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### The evolution of parental sex roles

Long, Xiaoyan

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# Chapter 6

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## Afterthoughts

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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 and 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 repeatedly 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.

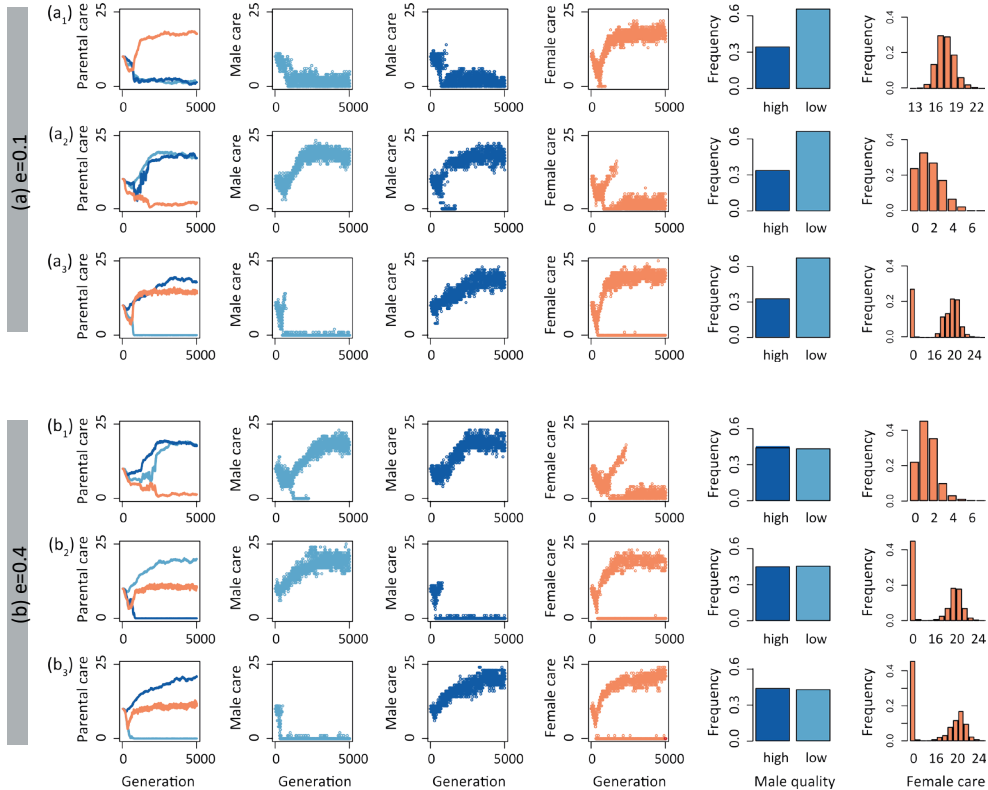
## CONDITION DEPENDENCE

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<sub>1</sub>)** Evolution of strongly female-biased care, with both types of male exhibiting a low level of care. **(a<sub>2</sub>)** 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<sub>3</sub>)** 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<sub>1</sub>)** Evolution of strongly male-biased care, with similar care levels in both types of male (similar to **(a<sub>2</sub>)**). **(b<sub>2</sub>, b<sub>3</sub>)** 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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