Weissing (2002). As we have seen in Chapter 3, such complementation is useful for various reasons. First, the results of Pen and Weissing (2002) are derived from fitness considerations that only allow the characterisation of evolutionary equilibria, but not whether these equilibria are attainable ('convergence stable') and/or evolutionarily stable (Geritz et al., 1998; see Appendix A in Van Boven & Weissing, 2004). By means of simulations we can check whether the equilibria discussed by Pen and Weissing (2002) are evolutionary attractors or whether perhaps evolutionary diversification ('evolutionary branching') occurs, as we encountered before in parental investment models (Chapter 3). Second, the analysis of Pen and Weissing (2002) implicitly assumes that the populations considered are monomorphic. As we have seen in Chapter 3, even transient periods of individual variation and polymorphism can be crucial for the course and outcome of evolution. Moreover, transient polymorphism often results in alternative stable states. Third, to ensure analytical tractability, mathematical models as those considered by Pen and Weissing (2002) have to be kept quite simple, thereby making a number of restrictive assumptions. For example, they assume that only females provide parental care and that only females control the sex ratio of their offspring. As we are interested in the care decisions of both parents, we here expand these models, considering evolution in both sexes. Individual-based simulation models can easily be extended, by adding all kinds of factors of biological interests. Moreover, such simulations have the advantage that they naturally incorporate individual variation and stochastic factors (e.g., mutations, genetic drift, demographic stochasticity) (DeAngelis & Mooij, 2005).

This chapter is structured as follows. We first consider the baseline scenario in which the costs of producing a son or a daughter are fixed and only the PSR can evolve. In this scenario we assume that only one sex provides care, and we investigate the implications of maternal, paternal, and biparental control of the sex ratio. We explore whether, and to what extent, our simulations recover Fisher's equal allocation principle and the analytical predictions of Pen and Weissing (2002). Besides, we investigate whether it matters which parent controls the primary sex ratio. In a second step, we consider a scenario where only one sex provides care and also determines the PSR. Now, not only the PSR is evolving, but also the level of parental care. The level of care is independent of offspring sex, but the costs of producing a son or a daughter are nevertheless different, as for the same care level more care time is required when raising the more expensive sex. We consider two sub-scenarios: one in which the PSR and the care level evolve independently, and second one in which both traits evolve in a coordinated fashion (implemented by genetic linkage). When investigating this scenario, we address questions as: To what extent does equal allocation still apply? Do the simulations confirm the analytical predictions of Pen and Weissing (2002)? Does the joint evolution of PSR and care level lead to different outcomes than PSR evolution for a fixed care level? Does it matter if PSR and care level can evolve in a coordinated manner (as in the case of linkage)? To what extent do we observe polymorphisms, which we encountered regularly in Chapter 3? In a third step, we extend the analysis further by allowing for the joint evolution of PSR, female care level, and male care level, without presuming that the sex that controls the PSR also provides parental care. This allows for a potentially intricate interplay of parental care and sex-ratio strategies. Now we address questions such as: Which care pattern, biparental or uniparental, is more likely to occur? To what extent are differences in the production costs of sons and daughters relevant for the evolution of the parental care pattern? If uniparental care is selected, which sex should be in charge of caring tasks: the sex that controls the PSR or the other sex? Does it matter (for the evolved care level and/or the evolved PSR) whether the PSR-controlling sex or the other sex does the caring? In a final step, we implement cost differences between sons and daughters in a different way. Here, we address the question: Do such modelling details matter for the evolutionary outcome?

5.2 THE MODEL

Population structure. The structure of our individual-based evolutionary model is similar to that of the models described in Chapters 3 and 4. We consider a sexually reproducing population with overlapping generations and a discrete time structure. To be concrete, we assume that a time unit corresponds to one day. The population consist of females and males that, on each day, can be in one of the following states: juvenile, mating, caring, or recovering from caring. In each of the three adult states, individuals have a mortality rate of 0.001 day^{-1}, resulting in an adult life expectancy of 1,000 days, a value we took as proxy for generation time in our simulations. Offspring mortality is density dependent, thus regulating population size. The degree of density dependence (see below) was chosen in such a way that the population consisted of approximately 4,000 individuals in all simulations reported.

Life cycle. Offspring surviving the nestling period enter the juvenile stage. After a maturation time of ten days (for both sexes) surviving juveniles start their adult life in the mating state. The males and females in the mating state pair up at random. Once paired, the male and female immediately switch to the caring state, rendering them unavailable for mating. If the sex ratio in the mating state is not 1:1, one or more individuals of the majority sex will be left unmated. These individuals remain in the mating state, where they have to wait until the next day for new mating opportunities. Individuals in the caring state stay in this state for a time period corresponding to either a predetermined parameter or an inherited care strategy. The duration of the care period can be sex-specific (T_m for the male parent; T_f for the female parent), but in the present study it cannot be adapted to the (sex) composition of the brood. Cost differences between sons and daughters arise because parents, when their care period is over, first have to recover from caring; the recovery period per son (R_s) may be different from the recovery period per daughter (R_d). When the recovery period is over, individuals switch back to the mating state. Individuals that do not care at all ($T = 0$) do not need to recover and return to the mating state the day after pairing. As previously stated, adults can die at any time and in any state. Hence, staying in any of the states for a prolonged period of time (in the mating state because of being a member of the majority sex; in the caring state because of a large value of T; in the recovery state because of having cared for offspring with a longer recovery period) is costly in terms of the expected future number of matings.

Offspring survival. Once a mating pair has formed, it produces a clutch of offspring. We assume that offspring survival depends strongly on the total parental effort $T_{tot} = T_f + T_m$, where T_f and T_m are the care durations of the female and the male parent, respectively. In addition, offspring survival is negatively related to the current population size N. To include both factors, we assume that for each offspring the probability to survive until fledging (= the juvenile state) is given by $S(T_{tot}) = (T^2_{tot}/(T^2_{tot} + D^2))/(1+ \gamma N)$. The first term $(T^2_{tot}/(T^2_{tot} + D^2))$ increases in a sigmoidal manner with total parental effort and describes the effect of parental care on offspring survival. The turning point of this function is at $T_{tot} = D$; accordingly, the marginal value of parental care is maximised at this level of care, which we call the 'demand' of the offspring. In a later study, we will consider differences in the demands of sons and daughters. Here, we assume that the demand of the offspring is not sex-specific; throughout, D was set to 20 days for both sons and daughters. The second term $(1+ \gamma N)$ is used to regulate population size N; γ is a positive constant determining the degree of density dependence. To ensure a sufficiently large population, γ was set to 0.003 in all simulations. As mentioned above, this choice results in a population size of about 4,000 individuals.

Differential costs of producing sons and daughters. There are various ways to implement cost differences in the production of sons and daughters in a model. We here chose for a variant where caring parents need a different recovery period after having cared for a son than after having cared for a daughter. This has the advantage that differential costs imposed on the parents do not have sex-specific consequences for their offspring. In our standard cost scenario, the parents have to recover for R_d days after having cared for a daughter and R_s days after having cared for a son. Hence, if a parent spends T days on caring, its total reproductive investment is $T+ R_d$ in case of a daughter and $T+ R_s$ in case of a son. Accordingly, $T+ R_d$ and $T+ R_s$ are the costs of raising a daughter or a son, respectively. In case of biparental care, the recovery period is distributed over the parents according to the care provided by them. Hence, it is given by $R \cdot (T_f/(T_f+ T_m))$ for the female parent and $R \cdot (T_m/(T_f+T_m))$ for the male parent, where R represents either R_d or R_s. In the simulations shown, the recovery period for the 'cheaper' type of offspring is equal to zero, while the recovery period for the more expensive type of offspring is either varied (in Fig. 1) or set equal to 15.

In our standard scenario, the recovery periods R_d or R_s are constant and independent of the parental care level. In Fig. 6, we consider an alternative scenario, where the recovery period after producing the cheaper type of offspring is equal to zero, while the recovery period after producing the more expensive type of offspring is proportional to T, the duration of the care period of the caring parent. In this variant of the model, the duration of the care period has therefore direct repercussions on the cost asymmetry. As constant of proportionality we chose 0.75, as $0.75 \cdot T = 15$ (the default recovery period after producing the more expensive sex) if T corresponds to D (= 20), the demand of the offspring.

Reproduction and inheritance. We consider a population of haploid individuals with four gene loci, each locus harbouring infinitely many alleles: the T_f-locus and the T_m-locus, which encode the duration of care when being a female or a male parent, respectively; and the s_f-locus and s_m-locus, encoding the probability of producing a son when the PSR is under maternal or paternal control, respectively. The T_f-locus and s_f-locus are only expressed in females while the T_m-locus and s_m-locus are only expressed in males. The value for T_f and T_f can take any natural number (including zero), whereas s_f and s_m are real numbers from the interval [0,1], in accordance with the general convention of quantifying sex ratios by the proportion of males shown in Chapter 4. When the PSR is under biparental control, it is given by $(s_f + s_m)/2$.

We consider two scenarios for the inheritance of care and sex ratio alleles. In the first scenario, the four gene loci are unlinked, and the allele an offspring receives at a given locus is drawn randomly from one of its parents (with 0.5 probability each), independently of the draws at the other loci. In the second scenario, the T_f- and s_f-alleles and the T_m- and s_m-alleles are linked and transmitted to the offspring as a pair. As a consequence, the maternal and the paternal care and PSR strategies can co-adapt with each other.

After a newborn offspring has inherited alleles from its parents, mutations can occur with probability $\mu = 0.005$ per locus. When a mutation occurs at the T_f-locus or the T_m-locus, the genetic value is either increased or decreased by 1, with equal probability. A mutation to a negative value was reset to zero. If a mutation occurs at the s_f-locus or the s_m-locus, the current value is modified by adding a small value to it. The mutational step size is drawn from a Cauchy distribution with location parameter 0 and scale parameter 0.01; the step size was limited to a maximal value of 0.05. A mutation to a negative value was reset to zero, whereas a mutation to a value greater than one was reset to one.

Initialisation and replication. In all simulations, the population was initialised with 1000 males and 1000 females. The s_f-locus and the s_m-locus were initialised at $s_f = s_m = 0.5$. The T_f-locus and the T_m-locus were initialised at $T_f = 20$, $T_m = 0$ when only females provide parental care, and $T_f = 10$, $T_m = 10$ when both parents initially care for the offspring. For each parameter combination, we ran at least 50 replicate simulations. Due to the high repeatability of the simulation results, we only present one representative replicate per setting.

5.3 RESULTS

Evolution of PSR when the costs of producing a son or a daughter are externally given. First, we explore the most fundamental scenario: only one parent, say the female, cares for the offspring, with a fixed level T_f. Only the PSR does evolve. Fig. 1a shows the evolutionary outcome for $T_f = 20$, assuming that the mother is the caring parent and that the sex ratio is under maternal control. According to Fisher's equal allocation principle, the evolutionarily stable PSR should lead to equal investment in sons and daughters, corresponding to $s(T_f+R_d) = (1 - s)(T_f+R_s)$ in our model. The corresponding PSR is called the 'Fisherian sex ratio'. Pen and Weissing (2002) arrive at a different conclusion. They show that Fisher's principle only holds true if the PSR and clutch size are optimised simultaneously. As the clutch size in our model is fixed at one, the latter condition is not satisfied. Moreover, the evolutionarily stable sex ratio depends on the trade-off between current and future reproduction and, hence, on the expected number of future matings of the caring parent. Using the reproductive value approach of Pen and Weissing (2002), we calculated the PSR expected by their theory (dashed lines in Fig. 1a), finding a perfect agreement of our simulation results with their predictions. This means that we do *not* find a Fisherian PSR, as the cheaper sex is overproduced in comparison to the equal allocation principle.

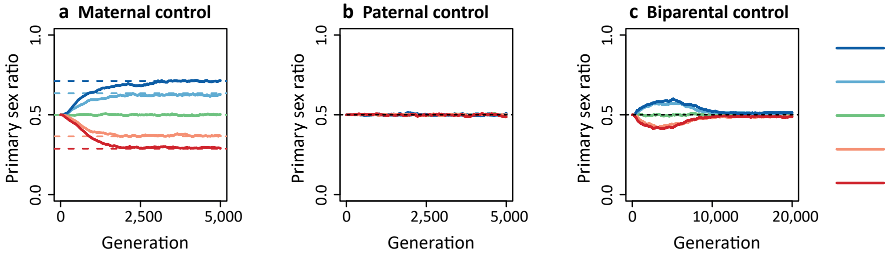


Figure 1. Evolution of the primary sex ratio when the production costs of sons and daughters are fixed parameters. The graphs depict evolutionary trajectories of the primary sex ratio (PSR) for a scenario where females provide a fixed amount of parental care while males do not provide care. The recovery period after maternal care depends on the sex being cared for and is determined externally. **(a)** When offspring sex is under maternal control, females overproduce the cheaper sex. The simulations (solid lines) converge to an equilibrium that coincides with mathematical predictions of Pen and Weissing (2002) (dashed lines). **(b)** When offspring sex is under paternal control, evolution leads to an unbiased PSR. **(c)** When both parents determine the sex ratio of their offspring, the cheaper sex is overproduced in an initial period (here: the first 10,000 generations), but in the end, an unbiased PSR evolves. The colours correspond to different cost scenarios (R_d, R_s: recovery period after caring for a daughter resp. a son). In all simulations, females care for 20 days ($T_f = 20$), males do not provide any care ($T_m = 0$), and the PSR is initialised at parity.

Mothers have typically been the focus of sex ratio theory, as many theoretical studies assume that the offspring sex ratio is exclusively controlled by females. Recent studies suggest that males may also be engaged in sex ratio control (reviewed in Douhard & Geffroy, 2021). Therefore, Fig. 1b considers a scenario where the male has substantial control over the PSR while the female is still the caring parent (T_f= 20). In line with standard theory, an unbiased PSR evolves in this case, as the males, which control the PSR, do not have to bear the costs of caring. In this situation, males and females have a conflict of interest regarding the PSR, as females would prefer to overproduce the cheaper sex.

Moreover, some empirical studies reveal that both sexes can be involved in determining the sex ratio of their offspring (Shuker et al., 2005; Macke et al., 2014). To investigate how sex-allocation strategy evolves when both parents have partial control over the PSR, we here simply assumed that the PSR is given by $(s_f + s_m)/2$. Fig. 1c shows the time trajectories of simulations with biparental control of sex allocation. In the first 10,000 generations, the cheaper sex is overproduced in the populations, but the magnitude of the PSR bias is less pronounced than it would be in the case when females have complete control over the PSR (Fig. 1a). Then, an unbiased PSR turns to be the evolutionary equilibrium. These findings suggest that under biparental control, sexual conflict over PSR leads to an evolutionary arms race, where the sex incurring the costs of reproduction tends to overproduce offspring of the cheaper sex, while the other sex bearing no reproduction costs counter-adapts to this strategy in order to attain an equal sex ratio. As a consequence, the sex bearing no costs of caring always 'wins' the arms race.

Joint evolution of maternal care level and PSR. Iteroparous species face two essential life-history trade-offs: the trade-off between current and future reproduction, and the trade-off between producing male or female offspring. In most studies, these trade-offs are explored separately from one another. In contrast, Pen and Weissing (2002) considered the realistic scenario that reproductive investment and PSR evolve jointly. They demonstrated that optimising reproductive effort and the sex ratio does not always result in equal allocation. To examine these findings, we extended our most basic model by allowing for the coevolution of the level of parental care and the PSR. We assume that the female does all the caring, and that the PSR is under maternal control.

Fig. 2 shows two representative simulations, all starting with a high level of female care (T_f = 20) and an unbiased PSR (s_f = 0.5). When daughters are more expensive to produce (Fig. 2a), females produce a larger number of sons (Fig. 2a_2). When sons are more costly to raise (Fig. 2b), a female-biased PSR evolves (Fig. 2b_2).No matter which sex is more expensive to generate, the female care level increases until it reaches a value close to 25, which exceeds the offspring demand (D = 20) (Fig. 2a_1,b_1). We think that this outcome can be explained by the trade-off between current and future reproduction: the long recovery period after rearing the most expensive sex reduces the mothers' expected number of future matings, making it profitable to invest more in current reproduction (Chapter 4).Moreover, polymorphisms in the PSR occur in most of the replicate simulations, with some of the females producing only sons and others producing only daughters (Fig. 2a_2,b_2).

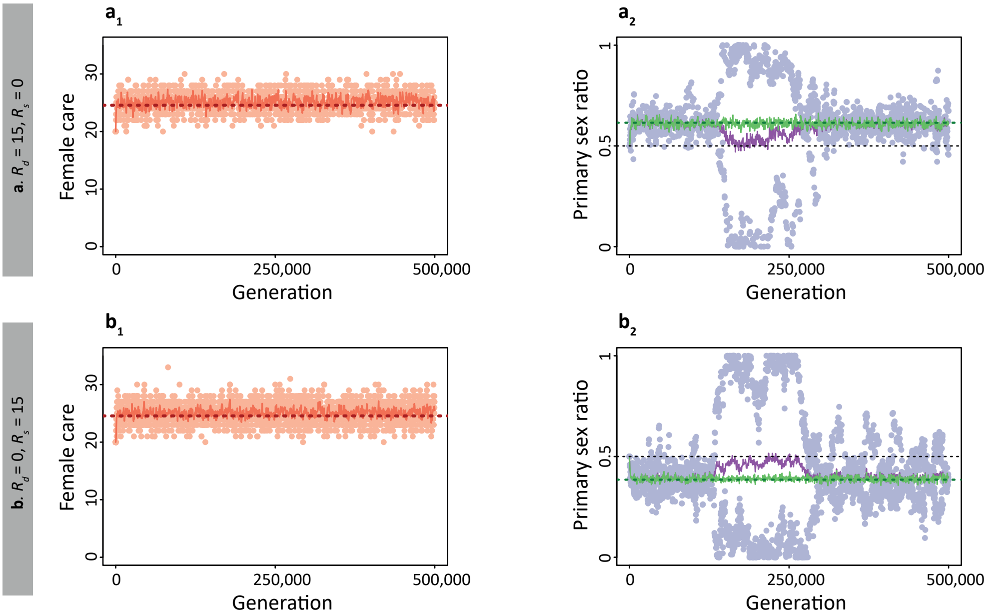


Figure 2. Joint evolution of maternal care level and PSR. Representative simulations for the case that the duration of maternal care (T_f) and the PSR, which is controlled by the mother (s_f), coevolve. **(a)** When daughters are more costly to raise, **(a_1)** a relatively high level of female care (exceeding the demand D = 20 of the offspring) evolves (solid red line), while **(a_2)** the average PSR in the population (green solid line) is biased towards males. **(b)** When sons are more costly, **(b_1)** the average female care level is similar to a1, while **(b_2)** the average PSR is female-biased. In these simulations, males do not provide care, and the female-care locus is unlinked to the PSR locus. Female care was initialised at 20 and the PSR was initialised at 0.5. <u>Graphical conventions:</u> Here, and in the following figures, solid red lines (as in a_1 and b_1) and solid green lines (as in a_2 and b_2) represent the average female care level and the average PSR that evolved in a simulation; dashed red lines (as in a_1 and b_1) and dashed green lines (as in a_2 and b_2) represent the evolutionarily stable female care level and the evolutionarily stable PSR predicted by the mathematical theory of Pen and Weissing (2002); red dots (as in a_1 and b_1) depict the T_f - values of individual females, while purple dots (as in a_2 and b_2) depict the PSR alleles (s_f- values) of individual females; solid purple lines show the average value of the PSR alleles in the female population. Notice that the average PSR (solid green line, the proportion of sons among the offspring produced in a time period of 1000 days) may differ from the average value of the PSR alleles (solid purple line).

Intriguingly, the occurrence of polymorphisms considerably lowers the bias in the average value of sex ratio alleles (s_f, indicated by solid purple lines), implying that the number of the two types of females is approximately equal. However, the average PSR (indicated by solid green lines) is still biased towards the cheaper sex, and the extent of bias is very close to that in the monomorphic population. This is due to the fact that females who exclusively produce the cheaper sex return to the mating market without any delay, resulting in an overproduction of the less expensive sex. Our findings, to some extent, support Kolman's (1960) argument that a population can have any degree of individual variability as long as the average sex ratio is in evolutionary equilibrium. Furthermore, our simulation results perfectly match with the analytical predictions of Pen and Weissing (2002) (dashed lines in Fig. 2), validating that the evolved sex-allocation strategy does not result in the overall investment in production for each sex being equal when the clutch size is constrained and trade-offs between current and future reproduction are considered.

We also checked two additional scenarios under the same assumptions, but with males having control over the sex of their offspring (Fig. S1) and both parents having control over the PSR (Fig. S2). In all circumstances, females provide a greater level of care than the offspring demand (Figs. S1a_1,b_1 and S2a_1,b_1), and the PSR is unbiased (Figs. S1a_2,b_2,a_3,b_3 and S2a_2,b_2). When the sex of the offspring is under paternal control, polymorphisms in the PSR also arise in some replicates (Fig. S1a_3,b_3). Taken together, identifying which sex is in control of the PSR is essential for predicting sex-allocation strategy, regardless of whether the parental investment in individual offspring is fixed (Fig. 1) or evolvable (Fig. 2).

Co-adaption of maternal care level and PSR. In the above simulations, we assumed that female care and sex-allocation strategies are inherited independently of one another. In Fig. 3, the two traits are assumed to be inked, and thus can co-adapt. In all replicate simulations, we observed polymorphisms in both PSR and maternal care effort. Importantly, parental care and sex ratio decisions are mutually dependent. When producing daughters is more costly (Fig. 3a), females who produce primarily daughters provide a relatively high level of care, whereas those who focus on producing sons offer a relatively low level of care (Fig. 3a_3). When the expense of raising sons is much higher (Fig. 3b), females who overproduce sons provide a higher level of care than those who overproduce daughters (Fig, 3b_3). In general, females devote more care to offspring of the more expensive sex than to those of the cheaper sex (Fig. 3a_1,a_3,b_1,b_3). This is because females who specialise in generating the most expensive sex face the longest recovery period, opting to provide more care in the current brood. In contrast to the results shown in Fig. 2, the extent of PSR bias increases when polymorphisms in parental care and sex ratio strategies emerge (see the solid green lines after generation 50,000 in Fig. 3a_2,b_2), suggesting that the cheaper sex is far more abundant when conditional sex allocation develops.

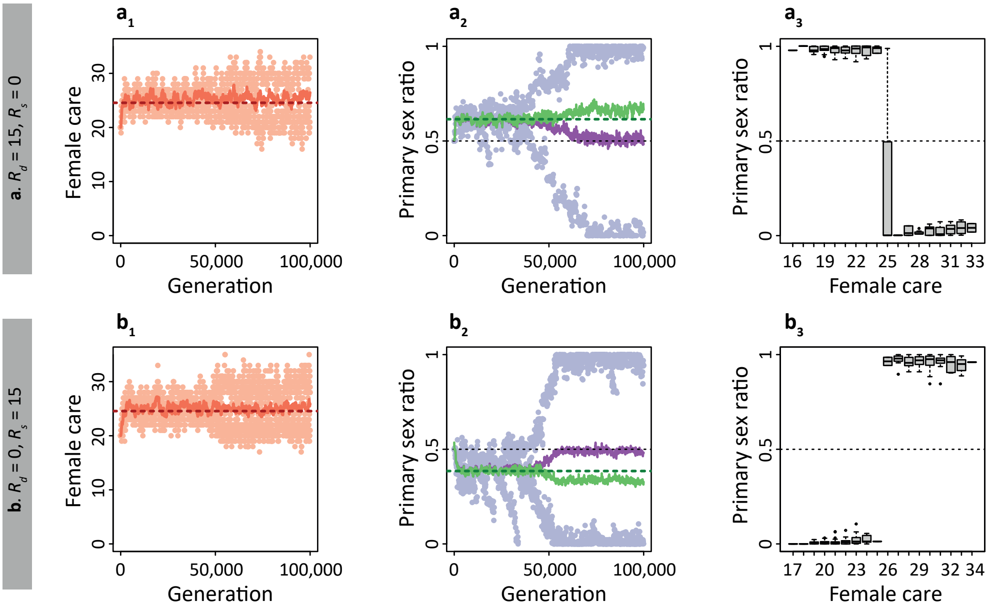


Figure 3. Co-adaption of maternal care level and PSR. The graphs show representative simulations for the same scenarios as in Fig. 2, but now for the case that the T_f - locus and the s_f - locus are linked, allowing the mother to adapt her care level to the PSR, and *vice versa*. Irrespective of whether **(a)** daughters or **(b)** sons are more costly to raise, $(\mathbf{a}_1,\mathbf{b}_1)$ a polymorphism in maternal care strategies and $(\mathbf{a}_2,\mathbf{b}_2)$ a polymorphism in PSR strategies evolve, $(\mathbf{c}_1,\mathbf{c}_2)$ with a strong association between female care level and the PSR. Notice that the emergence of polymorphism leads to a larger bias in average PSR (solid green line) than in the primordial monomorphic population. In all simulations, female care is initialised at 20 and the PSR is initialised at 0.5. Males do not care, and the PSR is under maternal control. See the caption of Fig. 2 for graphical conventions.

Joint evolution of PSR and parental sex roles. Previous research has primarily focused on the evolution of PSR (e.g., Shaw & Mohler, 1953; Bodmer & Edwards, 1960; Kolman, 1960; MacArthur, 1965; Leigh, 1970; Seger & Stubblefield, 2002; Pen & Weissing, 2002). However, the possibility of a reciprocal feedback from sex-allocation strategy to parental sex roles has largely been overlooked. To investigate the dynamic interplay between parental sex roles and sex-allocation strategy, we allowed female care and male care to coevolve with maternal PSR control. We assumed that genetic traits are inherited in a standard Mendelian way (no linkage), and that the recovery period is shared by the parents ($R\cdot(T_f/(T_f+T_m))$ for the female parent, and $R\cdot(T_m/(T_f+T_m)$) for the male parent).

Fig. 4 shows two representative simulations, both of which start with egalitarian biparental care ($T_f = T_m = 10$) and an even PSR ($s_f = 0.5$). When daughters are more costly to produce (Fig. 4a), males are selected to provide most (or even all) of the caring (Fig. 4a_1), and there is no bias in the average PSR (Fig. 4a_2). At the start, the female parent, who controls the offspring sex, has to spend an additional 7.5 days recovering from caring for a daughter, rendering them to produce more sons. As a result of this male-biased sex ratio, males are selected to care for their offspring (Chapter 4), which, in turn, eliminates the costs of caring in females, leading to an unbiased PSR in the end (similar to Fig. 1b).

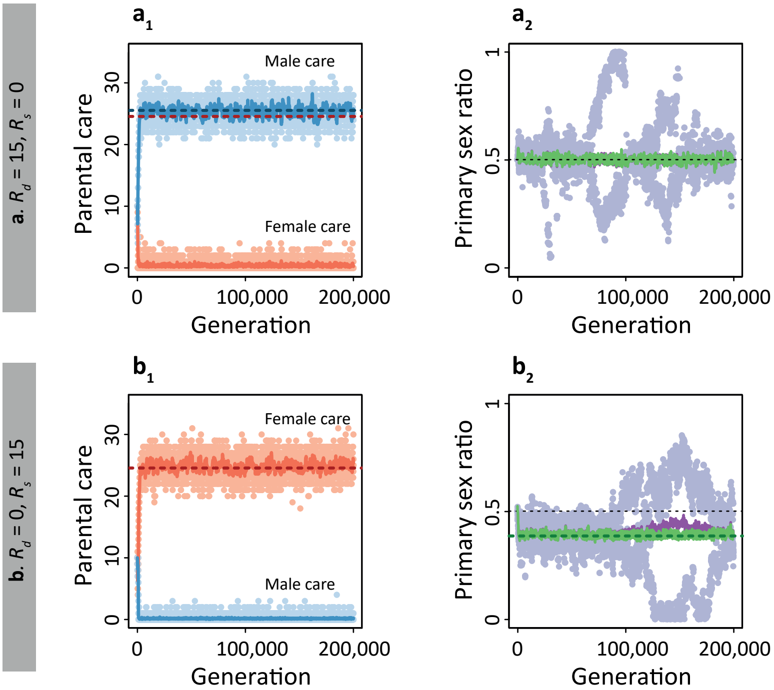


Figure 4. Joint evolution of PSR and parental care levels in both sexes. The graphs show the joint evolution of PSR, female care level, and male care level a scenario where the PSR is under maternal control and where the PSR and the care loci are transmitted independently. **(a)** When daughters are more costly to produce, **(a_1)** males are selected to provide all the care, while **(a_2)** an unbiased PSR at the population level is selected (although a polymorphism at the PSR locus occurs in some replicates). **(b)** When sons are more expensive to produce, **(b_1)** females are selected to provide all the care, and **(b_2)** these mothers produce a female biased offspring sex ratio. See the caption of Fig. 2 for graphical conventions.

In this case, the average male care level (see Fig. $4a_1$, the simulation result is shown by the solid blue line, and the analytical prediction of Pen and Weissing (2002) is indicated by the dashed blue line) is higher than the care level that develops in the scenario where biparental care cannot evolve at all (the analytical prediction for this scenario is indicated by the dashed red line, and the simulation outcome is shown by the solid red line in Fig. $2a_1$). In comparison to Fig. 2a, where the PSR is skewed towards the male (i.e., the cheaper sex), the unbiased PSR shown in Fig. 4a leads males to spend more time in the recovery state, hence increasing the investment in the current brood. Fig. 4b shows the circumstance where sons are more expensive to create. In this situation, strongly female-biased care evolves (Fig. $4b_1$), together with a female-biased PSR (Fig. b_2). Additionally, we discovered that the female population can be sporadically polymorphic in both scenarios, with some females producing a high proportion of sons and others generating a high proportion of daughters (Fig. $4a_2$,b_2).

With all other variables being equal, we examined the situation in which parents jointly control the sex of their offspring (Fig. S3). When it is more expensive to produce daughters, strongly male-biased care evolves (Fig. $S3a_1$), whereas strongly female-biased care evolves when it is more expensive to produce sons (Fig. $S3a_2$). Regardless of which sex provides care, an even PSR always results at equilibrium (Fig. $S3b_1$,b_2 ,the average PSR is indicated by pink lines).

Co-adaption of PSR and parental roles. In Fig. 4, each trait is inherited independently of the others. Fig. 5 shows a scenario in which parental care and sex ratio strategies are linked, with all other assumptions remaining the same as in Fig. 4. When daughters are more costly to raise (Fig. 5a), strongly male-biased care and an unbiased PSR evolve (Fig. $5a_1$,a_2), with polymorphisms in the PSR occurring occasionally (Fig. $5a_2$). In the presence of a PSR polymorphism, the female care level and the sex-ratio strategy are correlated: the PSR increases with the duration of female care (Fig. $5a_3$). When sons are more expensive to produce (Fig. 5b), female-only care and a female-biased PSR evolve (Fig. $5b_1$,b_2), with polymorphisms emerging in both female care and sex-allocation strategies (Fig. $5b_1$,b_2). Female care and PSR strategies are inextricably linked: females who exhibit a higher level of care specialise in son production, while those display a lower level of care specialise in daughter production (Fig. $5b_3$). Notably, the occurrence of polymorphisms results in a greater bias in the average PSR (solid green line) than in the monomorphic population.

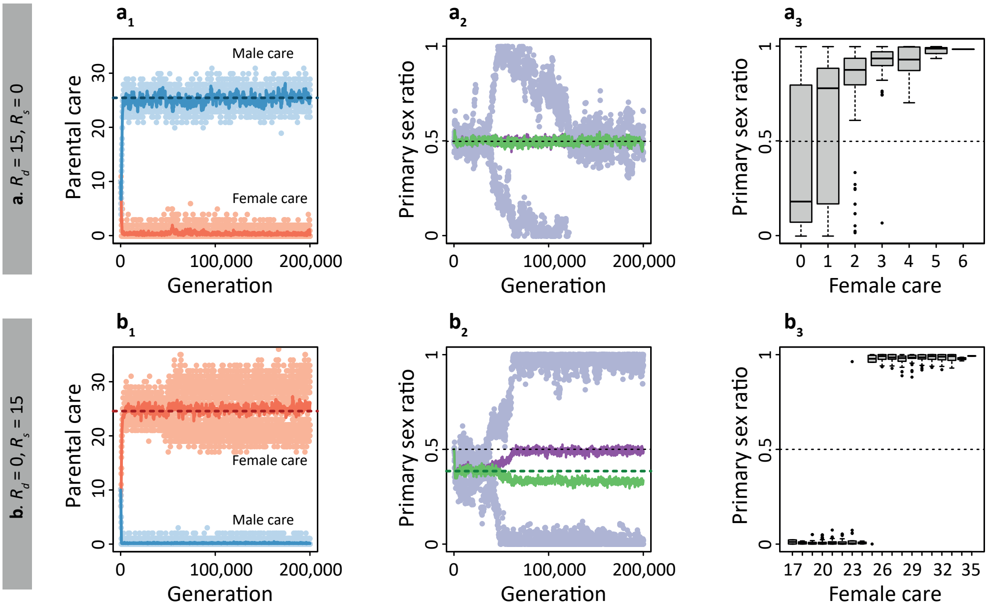


Figure 5. Co-adaption of PSR and parental care levels in both sexes. The graphs show the same situation as in Fig. 4, but now the care and the sex ratio loci are linked, allowing females (the sex controlling the PSR) to adapt the PSR to their care level. **(a)** When daughters are more costly to produce, **(a_1)** males are, as before, selected to provide all the care, while **(a_2)** the females produce an unbiased PSR at the population level. **(b)** When sons are more expensive to produce, **(b_1)** females are, as before, selected to provide all the care, but, in contrast to Fig. 4, **(b_2)** the average PSR at the population level is more skewed towards females. In (b), the female population is strongly polymorphic: some of the females provide a lot of care, and these females only produce sons **(b_3)**, while the other females provide much less care and only produce daughters. See the caption of Fig. 2 for graphical conventions.

Co-adaption of PSR and parental sex roles under a different cost scenario. Until now, all simulations have assumed that the recovery periods after caring for a son (R_s) or a daughter (R_d) are fixed. Here, we consider the same scenario as in Fig. 5, but with a recovery period that is proportional to each parent's own care level. Here, we assume that the recovery period after producing the more costly sex is given by $0.75 \cdot T$, while the recovery period after producing the cheaper sex is zero. With this assumption, we find a strong violation of Fisher's equal allocation principle, namely that the more expensive sex can be overproduced in the population (Fig. 6). When raising daughters is more expensive (Fig. 6a), strongly male-biased care and unbiased PSR evolved in the first 100,000 generations, followed by an increasing level of female care and a decreasing level of male care, as well as a female-biased PSR in the following 100,000 generations (Fig. 6a_1,a_2). This shift is triggered by the occurrence of polymorphisms in both female care and sex ratio strategies. The female population splits into two types after the 100,000th generation: one type focuses on producing daughters (who are the more costly sex, as their parents have to spend 0.75·T days to recover from caring for them) and provides a very low level of care (even no care). The other type predominantly produces sons (who are the cheaper sex, as their parents do not have to spend any recovery time before returning to the mating market) and provides a relatively higher level of care (Fig. 6a_3). The recovery time is essentially zero for both types of female. However, the females that primarily produces daughters also do not spend time caring and can thus return to the mating state much more quickly than the females that primarily produce sons; consequently, a female-biased PSR emerges in the population. Due to the occurrence of polymorphisms, the care pattern also switches from strongly male-biased care to the coexistence of biparental care and male-only care. In particular, when a son is born, both parents are involved in caring; however, when a daughter is born, only the male parent provides parental care (Fig. 6a_1,a_3). Fig. 6b shows what happens when sons are more expensive to produce. Now, strongly female-biased care develops, and the PSR is biased in favour of females (Fig. 6b_1,b_2). Despite the fact that the PSR polymorphism occurs (Fig. 6b_2), there is no correlation between female care and sex-allocation strategies (Fig. 6b_3). In comparison to the scenario where the total recovery period is fixed (see Fig. 3b, 5b), there is less individual variation in the female care level (Fig. 6b_1). This might be because the costs of caring increase in lockstep with parental investment in this case, preventing females from making large investment in the more expensive sex.

Additionally, we looked at the same scenario as in Fig. 6, but with males in charge of determining the sex of their offspring. Fig. S4 shows a mirror image of Fig. 6: male-only care and male-biased PSR evolve when daughters are more costly to produce (Fig. S4a), while female-biased care and male-biased PSR arise when sons are more expensive to produce (Fig. S4b). In the case of female-biased care, males participate in care tasks when daughters are produced, but they do not care for sons (Fig. S4b_3). Moreover, fig. S5 depicts the same situation as Fig. 6, but the recovery period after caring for the more expensive sex increases more slowly as care levels increase (here the recovery period after producing the more costly sex is given by 0.5·T). Similar to Fig. 6, when daughters are more costly to raise (Fig. S5a), males are selected to provide most of the caring (Fig. S5a_1), and females split into two types, with one type providing a higher level of care and specialising in producing sons, and the other type providing very little care and focusing on producing daughters (Fig. S5a_3). As a result, daughters are overproduced in the population (Fig. S5a_2). When sons become more expensive to produce (Fig. S5b), female-only care and female-biased PSR emerge, but without the polymorphisms in female care strategies exhibited in Fig. 5b.

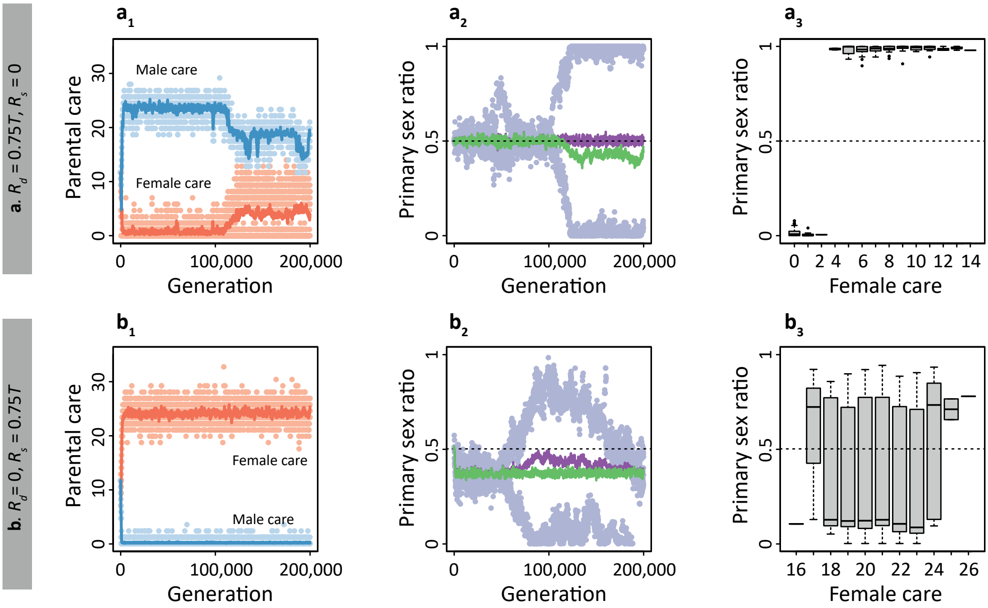


Figure 6. Co-adaption of PSR and parental care levels under a different cost scenario. The graphs show the same situation as in Fig. 5, but now the recovery period after caring is proportional to the parent's care level. **(a)** When daughters are more expensive to produce, **(a_1)** males are selected to provide more care, and two types of females evolve in the population: one type with a low-level care and the other type with a high-level care; **(a_2)** the PSR is unbiased when the population is monomorphic, but it becomes female-biased once polymorphism evolves; **(a_3)** there is a strong correlation between female care and the PSR when the female population is polymorphic: females with a higher level of care specialise in producing sons, whereas females with a lower level of care focus on producing daughters. **(b)** When sons are more costly to raise, **(b_1)** females are selected to provide care, **(b_2)** daughters are overproduced on average, **(b_3)** but there is no correlation between female care and the PSR. In this scenario, females and males stay in the recovery state for $0.75 \cdot T_f$ and $0.75 \cdot T_m$ days after caring for the offspring of the more costly sex, respectively. See the caption of Fig. 2 for graphical conventions.

5.4 DISCUSSION

We used individual-based simulations to investigate how the primary sex ratio coevolves with parental effort. Our simulations recovered some earlier analytical predictions and also produced several new insights. First, our baseline model (in which the PSR evolves in isolation, and the production costs of sons and daughters are fixed) predicts an overproduction of the cheaper sex, but to a different extent than predicted by Fisher's principle of equal allocation. The simulations confirm the analytical results of Pen and Weissing (2002), who demonstrated that equal allocation will only evolve when the clutch size and the PSR are optimised simultaneously. Moreover, our model demonstrates that identifying the parental sex that is in control of the PSR is essential for predicting the offspring sex ratio at evolutionary equilibrium. The cheaper offspring sex will only be overproduced if the caring parental sex is in full control of the PSR. Even in case of a large difference in the costs of raising a son or a daughter an unbiased PSR will evolve if the non-caring parent has full or partial control over the offspring sex ratio Second, when the PSR coevolves with parental investment in the absence of associations between parental care and PSR strategies, the evolved PSR is more biased than the equal allocation principle predicts. The average female care level and sex ratio strategy agree with the analytical predictions of Pen and Weissing (2002), but the evolutionarily stable PSR is, at the population level, either realised by a monomorphic population (where all individuals produce the same PSR) or by a polymorphic population (where individuals differ in the PSR produced). Third, In the presence of linkage between the genes determining the care level and the PSR, polymorphisms in care level and PSR strategies evolve rapidly. In this case, there is a strongly correlation between the care level and PSR: individuals with a higher level of care predominantly produce the more costly sex, while individuals with a lower level of care predominantly generate the cheaper sex. This condition- dependent sex allocation strategy results in the cheaper sex being even more abundant than it would be in the absence of condition dependence. Fourth, when the PSR coevolves with both maternal and paternal investment, the evolutionary interplay between the PSR and parental sex roles is even more intricate than previously anticipated. Cost differences in the production of male and female offspring induce a bias in the PSR, resulting in strongly sex-biased parental care, which in turn feeds back to affect the offspring sex ratio. In general, the cheaper sex is selected to provide parental care. If the caring sex is entirely responsible for the adjustment of the sex ratio of their offspring, the cheaper sex will be overproduced; otherwise, an unbiased PSR will evolve in the population. Last but not least, our model shows that the more costly sex can be overproduced (rather than underproduced, as predicted by Fisher's principle) when the cost differences in producing sons and daughters are not fixed but rather determined by care levels provided by each parent, suggesting that details do matter for the course and outcome of evolution.

To our knowledge, this study is the first to demonstrate the evolution of a condition-dependent PSR, where 'condition' refers to the genetic state at another gene locus, rather than on environmental states or the physical state of the parent. Under this conditional sex-ratio adjustment, the cheaper sex is more abundant than predicted by the equal allocation principle (Figs. 3 and 5b). This finding is in line with the analysis of Frank and Swingland (1988), who predicted an overproduction of the cheaper sex (in relation to the equal allocation principle) when the PSR is determined by a condition-dependent strategy. While Frank and Swingland (1988) were mainly concerned with environmental conditions (e.g., food resources, weather), our study suggests that their finding extends to situations where the PSR is conditional on genetic cues. The evolutionary outcome in our simulation aligns well with the 'genes as cues' principle of Olof Leimar and colleagues (Leimar, 2009; Dall et al., 2015). According to this theory, genetic cues can have a similar function as environmental cues in informing organisms about their selective environment and can hence guide the development of the phenotype. From this perspective, it is not too surprising that we arrive at the same conclusion as Frank and Swingland (1988).

Our model shares one feature with most other models where a condition-dependent PSR can evolve: typically, the evolved sex-ratio strategy is a 'bang-bang' strategy, where one type of sex is produced under one set of conditions, while the other type of sex is produced under the alternative conditions (see Figs.3, 5b, 6a, S4b and S5a). In species producing larger clutches, this would imply that most clutches only contain one type of offspring (either only sons or only daughters). Such extreme clutch sex ratios are rarely observed in nature, and a large number of empirical studies show that the PSR changes gradually in response to environmental conditions (e.g., Charnov et al., 1981; Daan et al., 1996; Wapstra et al., 2004). There are various options for bringing our simulation results better in line with such empirical findings. First, we assumed that an adjustment of the offspring sex ratio is not costly. Dependent on the system of sex determination, the costs of producing a sex ratio bias may increase with the degree of bias. It is conceivable that under such circumstances extreme sex ratios are not adaptive any more, as the benefits do not match the costs of extreme sex ratio control. Second, we assumed that care effort and PSR are completely linked, allowing for a perfect match between PSR and parental effort. It is conceivable that weakening genetic linkage will 'soften' the 'bang-bang' pattern observed under complete linkage.

Previous studies suggest that the maturation sex ratio (MSR) may be a good predictor of parental sex roles when there is no sex difference in adult life-history characteristics (Fromhage & Jennions, 2016; Chapter 4). The prediction is that the sex that is overrepresented at maturation should do all or most of the caring. Our results show that this assertion is not correct if the MSR reflects a PSR that coevolved with the parental care strategies of both parents. When producing female offspring are more expensive than producing male offspring, the PSR is biased in favour of males initially, favouring the male parent to provide most (or all) of the care (Figs. 4-6 and S3-S5). This is followed by the evolution of a male-biased PSR (Fig. S4a_2), an unbiased PSR (Figs. 4a_2, 5a_2 and S3a_2), or even a female-biased PSR (Figs. 6 and S5a_2). In contrast, females are selected to do most (or all) of the caring when female offspring are cheaper to raise than male offspring (Figs. 4-6 and S3-S5), corresponding to female-biased PSR (Figs. 4b_2, 5b_2, 6b_2 and S5b_2), unbiased PSR (Fig. S3b_2) or even male-biased PSR (Fig. S4b_2). From this, we conclude that the PSR (and the resulting MSR) does not necessarily predict the parental care pattern. Instead, the care decision of each parent is strongly affected by cost differences in raising sons or daughters. In general, the cheaper sex at the offspring stage is selected to do most (or all) of the caring later in life. Of course, the latter statement only holds under the provision that "all other things are equal". As we have shown in Chapter 4, the evolution of parental sex roles is also strongly affected by sex differences in life-history characteristics later in life. Therefore, further research into the relationship between cost differences, PSR, and parental sex roles is required, which also considers sex differences in maturation or adult mortalities at different life stages.

Our study illustrates that modelling details can be pivotal for the course and outcome of evolution. When we assume that recovery periods after caring for sons or daughters are fixed, and that the PSR and care efforts evolve in a coordinated fashion, mothers adapt her care level to the PSR in such a manner that with a higher level of care, they mainly produce the more expensive sex and with a lower level of care, they mainly produce the cheaper sex. In this way, the cheaper sex is overproduced in the population (Fig. 3). However, when we assume that the recovery periods after caring for offspring of each sex are proportional to care levels, there is a different correlation between care efforts and sex ratio strategies than that displayed in Fig. 3: high-care levels become associated with creating cheaper sex, while low-care levels become associated with rearing more expensive sex. As a result, the more costly sex, rather than the cheaper sex, gets overproduced in the end (Fig. 6). This suggests that the causal relationship between the PSR and parental care strategies is bidirectional, and that care must be taken in how to implement the costs of producing sons and daughters.

In the current study, differential costs of producing male and female offspring were implemented by introducing a recovery time depending on offspring sex. This way of modelling has the advantage that only the cost to the parent is manipulated, while keeping the 'needs' of the offspring constant. In many real-world situations, differential offspring costs arise as a result of differential offspring needs. This is, for example, likely to be case in sex dimorphic species, in which one of the sexes is larger than the other sex, and hence requires more parental resources in order to survive until fledging (Krijgsveld et al., 1998; Pen, 2000). In our model, such a scenario could be implemented by making the parameter D (specifying how offspring survival is affected by a given level of parental effort) sex-specific. It is possible that implementing differential offspring costs in terms of differential needs will lead to quite different conclusions than those reported here. Clearly, many questions are still unanswered and provide food for thought and future studies.

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5.6 SUPPLEMENTARY INFORMATION

This Supplement includes five supplementary figures:

Figure S1. Joint evolution of maternal care level and paternal PSR control.

Figure S2. Joint evolution of maternal care level and biparental PSR control.

Figure S3. Joint evolution of parental care levels in both sexes and biparental PSR control.

Figure S4. Co-adaption of parental care levels in both sexes and PSR under paternal control in a different cost scenario.

Figure S5. Co-adaption of PSR and parental care levels under a weakening influence of care levels on differential offspring costs.

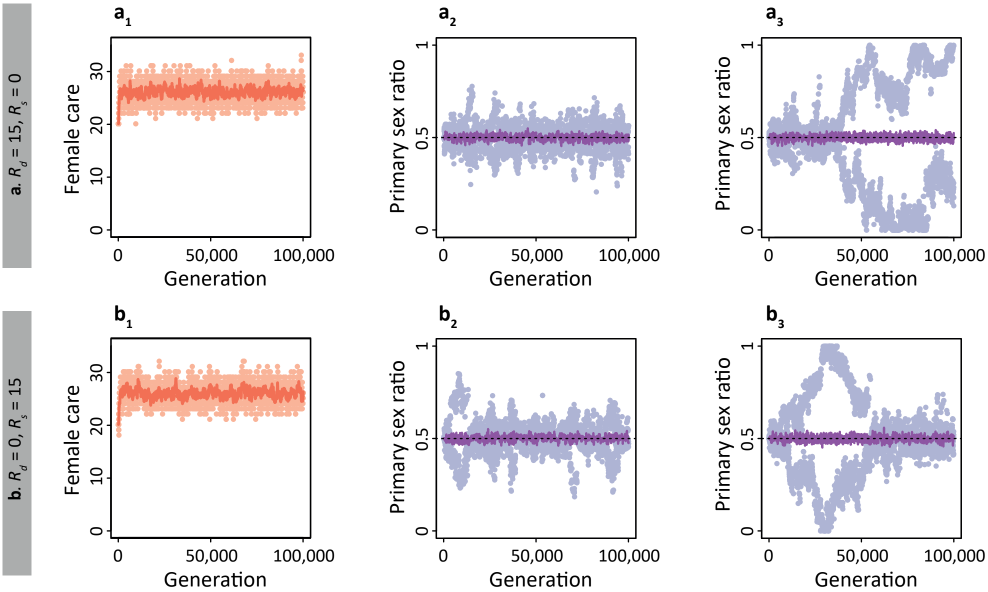

Figure S1. Joint evolution of maternal care level and paternal PSR control. Representative simulations for the same case as in Fig. 2, but with males in control of the sex ratio of their offspring. Similar to Fig. 2, **(a_1, b_1)** females provide a higher level of care than offspring demand ($D = 20$), regardless of whether **(a)** daughters are more costly to raise, or **(b)** sons are more expensive to produce. However, **(a_2, a_3, b_2, b_3)** the average PSR is always unbiased as males bear no costs of production. Moreover, the evolutionarily stable PSR can be reached by **(a_2, b_2)** monomorphic populations or **(a_3, b_3)** polymorphic populations. See the caption of Fig. 2 for graphical conventions.

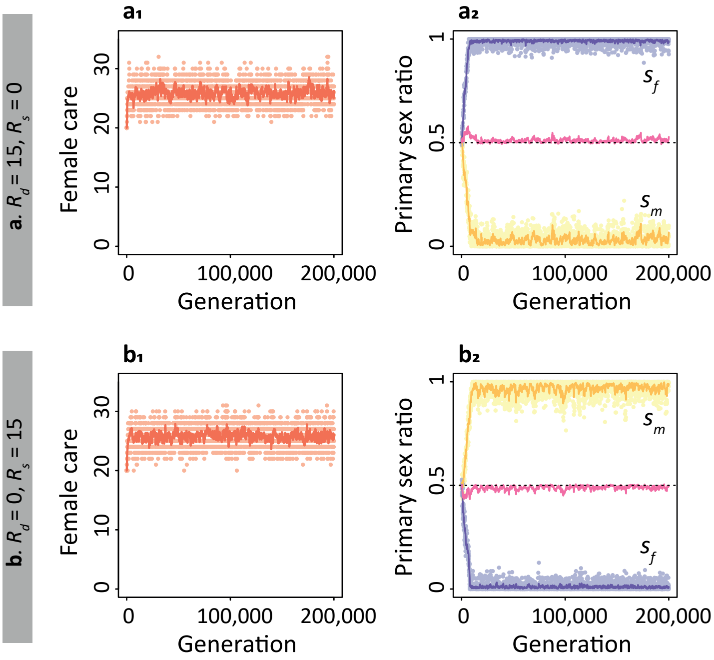

Figure S2. Joint evolution of maternal care level and biparental PSR control. Representative simulations for the same case as in Fig. 2, but with both parents in control of the PSR (= (s_f+ s_m)/2). Similar to Figs. 2 and S1, **(a_1, b_1)** females provide more care than their offspring demand (D = 20), irrespective of which sex is more expensive to produce. **(a)** When daughters are more costly to raise, **(a_2)** mothers are more likely to produce sons ($s_f \approx 1$, purple solid line), while fathers do the opposite ($s_m \approx 0$, yellow solid line) in order to achieve an unbiased PSR on average (pink solid line). **(b)** When sons are more costly to raise, **(b_2)** mothers desire to have primarily daughters ($s_f \approx 0$), while fathers counter-adapt to this strategy by favouring to create sons ($s_m \approx 1$), resulting in an unbiased PSR at the population level. Here, solid red lines (as in a_1 and b_1) and solid pink lines (as in a_2 and b_2) represent the average female care level and the average PSR that evolved in a simulation; solid yellow lines and solid purple lines (as in a_2 and b_2) represent the average value of s_m-alleles in the male population and s_f-alleles in the female population, respectively; red dots (as in a_1 and b_1) depict the T_f-alleles of individual females, while yellow and purple dots (as in a_2 and b_2) depict the PSR alleles of individual males and individual females, respectively.

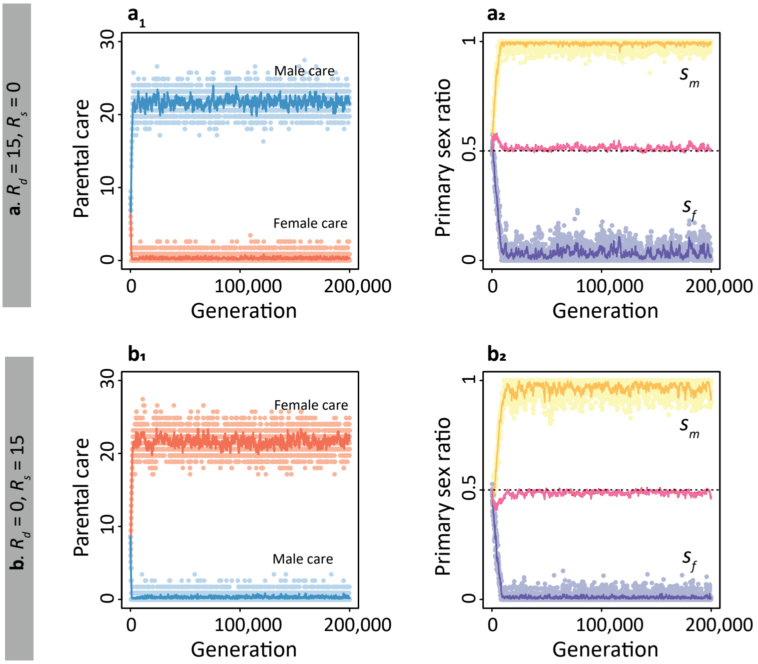

Figure S3. Joint evolution of parental care levels in both sexes and biparental PSR control. Representative simulations for the same case as in Fig. 4, but with both parents in control of the PSR (= $(s_f + s_m)/2$). Similar to Fig. 4, **(a)** when daughters are more costly to produce, **(a_1)** male-only care evolves; **(b)** when sons are more expensive to produce, **(b_1)** female-only care evolves. In both cases, **(a_2, b_2)** the average PSR is unbiased. See the caption of Fig. S2 for graphical conventions.

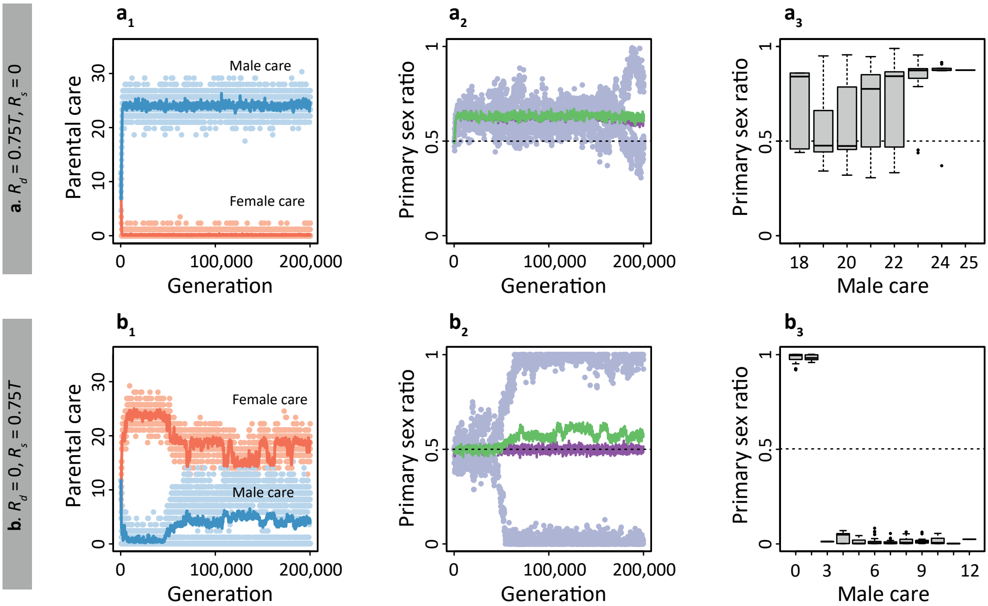

Figure S4. Co-adaption of parental care levels in both sexes and PSR under paternal control in a different cost scenario. The graphs show the same situation as in Fig. 6, but now males control the sex ratio of their offspring. **(a)** When daughters are more costly to raise, **(a$_1$)** males are selected to provide all of the care, **(a$_2$)** sons are overproduced in the population, **(a$_3$)** and there is no correlation between male care levels and the PSR. **(b)** When sons are more expensive to produce, **(b$_1$)** females are selected to do most of the care, and males split into two types: one type provides a low-level care and the other type provides a high-level care; **(a$_2$)** the PSR is unbiased when the population is monomorphic, but it is biased towards males once polymorphisms emerge; **(a$_3$)** there is a strong correlation between male care and the PSR when the male population is polymorphic: males with a higher level of care focus on producing daughters, whereas males with a lower level of care specialise in producing sons. In this scenario, females and males stay in the recovery state for $0.75 \cdot T_f$ and $0.75 \cdot T_m$ days, respectively. See the caption of Fig. 2 for graphical conventions.

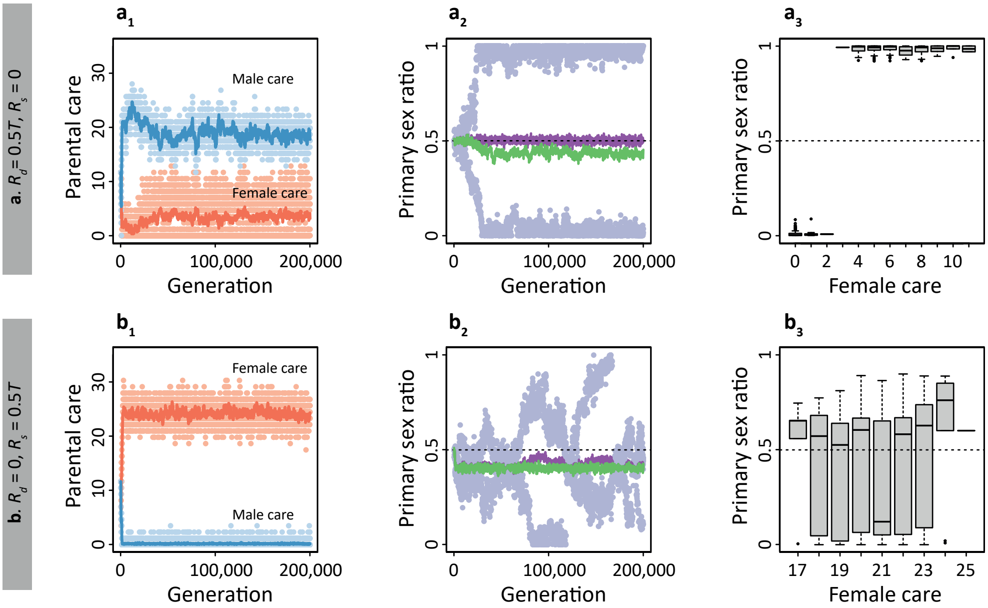

Figure S5. Co-adaption of PSR and parental care levels under a weakening influence of care levels on differential offspring costs. The graphs show the same situation as in Fig. 6, expect that the time required to recover from caring increases more slowly as care efforts increase. Here, female parents and male parents stay in the recovery state for 0.5 · T_f and 0.5 · T_m days after caring for the more expensive sex, respectively. Once again, the cheaper sex is selected to provide most (or all) of the care. In the case of male-biased care, the more expensive sex is overproduced when polymorphisms arise in the population. See the caption of Fig. 2 for graphical conventions.

Chapter 6

Afterthoughts

Xiaoyan Long

In this thesis I have addressed the question of how evolution shapes the behaviour of males and females in the context of mating and parenting. Towards achieving this goal, three chapters of my thesis investigated theoretical models by means of individual-based simulations. The simulation models are inspired by earlier mathematical models that derived evolutionary predictions about parental and mating strategies. In particular, Hanna Kokko and Mike Jennions (2008), as well as Lutz Fromhage and Mike Jennions (2016), have provided a substantial body of theory in this field. Therefore, one might ask why it is necessary to run simulations when mathematical models are already available. I hope that the outcome of my simulation studies has convinced the reader that a simulation approach has indeed something extra to offer.

In this chapter, I will close my thesis with some reflections on the use of individual-based simulations, with emphasis on three aspects: the emergence of polymorphisms, the coexistence of alternative stable states, and the implications of condition dependent behaviour. In my opinion, all three aspects are not sufficiently appreciated in the literature on the evolution of mating and parenting strategies. First, the neglect of polymorphism is apparent from the fact that dominant methods, such as the selection gradient method, implicitly assume that the population is in a monomorphic state (or that traits are distributed unimodally around the population average) most of the time. Second, analytical models sometimes predict alternative evolutionary outcomes, but they typically do not include stochasticity, which is crucial for understanding behaviour away from equilibrium, such as rapid switching between equilibria. Third, condition dependent behaviour, though highly relevant in real organisms, is not often considered in analytical models. This is understandable, as these models are already difficult to analyse in the absence of condition dependence. In contrast, conditional dependent strategies can fairly easily be incorporated in individual-based simulations. The sections below will discuss the three aspects in more depth and detail.

POLYMORPHISMS

Emergence of polymorphisms

The existence and evolutionary stability of polymorphisms has long been recognized in behavioural ecology. For example, classical models of evolutionary game theory, such as the Hawk-Dove game, predict the coexistence of different strategies (Maynard Smith & Price, 1973, Maynard Smith, 1982; Bergstrom & Godfrey-Smith, 1998; McNamara & Weissing, 2010). If the pure strategies under consideration (such as Hawk and Dove) are clearly differentiated, their coexistence can be fairly easily explained by negative frequency-dependent selection. In contrast, polymorphisms are more difficult to explain when the behaviour patterns are not discrete from the start, but have to become differentiated in small steps. This is the circumstance that is pertinent to this thesis because I considered quantitative traits (such as male and female parental effort) that vary due to mutations of small effect sizes.

For scenarios in which evolution proceeds in small steps, adaptive dynamics theory has made an important contribution by classifying situations in which polymorphism emerges from scratch. These situations correspond to so-called 'evolutionary branching points', which can be characterised analytically (Geritz et al., 1998), at least in case of one-dimensional phenotypic traits. In the course of evolution, such a trait first converges to an 'evolutionarily singular strategy', at which the selection gradient vanishes. If this singular strategy is not 'evolutionarily stable', the population undergoes diversifying selection. This results in evolutionary branching, with populations splitting into coexisting subpopulations that employ different strategies (Geritz et al., 1998; Dercole & Rinaldi, 2008). Accordingly, adaptive dynamics is a very useful tool for determining when polymorphisms are expected in the context of quantitative traits varying in one dimension. In Chapter 3, I applied a graphical variant of this approach (the inspection of Pairwise Invasibility Plots; see Fig. S3) to the case of egalitarian care. I showed that, similar to the simulations, egalitarian care rapidly converges to a singular strategy, where the population is exposed to disruptive selection. If the individuals would not have been able to make their parental behaviour dependent on their sex, branching would occur, where part of the population (irrespective of sex) would employ a low care level, while the other part would employ a high care level. This did not happen in my simulations, where the individuals could make their parental behaviour dependent on their sex. In this case, sexual conflict results in one of two alternative outcomes: either strongly female-biased care or strongly male-biased care.

This points to an important limitation of adaptive dynamics theory. This theory is well-developed for one-dimensional trait spaces, while multivariate analyses can only be conducted under very specific conditions (Leimar, 2009a). In particular, there is almost no theory available for the occurrence of evolutionary branching in multidimensional traits spaces. In my thesis, I was often interested in the joint evolution of several traits. For example, female parental effort coevolves with male parental effort (Chapter 3,4,5), female preferences and male ornaments evolve alongside with parental strategies (Chapter 3), and sex allocation strategies evolve in concert with parental investment per son and daughter (Chapter 5). In all these cases, polymorphisms systematically emerged, with branching occurring in both male and female parental care strategies (see Figs. 3, 4 and S2 in Chapter 3), and in both parental investment and primary sex ratio strategies (see Figs. 3, 5, 6, S4 and S5 in Chapter 5). A similar emergence of polymorphism in multivariate trait spaces has also been observed in other individual-based simulation studies (Botero et al., 2015; Gupte et al., 2021; Netz et al., 2021). As shown by Rueffler et al. (2016), such evolutionary branching events cannot easily be characterised mathematically anymore, and we are left with the conclusion that the emergence of polymorphism is not easy to predict when the trait space has several degrees of freedom.

Still, some progress can be made, by combining simulation results with mathematical analysis in a step-wise manner. To illustrate this, I used simulations to derive the distributions of male and female care levels at a certain time (see Fig. 3 in Chapter 3). Based on these distributions, I could calculate the fitness landscape and, hence, the selection gradient. This gradient then provided insights into whether selection is directional (and, if so, in which direction it proceeds), stabilising, or disruptive, explaining the time course of evolution until the next time step. In this way, a hybrid argumentation combining simulations and mathematical analysis is capable of explaining what actually happens, shedding some light on understanding the course of evolution when polymorphisms emerge in multiple traits simultaneously.

Implications of polymorphisms

Polymorphisms in several traits are frequently observed in many biological systems (e.g., Ross & Keller, 1995; Alonso-Blanco et al., 2004; Wellenreuther et al., 2014). In the behavioural sciences, they receive considerable attention under names as 'behavioural syndromes' or 'animal personalities' (Wilson, 1998; Gosling, 2001; Sih et al., 2004; Réale et al., 2007; Bell et al., 2009; Stamps & Groothuis, 2010). As mentioned above, the toolbox of mathematical biology often lacks the instruments to detect and predict such multidimensional polymorphisms. Accordingly, the occurrence of such polymorphisms is often overlooked. This neglect is problematic as it can lead to misleading conclusions. As shown in Chapter 3, the course of evolution in monomorphic (uni-modally distributed) populations is very different from polymorphic (bi-modally distributed) populations: while the selection gradient approach, which implicitly assumes that male and female populations are monomorphic, predicts a line of equilibria (or, in case of parental synergy, a single egalitarian equilibrium), the simulation approach predicts two alternative stable equilibria (either male- or female-biased care). This highlights that some of the standard tools of evolutionary theory, such as making predictions on the basis of selection gradients, should be applied with care when polymorphisms are to be expected.

My simulations provide the intriguing insight that even a very short-term polymorphism can have a dramatic effect on the course and outcome of evolution. This is exemplified at various places in my thesis (e.g., in Fig. 3 of Chapter 3 or in Fig. 1 below): first, the population is driven to a point where disruptive selection occurs in one or both sexes, leading to the emergence of polymorphism in one or both sexes. After a brief period of time, this polymorphism collapses, driving the population to one of two alternative equilibria. At equilibrium, all traces of polymorphism have disappeared. Therefore, this type of polymorphism can be easily neglected since it is transient and thus rarely observed, yet it can still be important for explaining patterns that actually occur in nature.

To close this part, I would like to point out that polymorphisms have many other implications for the course and outcome of evolution (reviewed in Sih, 2012 and Wolf & Weissing, 2012), for instance, they may enhance evolvability (Riederer et al., 2022) or facilitate speciation (Ingley & Johnson, 2014). Taken together, polymorphisms (even those that last for a relatively short period of time) have an important impact on ecology and evolution.

ALTERNATIVE STABLE STATES

Emergence of alternative stable states

Alternative stable care strategies occur repeatably in my simulations, although they are not observed in the analytical models of Fromhage and Jennions (2016). The discrepancy between simulations and analytical predictions may not be too surprising in the baseline model of Chapter 3 where mating is at random, the sexes do not differ in their life-history characteristics and parental synergism is not included. In this case the analytical model predicts a neutral line of equilibria along which a population can move by random genetic drift (Fromhage & Jennions, 2016). It is well known that systems with a connected set of equilibria are structurally unstable in the sense that a slight change in the model assumptions can dramatically change the dynamic behaviour of the model. For example, the famous line of equilibria in the classical model of Fisherian sexual selection (Fisher, 1930; Lande, 1981) vanishes when the slightest costs of female choosiness are incorporated in the model (Pomiankowski, 1987), or when the mapping between female preferences and male traits is only slightly perturbed (Van Doorn & Weissing, 2004). Therefore, it is perhaps unsurprising that the line of equilibria predicted by Fromhage of Jennions (2016) collapses to two stable equilibria in my simulations, as it is unavoidable that individual-based simulation models differ at least slightly from corresponding analytical models, for example, because stochasticity is automatically incorporated in these models.

However, structural instability alone does not fully account for the alternative stable states discovered in my simulations. When a small level of parental synergy is introduced in the model, the mathematical analysis of Fromhage and Jennions (2016) predicts an asymptotically stable equilibrium in which parents provide egalitarian biparental care. Now their model is structurally stable, but my simulation model (which follows the modelling framework of Fromhage and Jennions (2016) as much as possible) yields two alternative equilibria: strongly male-biased care and strongly female-biased care. The two equilibria correspond to two outcomes of sexual conflict over parental care: both parents have a joint interest in producing surviving offspring, but each parent prefers that their partner does most of the caring (Chapter 1). As long as the level of parental synergy is relatively small, this conflict is still intense, leading to an outcome where one sex is the ‘winner’ and the other sex is the ‘loser’ of the conflict.

I observed alternative stable states not only when the sexes are initially identical, but also when they differ in a variety of ways. For example, when females become choosy and males develop ornaments in response to female preferences, the two alternative care strategies still exist, together with two alternative mating strategies (see Fig. 6 in Chapter 3). Moreover, when the sexes differ in life-history characteristics, such as maturation rates and mating mortality rates, two alternative care patterns repeatably emerge (see Figs. 4 and S1 in Chapter 4). Therefore, alternative stable states can emerge in a wider range of configurations than previously thought.

Implications of alternative stable states

There is growing recognition that alternative stable states play a vital role in ecological systems. Many studies have found that if an ecosystem has alternative stable states, it can rapidly switch from one state to another when environmental conditions change, which is known as state shift in ecology (Holling, 1973; Scheffer et al., 2001; Beisner et al., 2003; Folke et al., 2004; Schröder et al., 2005). For example, freshwater lakes can rapidly shift from a clear-water state dominated by submerged vegetation to a turbid-water state dominated by phytoplankton when the nutrient influx is increasing (Scheffer et al., 1993; Scheffer, 1998); coral reefs can rapidly shift from a coral-dominated state to an algal-dominated state if conditions become more stressful (Done, 1992; Knowlton, 1992; Hughes, 1994); terrestrial grazing systems can rapidly shift from a densely vegetated state to a desert-like state when the grazing pressure is increased (Rietkerk & Van de Koppel, 1997; Van de Koppel et al., 1997). Intriguingly, these ecosystems do not transition from one state to another gradually, but rather abruptly when environmental parameters reach and cross a certain threshold (i.e., a bifurcation point). Once a state shift happens, it can be difficult to go back to the original state (which is usually a more desirable state), unless considerable changes are made to the environment conditions (Wissel, 1984; Yodzis, 1989). In some cases, such a state shift may even be irreversible due to hysteresis effects (Ludwig et al., 1997; May, 1997; Mumby et al., 2007; Isbell et al., 2013; Albrich et al., 2020), a phenomenon of great importance to ecologists and managers.

Alternative stable states have received much less attention in the evolutionary biology. Yet, it is not implausible that evolution may have quite different outcomes (Lehtonen & Kokko, 2012). In the case of parental care, many alternative care patterns are observed in taxa of closely related species (e.g., Reynolds & Székely, 1997; Chapter 2) or even in different populations of the same species (e.g., Van Dijk et al., 2012; Zheng et al., 2018). Comparative studies have concluded that parental care patterns are often evolutionarily labile (Reynolds et al., 2002; Gilbert & Manica, 2015; Furness & Capellini, 2019), implying that switches from one care pattern to a different one do regularly occur. Relatively few studies address such switching behaviour. For example, it has been argued that evolutionary transitions between parental care patterns can be triggered by changes in fertilization mode (Mank et al., 2005; Benun Sutton & Wilson, 2019), or changes in life-history characteristics (Klug et al., 2013). In my studies, I regularly encountered such transitions as well (e.g., Figs. 4, 5, S2, S6-S8 in Chapter 3; Figs. 4 and S1 in Chapter 4; Figs. 6, S4 and S5 in Chapter 5). However, these transitions were not driven by external changes, as environmental conditions were kept constant in all my simulations. This is less surprising than it may seem. In a stochastic dynamical system with alternative stable states, spontaneous transitions do regularly occur (see Chapter 3 for examples) in a predictable manner. The frequency of switches increases with the degree of stochasticity (in my models: with a decrease in population size; see Fig. S6 in Chapter 3) and decreases with the strength of attraction (in my models: factors reducing individual life expectancy; see Fig. S7 in Chapter 3). Interestingly, virtually all transitions in my simulations were preceded by the emergence of (transient) polymorphisms (see above). This is, for example, illustrated by Fig. 4 in Chapter 3. Moreover, while the system frequently exhibits one of the two states, one of the states shows much less stability than the other in some circumstances (see Figs. 4 and S1 in Chapter 4). From these results I conclude that the evolutionary lability of parental and mating patterns that is indicated by frequent transitions between patterns does not necessarily require an explanation in terms of changing environmental conditions or changing life history features of the organisms.

CONDITION DEPENDENCE

If individuals differ from each other in fitness relevant ways, then evolutionary theory predicts that organisms should take their ‘state’ or ‘condition’ into consideration when making decisions. This is a fundamental insight of evolutionary game theory, a field focusing on the evolution of behavioural strategies, where, by definition, a ‘strategy’ corresponds to a recipe on how to behave under all relevant conditions (Selten, 1983, McNamara & Weissing, 2010). Evolutionary game theory provides many examples that clearly demonstrate that condition-dependence can make all of a difference for the course and outcome of behavioural evolution (Selten, 1980). This is already evident from the first publication on this topic, where John Maynard Smith and George Price (1973) demonstrate that the evolution of condition-independent behaviour in the Hawk-Dove game leads to a mixed-strategy equilibrium, where escalated fights occur regularly, while the evolution of condition-dependent behaviour leads to a pure-strategy equilibrium where escalated fighting does not occur (see also Parker, 1974; Hammerstein, 1981; Maynard Smith, 1982; Van Doorn et al., 2003). Similarly, if behaviour is unconditional in the iterated Prisoner’s Dilemma game, cooperation will never get a foothold, while many cooperative equilibria exist in case of condition-dependent behaviour (Axelrod & Hamilton, 1981; Doebeli & Hauert, 2005; Van den Berg & Weissing, 2015).

Most models on the evolution of parental care address one dimension of condition dependence, namely that males may behave differently from females. Other aspects of condition dependence (see Harris & Uller, 2009; Kindsvater & Alonzo, 2014; Haaland et al., 2017; Ratikainen et al., 2018) are only rarely investigated. This could be because condition dependence makes mathematical analysis far more complex. In contrast, condition dependence can be easily incorporated into individual-based simulation models. Time constraints prevented me from investigating the implications of condition-dependent parental strategies in my thesis. But to indicate the importance of condition dependence, I here show some example simulations (Fig. 1) that are based on a simple toy model. To this end, I expanded the model in Chapter 3 by introducing two types of males: high-quality males associated with low adult mortality and low-quality males associated with high adult mortality. The quality condition was assigned to male offspring at birth, on the basis of external events (e.g., the weather during the first week in the nest), with a fixed proportion of male offspring labelled as high quality and the remainder as low quality. In this pilot study, males and female mate at random, and whenever a mating pair is formed, a single offspring is produced. The male parents make their care decisions based on their own quality. For simplicity, I assumed that the female parents have to make their decisions independently, without having information on the quality of their mate. Hence there are three evolving parameters: care effort when being a female, care effort when being a high-quality male, and care effort when being a low-quality male. In Fig. 1, I show some representative simulations, all starting with egalitarian biparental care. Some simulations converge to a single care strategy, which corresponds to strongly male-biased care or strongly female-biased care (Fig. 1(a_1,a_2,b_1)). In both cases, high- and low-quality males provide a similar level of care. Please note that transient polymorphisms arise in both sexes and play an important role in the evolutionary dynamics in these populations. Besides, some simulations converge to mixed care strategies in which female-only care, biparental care, male-only care, and biparental desertion all coexist in the same population (Fig. 1(a_3,b_2,b_3)). In these cases, high-quality males and low-quality males adopt different care strategies: in some populations high-quality males provide most (or even all) of the caring, while low-quality males provide no care (Fig. 1(a_3,b_3)), while in other populations low-quality males care for the offspring and high-quality males do not care at all (Fig. 1(b_2)). With different care strategies in males, the female population diverges, resulting in a permanent polymorphic state: a considerable fraction of individuals offers a high level of care, while others do not provide any care. Since females cannot make their care decisions according to their partners' quality and mating happens at random, all four care patterns coexist in the same population, as indeed has been observed in some species, such as Chinese penduline tits (*Remiz consobrinus*) (Zheng et al., 2018). Despite the fact that the model only considers a very simple condition dependence, the evolutionary outcomes are quite different from those found in Chapter 3. Of course, a much more thorough study is necessary to investigate the implications of condition dependence for the evolution of parental care patterns in more depth and detail.

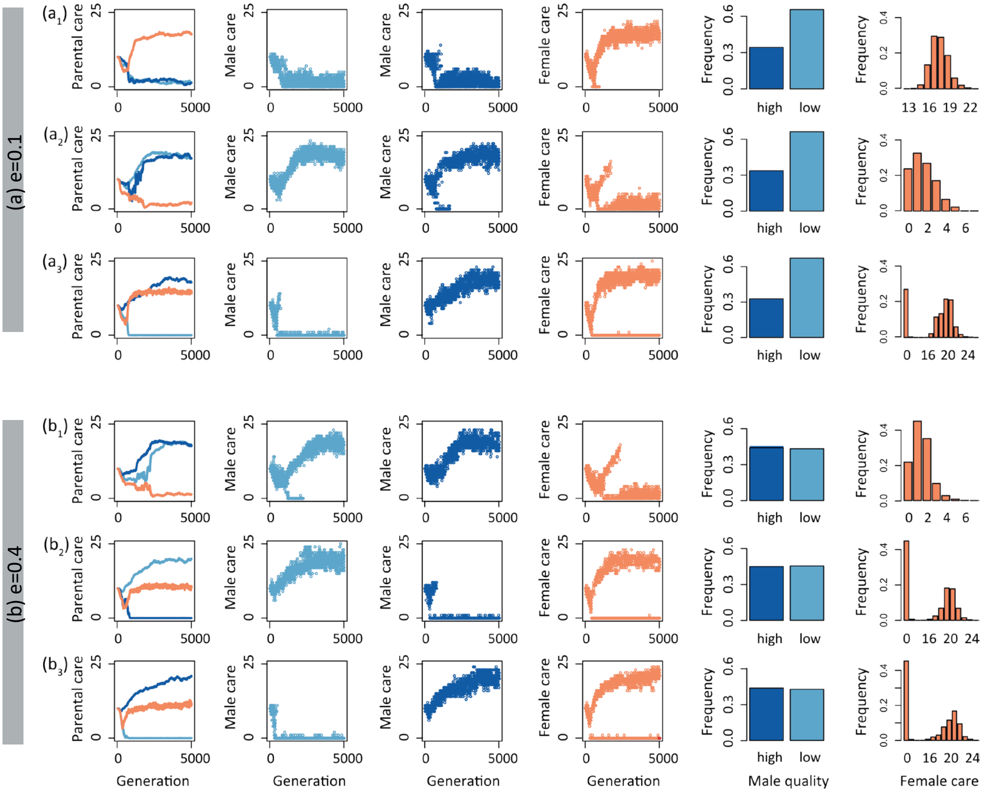

Figure 1. Evolution of parental roles when males differ in quality. The graphs shows six exemplary simulations for the evolution of sex-specific parental care when males differ in quality and can make their caring decisions dependent on their quality. Quality is a binary trait ('high-quality' vs. 'low-quality') that affects a male's mortality rate: $u_{high} = 0.001\ (1 - e)$ and $u_{low} = 0.001\ (1 + e)$, where e represents the effect size of quality difference. Quality is not heritable and assigned randomly to a male at birth; the probability of being assigned a high quality was 0.3 in all cases. Two scenarios are considered here, and for each scenario three replicate simulations are shown that illustrate qualitatively different evolutionary outcomes. In all simulations care levels unequal to zero showed a considerable degree of unimodal variation. We talk of 'polymorphism' when the distribution of care levels in a category is bimodal. **(a)** A relatively small effect of quality ($e = 0.1$). **(a_1)** Evolution of strongly female-biased care, with both types of male exhibiting a low level of care. **(a_2)** Evolution of strongly male-biased care, with similar care levels in both types of male. There is an initial period of polymorphism in females and high-quality males. **(a_3)** Evolution of a high level of care in high-quality males, no care in low-quality males, and a persistent polymorphism in female care. About 25% of the females do not care at all, while the remaining 75% show a high level of care. Notice that at the population level four types of parental care patterns coexist: biparental care, female-

only care, male-only care and biparental desertion. **(b)** A large effect of quality (*e* = 0.4). **(b_1)** Evolution of strongly male-biased care, with similar care levels in both types of male (similar to **(a_2)**). **(b_2 ,b_3)** Evolution of female polymorphism (50% no-care, 50% high level of care), associated with a high level of care in one type of male and a low level of care in the other type of male. Colours: red: females, dark blue: high-quality males, light blue: low-quality males. From left to right, the graphs show the time trajectories of (1) the average care levels of the three categories; the individual care levels in (2) low-quality males, (3) high-quality males, and (4) females; (5) the distribution of high- and low-quality males in the adult population; and (6) the distribution of female-care alleles in the final generation. Female mortality rates were fixed at 0.001.

In the above examples, condition dependence was supposed to be based on phenotypic characteristics (such as 'quality' or past experience) or on external characteristics, such as environmental cues. In Chapter 5 of this thesis, I found a very different form of condition dependence: individuals make their sex allocation decisions conditional on their care strategies which are entirely genetically determined. This is in line with the notion of Olof Leimar and his colleagues (Leimar, 2009b; Dall et al., 2015) that both environmental parameters and individuals' genotypes can provide reliable information for decision making. My study also shows that making decisions based on genetical cues and environmental cues may work in a similar manner. In my model where the costs of raising sons and daughters are fixed, parents with higher levels of care predominantly produce the more expensive sex, whereas parents with lower levels of care predominantly produce the cheaper sex (see Fig. 3 in Chapter 5). Under this conditional sex-ratio adjustment, the 'cheaper' sex is overproduced in the population. This is in line with the findings of Frank and Swingland (1988), who assumed that parents adjust the sex of the offspring based on environmental conditions (e.g., temperature, food availability): parents in the poor condition tend to overproduce the cheaper sex and parents in the good condition tend to overproduce the more costly sex. In this case, they also discovered that, at evolutionary equilibrium, the cheaper sex is overrepresented in the population. In my view, this whole field of condition-dependent mating and parental behaviour is underresearched, and I expect that future studies in this area will arrive at novel and surprising conclusions.

Until now, I have highlighted the power of individual-based evolutionary simulations. Should simulation approaches then replace analytical approaches? My answer is an emphatic NO! The biggest disadvantage of simulations is that numerous parameter combinations have to be investigated, which is computationally demanding and time consuming. As demonstrated in this thesis, in order to get somewhat representative findings, most of the chapters are based on tens of thousands of simulations. Therefore, seeing the forest through the trees can be challenging, at least in parameter-rich models. From this, it is extremely important to have analytical theory that can serve as a guideline. In my study, I profited a lot from the mathematical theory of Kokko and Jennions (2008) and Fromhage and Jennions (2016); their results served as a guideline for my simulations. Therefore, I advocate for a pluralistic approach in which mathematical theory sketches the broad outlines, while simulations are used to check the consistency of the mathematical approach and to expand the analytical findings to more realistic scenarios. In this way, the two approaches can go hand in hand, and eventually enrich each other.

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Summary
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Samenvatting

Summary

THE BAFFLING DIVERSITY OF PARENTAL SEX ROLES

In many animals, parents provide care to their offspring, such as building nests, or protecting and feeding the young. Species differ considerably in how parental care is distributed between the male and the female parent. Birds, for example, exhibit a remarkable variety of parental care patterns. In some species, only the female cares for their offspring. For instance, hummingbird mothers are the single caregivers, who build the nest, incubate the eggs, and feed and protect the chicks until they become independent. In other species, only the male is in charge of parental care. For instance, jacana fathers are typically the sole caregivers; they raise their offspring alone, without assistance from the mother. In still other species, both parents share the responsibilities for raising the offspring. Albatross parents, for example, pair for life and take care of the offspring together. Apart from that, parental care patterns can vary even within species. In Chinese penduline tits (*Remiz consobrinus*), for example, female-only care, biparental care, and male-only care all coexist in the same population.

The same type of diversity in 'parental sex roles' can be found throughout the animal kingdom. However, some broad patterns can be observed. For example, in mammals the female typically performs the majority of the care duties, in fishes males are most strongly engaged in parental care, and in birds biparental care is the most frequent care pattern. In this thesis, I attempt to explain the diversity of parental sex roles from an evolutionary perspective. I am particularly interested in understanding which care pattern is to be expected under which circumstances. To address this question, I employed two distinct research methods: evolutionary modelling, and the detailed comparison of parental care patterns in more than thousand species of birds.

UNDERSTANDING PARENTAL CARE PATTERNS IN BIRDS

Differences in environmental conditions and life-history traits have been proposed to explain the diversity of parental care patterns in birds. For example, avian species build two types of nests: open nests that are easily accessible, and closed nests that are only accessible through a small entrance. The eggs and chicks of open nests are much more exposed to predation and other risks than those of closed nests. One might therefore expect that, in order to reduce these risks, open nests require a higher level of cooperation between the two parents. To see whether this and other expectations agree with the patterns found in nature, I first collected a large set of data on 1101 bird species and subsequently investigated the statistical association between the parental care patterns in these birds and their ecological and life-history conditions. For this, a simple linear correlation analysis may be misleading; instead, sophisticated phylogenetic methods have to be employed. The reason for this is that closely related species are very similar to each other and should therefore not be considered as independent data points. For instance, in all albatross species the parents construct nests by making simple scrapes or mud mounds (completely exposed to the environment), and they share care duties almost equally. By applying simple linear correlation, one would find a strong association between open nests and high levels of parental cooperation. This conclusion, however, would be premature, as albatrosses share a great deal of evolutionary history and thus exhibit a high degree of similarity in terms of nest construction and parental care strategies.

Using a state-of-the-art comparative approach, which takes into account the shared evolutionary history among taxa, I demonstrated in **Chapter 2** that nest types do not accurately predict care patterns in birds. Instead, I showed that altricial and precocial species display distinct parental care patterns: altricial species, in which chicks are unable to obtain food and regulate the body temperature on their own, are associated with high levels of biparental cooperation, whereas precocial species, in which chicks are capable of feeding themselves soon after hatching, are associated with low levels of parental cooperation. Moreover, I discovered that species who live in groups are more likely to display biparental care than those who live solitary lifestyles. This finding suggests that the interaction within and between families may be an important determinant of parental strategies in birds, but further research is needed to decipher the mechanism.

MODELLING THE EVOLUTION OF PARENTAL CARE

Phylogenetic comparative analysis can provide us with some information about the patterns that exist in nature, but it does not necessarily provide explanations for how the patterns originate. To get a better sense of *how* and *why* various parental care patterns arise, constructing and analysing evolutionary models may be the most effective way. There are, of course, well-established models for the evolution of parental care. In these models, evolution is represented by differential equations, which are derived by the so-called 'selection gradient' method. This method assumes that evolution proceeds in the direction of steepest ascent of Darwinian fitness. As the selection gradient method neglects many details of the evolutionary process, it is not necessarily reliable. Therefore, I chose an alternative approach to modelling the evolution of parental care, namely individual-based evolutionary simulations, in which every single individual is represented by a digital agent that is tracked from birth to death. These individuals behave according to heritable parental strategies, which they pass on to their offspring. Successful parental strategies are represented in many offspring and therefore spread from one generation to the next. This way, I could explore how the parental care patterns evolve in the course of time.

Despite the fact that the assumptions underlying my individual-based models are very similar to those of the selection-gradient models, **Chapter 3** shows that the predictions of the two types of models are remarkably different. For the special case that male and female parents have the same properties, the selection-gradient method predicts a broad spectrum of biparental care patterns, ranging from strongly female-biased care to egalitarian biparental care to strongly male-biased care. In contrast, my individual-based model predicts that evolution will either result in an outcome where males do all the caring or in the opposite outcome of female-only care. Using a variety of methods, I could also show why the selection-gradient method often fails when applied to the evolution of parental care.

My individual-based simulations also lead to striking new insights. For example, the evolved parental care patterns turn out to be 'evolutionarily labile': an evolved care pattern that appears to be quite stable can switch to a completely new pattern in a brief period of time. For example, a population in which females provide most of the care can switch rapidly to a population in which males do most of the caring. This finding explains the puzzling fact that, frequently and unexpectedly, new parental care patterns pop up in phylogenetic trees. My simulations also shed new light on the interplay of sexual selection and parental care. If female preferences and male ornaments could evolve jointly with parental care strategies, again two alternative outcomes were possible, corresponding to either strongly male-biased care or strongly female-biased care. In the case of male-biased care, neither female preferences nor male ornaments evolved, while preferences and ornaments did evolve in the case of female-biased care. Moreover, the simulations suggest that, in contrast to conventional wisdom, the parental care pattern evolves first, setting the scene for the evolution female preferences and male ornaments.

PARENTAL SEX ROLES AND SEX RATIOS

The proportion of males and females in each cohort is not always the same. In most species, the ratio of males to females at birth is roughly 1:1, but this can shift considerably later in life. For example, if one of the sexes is engaged in a high-risk lifestyle, resulting in a high mortality rate for that sex, members of the sex with a low-risk lifestyle will become increasingly abundant in the population. In the literature, there are some theories that link parental sex roles to sex ratios. The basic idea is that the most abundant sex should take on more care duties than the less abundant sex.

Using the model of Chapter 3, I systematically investigated the interplay between sex ratios and parental care patterns in **Chapter 4**. To create sex ratio biases, I considered sex-differences in the life cycle of individuals. For example, the sexes were supposed to differ in their maturation rate or in their mortality rate at a certain breeding stage (e.g., the stage where mating happens and the stage where parents provide parental care). By and large, my simulations confirm that the more common sex is associated with a higher level of parental care, but for different reasons than the literature suggests. Moreover, in a subset of simulations strongly sex-biased care evolved in the absence of sex ratio bias. Sometimes, evolution even led to the opposite pattern than generally predicted: in these cases the overrepresented sex provided less parental care than the underrepresented sex. Thus, it is difficult to predict parental sex roles on the basis of the sex ratio. Instead, I discovered that the processes by which the sex ratio becomes biased play a crucial role in the evolution of parental care patterns. Importantly, my findings indicate that parental care patterns are the cause, rather than the effect, of biased sex ratios.

The current discussion about the role of sex ratios in the evolution of parental care focuses mainly on the number of adult individuals. In **Chapter 5** I shifted the focus to the sex ratio at conception. This sex ratio is supposed to be unbiased when there is no difference in producing sons and daughters. However, when one of the sexes is cheaper to produce than the other sex in that it requires less attention and care from parents, the cheaper sex is expected to be overproduced in the population. By allowing the sex ratio at conception to evolve in tandem with male care and female care, I showed that the offspring of the cheaper sex are, in a sense, predestined to provide parental care in later life.

REFLECTIONS ON EVOLUTIONARY MODELLING

I have attempted to understand how evolution shapes parental behaviours of males and females in this thesis. To achieve this goal, three chapters of my thesis (Chapters 3-5) constructed theoretical models by employing individual-based simulations. These chapters show that simulation outcomes deviate substantially from the predictions made by traditional models. To further understand the causes of these discrepancies, in **Chapter 6** I reflect on two factors that are essential for understanding the parental care patterns in my simulations. One is the occurrence of polymorphisms (e.g., low-level care and high-level care strategies coexist in both males and females), and the other is the occurrence of condition dependence (e.g., parents make their care decisions based on their own quality). These two components are typically overlooked in standard parental care theories, as they are not easy to incorporate into the toolbox of evolutionary models. I hope that my thesis has shown the added value of individual-based simulations in making evolutionary predictions. This is not to say that classical methods should be discarded from the toolbox. Instead, I believe that the two approaches, when applied in concert, complement one another very well.

Samenvatting

DE VERBIJSTERENDE DIVERSITEIT VAN OUDERLIJKE GESLACHTSROLLEN

Bij veel dieren zorgen ouders voor hun nakomelingen, bijvoorbeeld door het bouwen van nesten of het beschermen en voeden van de jongen. Soorten verschillen aanzienlijk in de manier waarop ouderlijke zorg wordt verdeeld tussen de mannelijke en de vrouwelijke ouder. Vogels vertonen bijvoorbeeld een opmerkelijke verscheidenheid aan ouderlijke zorgpatronen. Bij sommige soorten zorgt alleen het vrouwtje voor de nakomelingen. Kolibriemoeders zijn bijvoorbeeld de enige verzorgers die het nest bouwen, de eieren uitbroeden en de kuikens voeden en beschermen totdat ze onafhankelijk zijn. Bij andere soorten is alleen het mannetje verantwoordelijk voor de ouderlijke zorg. Zo zijn jacana-vaders meestal de enige verzorgers; ze voeden hun kroost op zonder hulp van de moeder. Bij nog andere soorten delen beide ouders de verantwoordelijkheid voor het grootbrengen van het nageslacht. Albatros-ouders vormen bijvoorbeeld een koppel voor het leven en zorgen samen voor het nageslacht. Ouderlijke zorgpatronen kunnen zelfs binnen een soort variëren. Bij Chinese buidelmezen (*Remiz consobrinus*), bestaan ouderlijke zorg door de vrouwtjes, zorg door twee ouders en zorg door alleen de mannetjes allemaal naast elkaar in dezelfde populatie.

Dezelfde soort diversiteit in ‘ouderlijke geslachtsrollen’ is te vinden in het hele dierenrijk. Hier kunnen enkele brede patronen worden onderscheiden. Bij zoogdieren voert het vrouwtje bijvoorbeeld typisch de meeste zorgtaken uit, bij vissen zijn de mannetjes het sterkst betrokken bij de ouderlijke zorg en bij vogels is zorg door beide ouders het meest voorkomende zorgpatroon. In dit proefschrift probeer ik de diversiteit van ouderlijke geslachtsrollen te verklaren vanuit een evolutionair perspectief. Ik ben er vooral in geïnteresseerd om te begrijpen welk zorgpatroon onder welke omstandigheden te verwachten is. Om deze vraag te beantwoorden, heb ik twee verschillende onderzoeksmethoden gebruikt: evolutionaire modelleringen en een gedetailleerde vergelijking van ouderlijke zorgpatronen bij meer dan duizend vogelsoorten.

OUDERLIJKE ZORGPATRONEN BIJ VOGELS BEGRIJPEN

Verschillen in omgevingscondities en levensgeschiedeniskenmerken zouden de diversiteit van ouderlijke zorgpatronen bij vogels kunnen verklaren. Vogelsoorten bouwen bijvoorbeeld twee soorten nesten: open nesten die gemakkelijk toegankelijk zijn en gesloten nesten die alleen toegankelijk zijn via een kleine ingang. De eieren en kuikens van open nesten zijn veel meer blootgesteld aan predatie en andere risico's dan die van gesloten nesten. Je zou dus kunnen verwachten dat, om deze risico's te verkleinen, open nesten een hogere mate van samenwerking tussen beide ouders vereisen. Om na te gaan of deze en andere verwachtingen overeenkomen met de patronen die in de natuur worden gevonden, heb ik eerst een grote hoeveelheid gegevens verzameld van 1101 vogelsoorten en vervolgens het statistische verband onderzocht tussen de ouderzorgpatronen bij deze vogels en hun ecologische en levensloopomstandigheden. Hiervoor een eenvoudige lineaire correlatieanalyse gebruiken kan misleidend zijn; in plaats daarvan moeten geavanceerde fylogenetische methoden worden gebruikt. De reden hiervoor is dat nauw verwante soorten erg op elkaar lijken en daarom niet als onafhankelijke gegevenspunten mogen worden beschouwd. In alle albatrossoorten bouwen de ouders bijvoorbeeld nesten door eenvoudige nestkuilen of modderhopen te maken (die volledig zijn blootgesteld aan de omgeving), en ze delen de zorgtaken bijna gelijk. Door een eenvoudige lineaire correlatie toe te passen, zou men een sterk verband vinden tussen open nesten en een hoge mate van ouderlijke samenwerking. Deze conclusie zou echter voorbarig zijn, aangezien alle albatrossoorten een groot deel van hun evolutionaire geschiedenis delen en daardoor sowieso een hoge mate van overeenkomst vertonen in de manier waarop ze hun nest bouwen en ouderzorg inrichten.

Met behulp van state-of-the-art vergelijkingen, die rekening houden met de gedeelde evolutionaire geschiedenis van taxa, heb ik in **hoofdstuk 2** aangetoond dat nesttypen zorgpatronen bij vogels niet nauwkeurig voorspellen. In plaats daarvan liet ik zien dat nestblijvers en nestvlieders verschillende en typerende ouderlijke zorgpatronen vertonen: nestblijvers, soorten waarvan de kuikens niet in staat zijn om zelfstandig voedsel te verzamelen en de lichaamstemperatuur te reguleren, zijn geassocieerd met een hoge mate van samenwerking tussen beide ouders, terwijl nestvlieders, soorten waarvan de kuikens in staat zijn zichzelf snel na het uitkomen te voeden, geassocieerd zijn met een lage mate van samenwerking tussen beide ouders. Bovendien ontdekte ik dat soorten die in groepen leven, meer kans hebben om zorg door beide ouders te vertonen dan soorten die solitair leven. Deze bevinding suggereert dat de interactie binnen en tussen families een belangrijke bepalende factor kan zijn van ouderlijke strategieën bij vogels, maar verder onderzoek is nodig om dit mechanisme te ontrafelen.

HET MODELLEREN VAN DE EVOLUTIE VAN OUDERLIJKE ZORG

Fylogenetische vergelijkende analyses kunnen ons enige informatie verschaffen over de patronen die in de natuur voorkomen, maar geven niet per se verklaringen voor het ontstaan van deze patronen. Om een beter beeld te krijgen van *hoe* en *waarom* verschillende ouderlijke zorgpatronen ontstaan, is wellicht het construeren en analyseren van evolutionaire modellen de meest effectieve manier. Er zijn natuurlijk gevestigde modellen voor de evolutie van ouderlijke zorg. In deze modellen wordt evolutie weergegeven door differentiaalvergelijkingen, die worden afgeleid met de zogenaamde 'selectiegradiënt'-methode. Deze methode gaat ervan uit dat het verloop van evolutie in de richting van de snelste toename van de Darwinistische 'fitness' is. Omdat de selectiegradiëntmethode veel details van het evolutionaire proces negeert, is deze mogelijk niet betrouwbaar. Daarom koos ik voor een alternatieve manier om de evolutie van ouderlijke zorg te modelleren, namelijk 'individual-based' evolutionaire simulaties, waarin digitale individuen worden gevolgd van geboorte tot de dood. Deze individuen gedragen zich volgens erfelijke ouderstrategieën, die ze doorgeven aan hun nakomelingen. Succesvolle ouderstrategieën zijn vertegenwoordigd in veel nakomelingen en verspreiden zich daarom van de ene generatie op de andere. Zo kon ik onderzoeken hoe ouderzorgpatronen in de loop van de tijd evolueren.

Ondanks dat de aannames die ten grondslag liggen aan mijn 'individual-based' modellen sterk lijken op die van de selectie-gradiënt modellen, laat **hoofdstuk 3** zien dat de voorspellingen van de twee typen modellen opmerkelijk verschillend zijn. In het speciale geval dat mannelijke en vrouwelijke ouders dezelfde eigenschappen hebben, voorspelt de selectie-gradiëntmethode een breed spectrum van zorgpatronen door beide ouders, variërend van zorg door voornamelijk vrouwtjes, tot zorg egalitair verdeeld over beide ouders, tot zorg door voornamelijk mannetjes. Daarentegen voorspelt mijn 'individual based' model dat evolutie uiteindelijk zal leiden tot ofwel zorg uitsluitend door mannetjes, ofwel uitsluitend door vrouwtjes. Met behulp van verschillende methoden kon ik ook aantonen waarom de selectie-gradiëntmethode vaak faalt wanneer deze wordt toegepast op de evolutie van ouderlijke zorg.

Mijn 'individual-based' simulaties leidden ook tot opvallende nieuwe inzichten. Zo blijken de geëvolueerde ouderzorgpatronen 'evolutionair labiel': een geëvolueerd zorgpatroon dat vrij stabiel lijkt te zijn, kan in korte tijd omschakelen naar een geheel nieuw patroon. Een populatie waarin vrouwen de meeste zorg verlenen, kan bijvoorbeeld snel overschakelen naar een populatie waarin mannen de meeste zorg leveren. Deze bevinding verklaart het raadselachtige feit dat, vaak en onverwacht, nieuwe ouderlijke zorgpatronen opduiken in fylogenetische bomen. Mijn simulaties werpen ook nieuw licht op het samenspel van seksuele selectie en ouderlijke zorg. Als vrouwelijke voorkeuren en mannelijke ornamenten samen met ouderlijke zorgstrategieën konden evolueren, waren er opnieuw twee verschillende uitkomsten mogelijk. Deze komen overeen met zorg door voornamelijk mannetjes, of door voornamelijk vrouwtjes. Als voornamelijk mannetjes voor de kinderen zorgen, evolueerden noch vrouwelijke voorkeuren, noch mannelijke ornamenten. Als voornamelijk vrouwtjes zorgen, evolueerden er wel voorkeuren én ornamenten. Bovendien suggereren de simulaties dat, in tegenstelling tot de gangbare opvatting, het ouderlijke zorgpatroon het eerst evolueert, wat vervolgens de toon zet voor de evolutie van vrouwelijke voorkeuren en mannelijke ornamenten.

OUDERLIJKE GESLACHTSROLLEN EN GESLACHTSVERHOUDINGEN

In een cohort is het aandeel mannen en vrouwen niet altijd hetzelfde. Bij de meeste soorten is de verhouding tussen mannetjes en vrouwtjes bij de geboorte ongeveer 1:1, maar dit kan later in het leven aanzienlijk veranderen. Als een van de seksen bijvoorbeeld een risicovolle levensstijl heeft, wat resulteert in een hoog sterftecijfer voor dat geslacht, zullen leden van het geslacht met een laag risicovolle levensstijl steeds hoger vertegenwoordigd zijn in de populatie. Er zijn een aantal theorieën die de geslachtsrollen van de ouders koppelen aan de geslachtsverhoudingen. Het uitgangspunt is dat het oververtegenwoordigde geslacht meer zorgtaken op zich zou moeten nemen dan het ondervertegenwoordigde geslacht.

Door middel van het model uit Hoofdstuk 3 heb ik in **Hoofdstuk 4** de wisselwerking tussen geslachtsverhoudingen en ouderlijke zorgpatronen systematisch onderzocht. Om over- of ondervertegenwoordiging van geslachten te creëren, heb ik rekening gehouden met geslachtsverschillen in de levenscyclus van individuen. Zo werden bijvoorbeeld de geslachten verondersteld te verschillen in de snelheid waarmee ze volwassen worden of verschilden ze in hun sterftekans tijdens een bepaald voortplantingsstadium (bijvoorbeeld het stadium waarin de paring plaatsvindt en het stadium waarin ouders ouderlijke zorg verlenen). Over het algemeen bevestigen mijn simulaties dat het oververtegenwoordigde geslacht geassocieerd is met meer ouderlijke zorg, maar om andere redenen dan de literatuur suggereert. Bovendien evolueerde er, in een deel van de simulaties, ouderlijke zorg door voornamelijk één van de seksen terwijl er geen sprake was van afwijkende geslachtsverhoudingen. Soms leidde de evolutie zelfs tot het tegenovergestelde patroon dan dat algemeen wordt voorspeld: in deze gevallen bood het oververtegenwoordigde geslacht minder ouderlijke zorg dan het ondervertegenwoordigde geslacht. Het blijkt dus moeilijk om geslachtsrollen van ouders te voorspellen op basis van de geslachtsverhouding. In plaats daarvan ontdekte ik dat de processen waardoor de geslachtsverhouding verandert een cruciale rol spelen in de evolutie van ouderlijke zorgpatronen. Bovenal geven mijn bevindingen aan dat ouderlijke zorgpatronen eerder de oorzaak dan het gevolg zijn van scheve geslachtsverhoudingen.

De huidige discussie over de rol van geslachtsverhoudingen in de evolutie van ouderlijke zorg richt zich vooral op het aantal volwassen individuen. In **hoofdstuk 5** verleg ik de focus naar geslachtsverhoudingen bij de conceptie. Als er geen verschil is tussen het produceren van zonen en dochters, hoort deze geslachtsverhouding gelijk te zijn. Wanneer één van de geslachten echter met minder kosten kan worden voortgebracht dan het andere geslacht, omdat het minder aandacht en zorg van de ouders vereist, is de verwachting dat dit ‘goedkopere’ geslacht in de populatie wordt overgeproduceerd. Door de geslachtsverhouding bij de conceptie samen te laten evolueren met de zorg door mannetjes en vrouwtjes, heb ik laten zien dat de nakomelingen van het ‘goedkopere’ geslacht in zekere zin zijn voorbestemd om op latere leeftijd ouderlijke zorg te verlenen.

BESCHOUWINGEN OVER EVOLUTIONAIR MODELLEREN

In dit proefschrift heb ik geprobeerd te begrijpen hoe evolutie het ouderlijk gedrag van mannetjes en vrouwtjes vormt. Om dit doel te bereiken, construeerde ik in drie hoofdstukken van mijn proefschrift (hoofdstukken 3-5) theoretische modellen met ‘individual-based’ simulaties. Deze hoofdstukken laten zien dat simulatie-uitkomsten aanzienlijk afwijken van de voorspellingen van traditionele modellen. Om de oorzaken van deze discrepanties beter te begrijpen, reflecteer ik in **hoofdstuk 6** op twee factoren die essentieel zijn voor het begrijpen van de ouderlijke zorgpatronen in mijn simulaties. Eén daarvan is het optreden van polymorfismen (zoals het naast elkaar bestaan van “veel-zorg-geven” en “weinig-zorg-geven” strategieën in zowel mannetjes als vrouwtjes), en de andere is conditie afhankelijkheid (als bijvoorbeeld ouders hun zorgbeslissingen nemen op basis van hun eigen kwaliteit). Deze twee componenten worden doorgaans over het hoofd gezien in standaard theorieën over ouderlijke zorg, omdat ze niet gemakkelijk kunnen worden opgenomen in de gereedschapskist van evolutionaire modellen. Ik hoop dat mijn proefschrift de toegevoegde waarde heeft aangetoond van ‘individual-based’ simulaties voor het maken van evolutionaire voorspellingen. Dit wil niet zeggen dat klassieke methoden uit de gereedschapskist moeten worden genomen. In plaats daarvan geloof ik dat de twee benaderingen, wanneer ze samen worden toegepast, elkaar zeer goed aanvullen.

Acknowledgements

I have been putting off writing this chapter because completing it would mean the end of both my PhD journey and my life in Groningen. So far in my life, I can honestly say that pursuing a PhD has been the most challenging, but ultimately rewarding, experience I have had. Completing this thesis would not have been possible without the help of a large number of people. Therefore, I would like to express my sincere appreciation to everyone who has contributed to making this possible.

First of all, I would like to thank my supervisors. Tamás, it is largely due to your support and encouragement that I get the opportunity to do a PhD. I met you in a workshop in China, where you gave fascinating talks about parental care, sexual selection and mating systems in animals. Then I got the chance to visit you in Bath, where I had conducted my first phylogenetic comparative study for my bachelor thesis under your supervision, as well as attended my first international conference with your encouragement and financial support. Throughout my time in Bath, I developed an increasing interest in understanding the evolution of animal behaviours, particularly parental care. Therefore, you helped me to apply for the CSC scholarship, enabling me to pursue PhD research at the University of Groningen under the supervision of you and two additional amazing supervisors from Groningen: Jan and Franjo. Despite the fact that we did not work together much during my PhD (mostly because a bike accident resulted in my being unable to conduct fieldwork on Kentish plovers), your mentorship and support were essential for all of the research presented in this thesis.

Jan, I will be eternally grateful for the freedom you gave me to explore my own path, as well as the advice and support you provided whenever I needed it. Having the opportunity to attend conferences with you has been a pleasurable experience. I really appreciate that you have introduced me to a number of researchers. Besides, you are the first person to tell me not to work too hard and to instill in me the importance of maintaining a healthy work-life balance. Thanks for making our group outings happen (including my first Treasure Hunt in Groningen and BBQs in both your old and new gardens). Also, thanks for inviting my dad and me to the annual Conseco/BPE Kerstborrel/Tapas Evening, the first party my dad attended while abroad.

Franjo, you are the person to whom I owe the most gratitude. For the first two years of my PhD, I felt completely lost as a result of the cancellation of fieldwork and the prolonged recovery period following knee surgery, but you took me under your wing and introduced me to the world of theoretical research. Although I had no prior experience with theoretical modelling at the time, you helped me in making up for my lack of knowledge, allowing me to gain expertise in developing evolutionary models in a relatively short period of time. And you have always praised me when I achieved something, which helps a great deal in reestablishing my confidence. In the last three and a half years, you have guided me through numerous aspects of scientific practices and have supported me at every step of my career development. There are no words to adequately express how grateful I am for all of your guidance and support. I sincerely hope that I will have the opportunity to collaborate with you on future projects.

I would also like to express my gratitude to Sander van Doorn, who has always been willing to answer my numerous questions about mathematical models. And I also want to thank Yang Liu, my awesome undergraduate mentor, for introducing me to the world of scientific research and supporting me in various manners.

I would like to thank the reading committee, Prof. Hanna Kokko, Prof. Sasha Dall and Prof. Ido Pen, for taking the time to read my thesis and for providing constructive feedbacks on my work.

A heartfelt thank you to Joyce and Marten for being my wonderful Dutch parents as well as being my paranymphs. You two make me feel like I have a family in Groningen, especially when you said that there is always a room for me if I come to visit. I will be eternally grateful to you for the kind support you provided me during and after my knee surgery, which greatly assisted me in returning to a normal life. I really appreciate you inviting my father and me to dinner. As a result, my parents have not been overly worried that I am alone in a foreign country with a 'broken' knee since my father returned to China. Thank you also for every dinner you prepared for me, which completely changed my impression on Dutch cooks (Marten, you are the best chef in Groningen). I cannot thank you two enough for everything you have done for me over the years.

I collected data for my first project at the Evolution and Biodiversity research group in Bath. I want to thank Narhulan and Jose for making me feel at ease in the group. Chufei, Tie and Ting, thanks for your great friendship. Visiting London with you will undoubtedly remain indelible in my memory. Ana, thank you very much for hosting me at your place.

I then started my journey in Groningen as a member of the BPE group and the TRÊS group. Reinaldo, my Chilean brother, thank you for helping me integrate into the BPE group. I had a wonderful time with you and Camila, and I will definitely visit you in Chile one day. Martje, you are the most amazing friend I could ever have. You instill in me the feeling of belonging in a foreign country. You were always there for me when I was feeling down. To cheer me up, you even made soymilk using a recipe from my grandma. Thank you very much for everything you have done for me. Sara, I knew we were going to be close friends after meeting you for the first time. I have always thought of you as the Italian version of myself, with a similar body size and a similar desire for good food. I thoroughly enjoyed every moment we spent together, including the hours we spent chatting on the street in the freezing cold. Michela, it was a pleasure to host you and Luce, and it brought back wonderful memories. I really appreciate all of your assistance with my thesis submission. Mirjam, you are a wonderful friend from whom I have gained a great deal of knowledge about Dutch culture. Traveling to Spain with you and Sara, as well as our Game of Thrones dinner nights (with you, Sara, and Marjie), will always be memorable experiences in my life. Maaike, I had a great time on the bike trip with you; the most memorable scene was when you made coffee for me on the small camping stove. Also, let's perform at least one song for our band, 'the Fun Club,' before I leave. Marco, thank you very much for the birdwatching trip and for double-checking my Dutch summary. Chistina, thank you for keeping me company during the lockdown; otherwise, I would have gone insane. Your texts encouraging me to complete my thesis were also greatly appreciated. Blanca, it was a great pleasure hosting you at my place. Especially when I was stressed out about the mathematical modelling exam, it was your grocery shopping that helped me unwind. I am very looking forward to visiting you in Madrid this summer. Jia, thank you for your insightful discussion about parental care patterns in Penduline tits. I wish you the best of luck with your thesis and please let me know if there is anything I can do to help. Wenxia, Gaoyang, Xia, Donghui, Lisheng and Long, thank you for the pleasant evenings we spent together (many amazing Chinese food). Gaoyang, Xia, and Donghui, I wish you the best of luck with your PhD projects.

My life, both inside and outside of academia, has been enriched by the people I met in the MARM group. Therefore, I would like to express my thankfulness to the entire MARM group. Apu, you are the most special one. I consider myself extremely fortunate to have met you, someone with whom I genuinely enjoy spending every second. Those times when we went for a run in the snow, spent the entire night walking around Noorderplantsoen, and of course, the countless dinners, coffees, and drinks that we shared will remain in my memory forever. I am very grateful to have you as a best friend, and I sincerely hope that we will have the opportunity to live in the same city in the future. Jana, it has been a great pleasure to collaborate with you on various projects (including Botero's project and journal clubs) and even more to be your friend. You are such a smart and nice person; I have learned a lot from you. I am overjoyed that we will continue working on our projects after I defend my thesis. And it was because of you that I began to enjoy outdoor activities at night, most notably when you and Apu were present. I am also very proud of you for being able to handle spicy food so well now. Eva, I would like to express my gratitude to you for assisting me in translating my English summary into Dutch, especially considering the time constraints and the fact that you had to do it on the train. Magdalena, thank you very much for organising everything for us, including group meetings. Also thanks for showing me the Poland supermarket, where I can find very tasty sausages. Boris, you are a great swimming instructor because I can now swim much faster than before. Christoph, thank you for contributing your critical thinking to the group discussion, which makes it more enjoyable. Although you made up a lot of stories, I enjoyed spending time with you. I am not sure if you are going to be an amazing

DJ, but perhaps a storyteller. Jacob, thanks for your friendship and for the wonderful evenings we spent together. Inès, I had a great time preparing for our group meeting's paper discussion with you. I also loved the pasta you made for us. Pratik, many thanks for always attempting to help with R-related issues and for your great feedbacks on my projects. Timo and Stefano, thank you for the stimulating discussions at the group meetings and for your great company at the parties. Hanno, thank you very much for checking my C++ code and for your fantastic suggestions for increasing simulation speed; otherwise, I might need two more years to complete my thesis. Joke, thanks for the computing advice. Emiliano, thank you for your help in resolving programming issues when I was just getting started with simulations, as well as for sharing your life experiences. With your lovely smiles, Ingeborg, you always try your best to help me with various issues, for which I will be eternally grateful. Stefany, thank you for providing grant information and for your advice on thesis printing. I hope we will have a proper graduation celebration for you in the near future.

To Frigg, Marianthi, Elisa, Euan, Janet, Pedro, Shu, Yang, Tianjian, Lucas, Joshua, Theo, Albertas, Karen, Helen, Kevin, Thijs, Omer, Marta, Marina, Miguel, Anni and all the other cool members of the groups of BPE and TRÊS over these years: Thank you for the stimulating discussions and pleasant conversation during the coffee break.

I would like to express my gratitude to two special groups. One is the 'Panixue Schnee group', in which I spent time with Apu and Jana, going for walks surrounded by numerous adorable cats, making a lovely snowman, and discussing potential collaboration on a future project about personality, parental care, and evolvability. The other one is the 'RC-Boat', which is the best boat house in Groningen. Raph and Claire, I appreciate how you always made me feel welcome when I showed up at your door without making an appointment. You make my stay in Groningen even more memorable because I know that no matter what happens, there is always one place I can go to 'recharge my batteries'.

There are numerous people who have indirectly contributed to the completion of this thesis. I would like to express my heartfelt appreciation to Yanning (Yuhong) for feeding me while I worked on my thesis and for sharing beautiful photos from Africa that refresh my minds. Thank you, Xiangxiang, for always making time to meet me for a cup of coffee whenever I called. Having a conversation with you always helps to relieve my stress. To my old and good friends 娜泡, 珮珮, 小苹果, 洁芸妈, 江胖, 小左, 恺恺, 张阿爷, 瑞瑞, 可羚, 俏仪, 志洁, 凯驰, 世桂, 阳之, 天萌, 灿爷, lingling, 子劢: I greatly appreciate your efforts in sustaining our friendship over the years.

最后，感谢我的爸爸妈妈和外婆。谢谢你们从小到大一直支持我，没有给过我任何束缚。你们说希望我做一只自由快乐的小燕子， 我希望你们在将来需要陪伴的时候我可以陪在你们身边。我非常想念你们，想和你们一起走在街上晒晒太阳。希望国内疫情可以快快好起来。

About the author

Xiaoyan Long was born in Sichuan, China on December 12 of 1993. In 2012, Xiaoyan started undergraduate studies in Ecology at the Sun Yat-sen University, China. In 2016, she obtained a CSC scholarship to pursue her PhD in the groups of Franjo Weissing (Modelling Adaptive Response Mechanisms) and Jan Komdeur (Behavioural Evolutionary Ecology) at the University of Groningen, the Netherlands. She has broad research interests, including parental care, mate choice, cooperation and conflict, and competition. Her eventual career goal is an academic position studying the evolution of animal behaviour, using a combination of theoretical and empirical approaches. In June 2022, she will begin her postdoctoral research at the University of Freiburg, Germany.

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