The evolution of paternal care can lead to population growth in artificial societies

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HIGHLIGHTS

- An agent-based model that relates paternal care and population dynamics is reported.
- Females elicit and exploit paternal care when their reproductive costs are high.
- Females reproduce faster and populations grow when paternal care is selected.
- Majority of simulations go extinct regardless of differences in reproductive costs.
- Sex-based differences in reproductive costs are not enough to produce paternal care.

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ABSTRACT

Evolutionary models of paternal care predict that when female reproductive effort is higher than male reproductive effort, selection might favour the emergence of unconditional male cooperation towards females, even when the latter group does not reciprocate. However, previous models have assumed constant population sizes, so the ecology of interacting individuals and its effects on population dynamics have been neglected. This paper reports an agent-based model that incorporates ecological dynamics into evolutionary game dynamics by allowing populations to vary. As previous models demonstrate, paternal care only evolves when female reproductive effort is higher than that of males, and the optimal strategy for females is to exploit male unconditional cooperation. The model also shows that evolution of this behaviour drives some simulations towards regimes of population growth. Thanks to the evolution of paternal care, females' inter-birth intervals are shortened and causing them to reproduce faster. Thus, it is suggested that the evolution of paternal care in species with differential reproductive effort between sexes could be associated to population growth. Nevertheless, the modelled evolutionary dynamics are stochastic, so differences in reproductive effort are necessary but not sufficient conditions for the evolution of paternal care.

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1. Introduction

Paternal care, a suite of behaviours by a mature male is a rare phenomenon among mammals. Direct infant care by males occurs in fewer than 5% of mammals. Evolutionary biology provides a canonical explanation to the rarity of this behaviour. The concept of *reproductive effort* (Trivers, 1972) identifies a particular fitness trade-off. Reproductive effort consists of two components, *mating costs* and *parental investment*. Mating costs measures the energy spent for attracting and accessing sexual partners. Parental investment measures the energy costs of all behaviours that enhance the fitness of current offspring. Therefore, reproductive effort refers to all forms of parental expenditure associated with producing and rearing a child that, at the same time, limits the parents' ability to invest in another child. A fitness trade-off is presumed to exist between the immediate fitness increment parents receive from enhancing the survival of their offspring and the delayed fitness parents gain from future reproduction, the former coming at the expense of the latter (Clutton-Brock, 1989). Internal gestation and obligatory post-partum suckling in mammals yield a reproductive difference in the rate at which males and females can reproduce: during the long period between gestation and children's maturity (usually after weaning) females cannot reproduce, whilst males can (Geary, 2000). When this situation is combined with the ability of females to care effectively for their offspring, this reproductive difference results in males focusing on mating effort through sexual competition (and away from paternal investment), while most of the parental investment offspring require to survive depends on females (Smith, 1977).

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Humans follow the same taxonomic bias found in mammals: since males experience lower levels of *minimum* parental investment than females do, they spend less on parenting and instead show a greater eagerness to engage in mating (Baumeister et al., 2001; Schmitt, 2005). Women must incur the differential costs of internal fertilisation, placentation, gestation, and periods of lactation that can last several years in foraging environments (Key, 2000; Quinlan and Quinlan, 2008). Human mothers also produce the largest and slowest-maturing babies among primates (DeSilva, 2011). But despite producing the most costly babies, humans breed the fastest. Whereas interbirth intervals are estimated at around 4 years in gorillas, 5.5 years in wild chimpanzees, and 8 years in orangutans, in foraging societies, inter-birth intervals average just 3.5 years (Key, 2000). Therefore, years before a human mother's previous children are self-sufficient, she will give birth to another infant, and the care these dependent youngsters require will exceed that of which the mother by herself can supply (Hrdy, 2009). Given their high energetic burden of reproduction, human mothers need the help of others, including real or possible fathers.

In *cooperative breeding* species, females and males help raise offspring that are not necessarily their own (Bergmüller et al., 2007). Male investment in their offspring is shown in many models of cooperative breeding in human evolution (Anderson et al., 1999; Belsky et al., 1991; Bogin, 2010; Fernández-Duque et al., 2009). However, across and within cultures, fathers greatly vary in the manifestation of paternal care, ranging from complete absence or aloofness, to great intimacy and direct care (Hewlett, 1993; Hurtado and Hill, 1996). Thus, as Hrdy (2000) stated, there is no empirical evidence nor theoretical bases for assuming that mothers could count on fathers to give a higher priority to provisioning children they already have (a costly behaviour for themselves) rather than seeking additional mates (and thus maximise their fitness). The questions analysed by this research are the following: under which evolutionary circumstances mothers could have elicited costly cooperation from males in the form of paternal care; and what consequences does this male investment in breeding activities have on reproduction rates and population dynamics.

Computational models of paternal care (Key and Aiello, 2000) have assumed that breeding activities, in which cooperation is not guaranteed, can be modelled using *evolutionary game theory*, in particular, employing the iterated Prisoner's Dilemma (IPD) (Axelrod, 2006; Axelrod and Hamilton, 1981), the leading paradigm to explain cooperative behaviour in the biological and the social sciences (Colman, 1995; Nowak, 2006). Here, I also decided to use the IPD. Recent studies have, nonetheless, challenged the suitability of the IPD to model the evolution of paternal care. An alternative game that has proved successfully in reproducing real data is the iterated *snowdrift game* (ISD). Both IPD and ISD games assume that partners have a common interest in their current brood. However, there is conflict between them because each parent would prefer its mate to provide the majority of parental investment. The main difference between these two games lies in what is the best response to a partner's defection: while for the IPD the best reply is defection, in the ISD it is cooperation. Thus, for instance, Van Dijk et al. (2012) found that in penduline tits (*Remiz pendulinus*), when facing their partners' desertion, both females and males do best by caring for their brood alone. Therefore the authors conclude, penduline tits do not appear to be playing the IPD at the population level, but the ISD instead. But this might not always be the case. Different life histories (especially different configurations of reproductive effort for males and females), and also different breeding behaviours can alter the progenitor's contingent payoff of cooperation and defection in their reproductive strategies. For instance, in species in which mothers cannot care effectively for offspring alone, they confront the difficult challenge of producing viable offspring without having the ability to do so. This reproductive scenario is better captured by the IPD, since mothers

facing a non-cooperative partner do best by abandoning the futile enterprise of rearing an infant alone (for tamarins see Bardi et al., 2001; for humans see Hrdy, 2009). This is the expected result unless these mothers have safe and available alternatives, such as relying on shared care and support (i.e., cooperative breeding or allomothering) and/or on paternal care. For this reason, in this paper I explore the evolution of paternal care in the context of disparity of reproductive effort between sexes and cooperative breeding systems using the IPD modelling approach.

Trivers (1971) was the first in analysing a scenario in which cooperation might emerge among selfish individuals through his theory of *reciprocal altruism*: if individuals assist each other in turns, and the costs of cooperation are relatively low to donors while the benefits are high to recipients, reciprocal cooperation could evolve among related and unrelated individuals. In these models, paternal care has been compared to male 'unconditional cooperation' (or 'pure altruism') towards females who do not reciprocate: this male cooperative behaviour, although beneficial for females, is costly for themselves. The same definition of paternal care is used here.

Agent-based models (ABM) about the evolution of paternal investment (Key and Aiello, 2000), have shown that male agents will tend to cooperate unconditionally with females (that is, males will choose to cooperate even when reciprocation is absent or uncertain) to help females pay for their high reproductive effort. Females in these models value males as sources of paternal investment, and they behave strategically. For this to occur, female reproductive effort must be much higher than that for males. Females also must punish uncooperative males, by excluding them from future cooperation, and exploit altruistic males. Over evolutionary time, non-cooperative males will tend to reproduce less and, therefore, their strategies will tend to vanish from the agent population. Finally, by exploiting male unconditional cooperation, female agents might offset their high reproductive burden, and since male reproductive effort is smaller than that of females, they can afford to receive the sucker payoff when playing against females. However, those ABMs have assumed constant population sizes, so the ecology of interacting individuals, the evolution of different reproductive strategies and their effect on population dynamics has been neglected. This is the gap this paper seeks to fill.

The reported ABM aims at simulating the evolution of paternal care and at studying its effect on population growth. It incorporates ecological dynamics into evolutionary game dynamics by allowing populations to vary. Thus, the possible mechanisms that link the reproductive effort of sexes, the evolution of reproductive strategies (in particular, of paternal care) and population growth or decay can be identified. Our hypothesis is that the evolution of paternal care, in a context of sex-based differences of reproductive effort, should result in sustained population growth, because mothers that receive unconditional cooperation from males are able to reproduce faster. It is predicted that, thanks to the evolution of male unconditional cooperation and the consequent exploitative behaviour of females, mothers will be able to reach the energy costs of reproduction sooner. Consequently, their inter-birth intervals will be shortened, reproducing faster, and hence populations describe regimens of growth. To test this hypothesis, the ABM is introduced, describing in detail its entities, state variables and modelled mechanisms (Section 2). General results and analyses are reported in Section 3. Then, the paper focuses on the link between the evolution of paternal care and population dynamics (Section 4), and latter on the evolution of reproductive strategies in inter-sex interactions (Section 5). Model results and main predictions are discussed by referencing the literature on the evolution of cooperation, breeding strategies in mammals and group selection models (Section 6). The paper finishes with some concluding remarks (Section 7).