

MATHEMATICAL MODELLING OF THE
EVOLUTION OF HUMAN BEHAVIOURS
AND STRATEGIC CHOICE

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A thesis submitted in fulfilment of
the requirements for the degree of
Doctor of Philosophy

Faculty of Science
School of Mathematics and Statistics
The University of Sydney

2019

ABSTRACT

Evolutionary anthropology seeks answers to the eternal philosophical question: how have we come to be? Studies in evolutionary anthropology attempt to explain the evolution of uniquely human behaviours by investigating the mechanisms that drive different trajectories. In this thesis dynamic mathematical models are built to investigate the tradeoffs defining divergent evolutionary pathways of strategic choice. This is done by comparing evolutionary equilibria at great ape-like and hunter-gatherer-like life histories.

One investigation considers the evolution of pair bonding in humans. Mate guarding that pays off in increased likelihood of obtaining paternities outperforms strategies of paternal care at hunter-gatherer-like male-biased sex ratios while multiple mating is the evolutionary equilibrium at chimpanzee-like female-biased sex ratios. This demonstrates the promise of mate guarding as a pathway to social monogamy and links male reproductive strategies to the grandmother hypothesis through sex ratio dependence.

Competition and care as male reproductive strategies are then investigated more generally in an ordinary differential equation model. Equilibria depend on life history and benefit parameters.

An integro-difference equation model that explores the effect of non-parental imitation on the coevolution of low fertility at high socio-economic status is also given, applying Darwinian selection to a contemporary case of cultural evolution.

This thesis shows that competitive strategies often pay off at human-like parameters despite the possibility of increased offspring survivorship through care. However, coexistence or persistence of a non-competitive strategy may also occur under specific parameters.

Uncovering drivers of the evolution of different male reproductive strategies is important for guiding further research and shedding light on why we are so different from other great apes.

PUBLICATIONS AND PRESENTATIONS

PUBLICATIONS

Chapter 2 of this thesis is published as:

Loo, S., Chan, M., Hawkes, K., Kim, P. (2017). Further mathematical modelling of mating sex ratios & male strategies with special relevance to human life history. *Bulletin of Mathematical Biology*, 79(8), 1907-1922. DOI: 10.1007/s11538-017-0313-2.

I co-designed the study, analysed the simulations and wrote the drafts of the manuscript.

Chapter 3 of this thesis is published as:

Loo, S., Hawkes, K., Kim, P. (2017). Evolution of male strategies with sex-ratio-dependent pay-offs: connecting pair bonds with grandmothering. *Philosophical Transactions of the Royal Society B*, 372(1729). DOI: 10.1098/rstb.2017.0041.

I designed the study, analysed the simulations and wrote the drafts of the manuscript.

PRESENTATIONS

The Show-Off Hypothesis: The evolution of large-game hunting, and signalling like peacocks. *Society of Mathematical Biology (SMB)*, 2018, University of Sydney, NSW.

Cultural evolution of low fertility at high socio-economic status. *Women in Mathematics Special Interest Group (WIMSIG)*, 2017, University of Adelaide, SA.

Evolution of male reproductive strategies with sex-ratio dependent payoffs. *Australia and New Zealand Industrial and Applied Mathematics (ANZIAM)*, 2017, Hahndorf, SA.

An agent-based model of the evolution of large-game hunting in hunter-gatherer communities. *Joint meeting of the European Society for Mathematical and Theoretical Biology and the Society for Mathematical Biology (ECMTB/SMB)*, 2016, University of Nottingham, UK.

A mathematical investigation into the effect of large-game hunting in hunter-gatherer populations. *Australia and New Zealand Industrial and Applied Mathematics (ANZIAM)*, 2016, Canberra, ACT.

Agent-based modelling of hunter-gatherer populations. *University of Wollongong Mathematical Biology Workshop*, 2015, Wollongong, NSW.

ACKNOWLEDGEMENTS

The culmination of the past four years that you now hold in the palms of your hands was completed in no shape or form, by an individual alone, but only through the sustenance, provision and support of countless individuals. These are only some of them.

My deepest gratitude to my supervisor Peter Kim for his guidance and support through metaphor, encouragement and mathematics. Thank you for pushing me to conquer the greatest of mathematical mountains by traversing its rocky path through both exploration and teleportation. Your intellect and humility are both respectable and inspiring.

To Kristen Hawkes, not only for her guidance in the anthropological concepts studied here, but also for her boundless enthusiasm and inspiration in research. Thank you for your many clarifying emails and ongoing encouragement.

Thanks to Ulf Dieckmann for his guidance during my time at the International Institute of Applied Systems Analysis, in the Young Scientist's Summer Program of 2017. Chapter 5 was completed during this time.

To my parents, thank you for all your help in editing, proofreading and feeding me. Thank you for growing me in more ways than just the contents of this thesis. To Kevin, for paving a way before me.

For partnering with me through this whole journey, Luke. Thank you for believing in me and encouraging me every day.

I would not have managed to complete this thesis without the strength of God, who is strong when I am weak, and who sustains and strengthens even when there feels like there is none left to give.

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ABBREVIATIONS

ODE	Ordinary differential equation
ASR	Adult sex ratio
OSR	Operational sex ratio
PC	Paternal care of dependants
MG	Mate guarding
MM	Multiple mating

INTRODUCTION

The application of mathematical modelling to the investigation of social behaviours has been an increasingly growing field of curiosity in recent decades (e.g. Chan *et al.*, 2016; Jennions and Fromhage, 2017; Kokko, 2008; Laland, 1993; Schacht and Bell, 2016). The techniques and models developed within mathematical modelling have the power to illuminate and inform hypotheses regarding interactions and behaviours between populations. For example, between cells, insects, or individuals investing in competing behavioural strategies. Our own daily interactions with society and the world around us may lead us to think that attempting to simplify or quantify human behaviour is too complex, as choices and strategies appear to exist outside of straightforward algorithms. How can one possibly attempt to express human interaction by using simply a few variables? This is what I venture to do in this thesis. Drawing from various disciplines and fields of research, I use mathematical modelling to shed light on some of the mysteries of human behaviour and evolution.

Creating mathematical models that allow for the investigation of mechanisms of individual behaviour is a useful tool in obtaining evidence to either support or negate existing hypotheses. Such modelling techniques are able to marry interdisciplinary information and develop quantitative analysis that can inform the problem at hand. Gatenby and Maini (2003, p.76) emphasise the indispensability of "[developing] mechanistic models that provide real insights into critical parameters that control system dynamics". This marriage between mathematical modelling and behavioural interactions is the intersection in which this thesis sits.

Questions within evolutionary anthropology and cultural evolution are investigated through the lens of dynamical systems. I develop models of human behavioural strategies with an emphasis on the male side of the story of human life history, and in doing so seek to uncover some of the mechanisms that drive the evolution of uniquely human, counter-intuitive behaviours and traits. What are the selection pressures leading to monogamy in humans? Why do males tend towards competition over caring behaviours? Can we learn more about the mechanisms that drive modern societies to low fertilities?

1.1 HUMAN LIFE HISTORY AND MATHEMATICAL MODELLING

The eternal philosophical question, "Where do we come from?" is pervasive in human experience and informs and inspires evolutionary anthropological research. The studies in this thesis seek answers to this question and consider the selection pressures and mechanisms by which we as humans have come to be unique in the ways that we interact with and manipulate the world around us. Some of these differences include large brains, long postmenopausal life spans, and long interbirth intervals.

Persistence of different behaviours is often dependent on the tradeoff between effort invested in reproduction and effort invested in somatic maintenance. Life history theory explores these tradeoffs by considering determinants relating to specifics of growth, fertility and mortality. For example, costs of increasing the success of reproduction may trade off with a reduction in energy spent on physical or somatic maintenance and immunity. Energy is redirected or diverted, following pathways that increase fitness. It is the balance of these tradeoffs that establishes evolutionarily stable strategies.

It is the combination of selection pressures influencing mortality and fertility that will favour a particular life history strategy, and models reveal that small changes in these selection pressures can have large effects on the optimal life history. (Mace, 2000, p.8)

Exploring these tradeoffs and finding the tipping point between the costs and benefits of competing strategies can help us understand the selection pressures that drive changes to behaviour and, in particular, that so sets us apart from our closest cousins, the great apes. Is it possible to quantify and compare these tradeoffs in order to track changes in evolutionary trajectories? Investigations of this are based on the theory of natural selection, originally established by Darwin (1871). This work has shaped studies of humanity ever since.

Studies of modern hunter-gatherers and other small-scale societies are crucial in understanding human evolution and the selection pressures of ancestral humans. While

few hunter-gatherer or foraging communities exist in the modern world, there has been much ethnographic and demographic interest in these people groups. Throughout anthropological literature, ethnographic data is available for many of these people groups, as well as the great apes (e.g. Hawkes *et al.*, 1991, 2001; Hill *et al.*, 2001, 2007; Hill and Hurtado, 1996; Howell, 1979; Blurton Jones, 2016; Muller and Wrangham, 2014). Ethnographic and archaeological research of populations such as these provide a guide to thinking about human behaviour within an environment representative of human ancestral lifestyles, in particular considering the trajectory of human behaviour had modern healthcare and contraception not intervened (von Rueden *et al.*, 2014). Marlowe (2005) further highlights the importance of this information in evolutionary anthropology and evolutionary biology, stating that "the ethnographic record of foragers provides the only direct observations of human behaviour in the absence of agriculture, and as such is invaluable for testing hypotheses about human behavioural evolution" (Marlowe, 2005, p.1).

In exploring human life history, there has been much interest in the mechanisms of female postmenopausal life span, mate guarding and pair bonding, and large-game hunting. These behaviours, observed in hunter-gatherers, are uniquely human and at first glance counter-intuitive. Natural selection might assume the persistence of strategies that produce more surviving offspring. However, this is often not the case. Selfish behaviours, or behaviours that reduce the fitness of the population as a whole, can persist by mechanisms of maladaptive competition and costly signalling (as modelled by Grafen, 1990a,b, for example), winning over strategies that seem more beneficial to the group. Such mechanisms are sometimes difficult to prove by exposition.

The interdisciplinary partnership of anthropology and mathematics has been instrumental in the exploration of hypotheses surrounding these behaviours by quantifying and analysing the long-term equilibrium evolutionary benefits of these behaviours (e.g. Grafen and Ridley, 1983; Grafen, 1990b,a; Hawkes *et al.*, 1995; Kim *et al.*, 2012, 2014; Kokko and Jennions, 2003, 2008; Schacht and Bell, 2016). However while a wide range of models exist for the investigation of questions in evolutionary anthropology, much

of this research is founded in ideas of game theory, and specifically, optimal foraging theory or fitness maximisation (Charnov, 1976; Hill *et al.*, 1987; Smith, 1972; Pyke *et al.*, 1977), or statistical analysis of empirical data. Dynamical systems modelling of behavioural strategies is lacking, and generally under appreciated by the mathematical world.

In this thesis, I follow the instructive work of Hawkes *et al.* (1995) to investigate the evolution of male reproductive strategies. These studies are given in Chapters 2 and 3, where I explore the possibility of mate guarding as an avenue to pair bonding in humans. Hawkes *et al.* (1995) investigated the tradeoffs between three strategies (mate guarding, care and multiple mating), and showed persistence of mate guarding in a wide range of situations. However, pair bonding is rare in mammals. This begs the question, what drives the evolution of pair bonding in some populations, but not others?

One suggestion follows from Coxworth *et al.* (2015), who note the shift in adult sex ratio that emerges as postmenopausal longevity evolved in humans. As ecological changes created a fitness opportunity for subsidies provided by 'grandmothers', the increase in longevity caused a shift in adult sex ratios from female-biased ape-like sex ratios to male-biased hunter-gatherer-like sex ratios. This is the result of males remaining fertile until old age, but the female age of menopause staying around 45 despite the increased longevity. These male-biased sex ratios cause an increase in male competition as female mates per male become scarce. Thus, the payoffs to male reproductive investment necessarily shift as sex ratios change. This is the premise of research conducted in Chapters 2 and 3. I investigate the effect of changing sex ratios on the evolution of male reproductive strategies, and align these discoveries with demographic studies of chimpanzees and hunter-gatherers.

In the first model in Chapter 2, I critique a model from the literature (Schacht and Bell, 2016) and develop an ordinary differential equation model to investigate the effect of sex ratios on male reproductive strategies. I show that the winning strategy is highly dependent on the sex ratio. In Chapter 3, I continue this investigation by making expli-

cit assumptions that were implicit in previous models. I develop a difference equation model in order to accurately model the male's dilemma, where increased production raises the payoff for theft (Hawkes *et al.*, 1995; Tullock, 1974). By explicitly studying inefficiencies in guarding and emphasising that paternities should be necessarily uncertain regardless of the number of pairs formed, I investigate the dependence of male reproductive strategies on both the adult sex ratio and the efficiency of guarding.

In these models, mate guarding trades off with alternative strategies of care and multiple mating, but care is an insufficient explanation for the evolution of pair bonding, as it fails to outcompete guarding at male-biased sex ratios. At these hunter-gatherer-like sex ratios, the scarcity of females relative to males creates a selection pressure for traits that increase one's competitive standing for paternities amongst peers. It is competition that outperforms care in this investigation of pair bonding.

In Chapter 4, I then consider a general model of the male mating strategies of competition and care, where competition pays off in increased likelihood of obtaining paternities and care pays off in differential offspring survival. This addresses the question of sex-role divergence, and explores why males tend towards competition over caring strategies. The investigation follows from the Fisher condition (Fisher, 1930), which highlights the importance of gametic differences on strategic investment. Since male gametes are small but more numerous compared to females' large but fewer gametes, males are able to bear the cost of producing more gametes that go wasted in competition. I develop a model of this interaction between the costs of care and competition and apply this model to the problem of large-game hunting.

Ethnographic studies of the Hadza people in Tanzania highlight the uniqueness of human large-game hunting, where investment in large-game hunting does not return direct offspring survival benefits (Hawkes, 1991; Hawkes *et al.*, 1991; Hawkes, 1993; Hawkes *et al.*, 2001; O'Connell *et al.*, 1988). While the classical hunting hypothesis (Lancaster and Lancaster, 1983; Washburn and Lancaster, 1968) would propose that this strategy evolves out of paternal care, where the successful capture of game results in

the direct provisioning of offspring, this optimistic hypothesis fails to align with ethnographic research. There is no observed correlation between the success of hunters and the differential provisioning of their offspring. Instead, the show-off hypothesis proposes that this behaviour is a costly signal and investment increases one's likelihood of obtaining paternities as others defer to better hunters (Hawkes, 1991; Hawkes *et al.*, 1991; Hawkes, 1993). This is supported by the observation that successful hunters are deemed better mates and subsequently obtain more paternities (Hawkes *et al.*, 2001). Investment in one's deferential competitive standing amongst peers is key to understanding this tradeoff. When do selection pressures drive the evolution of competition and increased likelihood of paternities over provisioning and increased offspring survivorship?

1.2 CULTURAL EVOLUTION

Techniques and concepts from evolutionary anthropology and evolutionary biology are often employed in questions regarding the cultural evolution of behaviours in contemporary society (Boyd and Richerson, 1985; Mace, 2000; Mesoudi *et al.*, 2007; Mesoudi, 2011; Richerson and Boyd, 1984). Using Darwinian evolution theory, mechanisms that drive the evolution of culture can be explored. In Chapter 5, a novel dynamic mathematical model of the cultural evolution of low fertility at high socio-economic status is explored. Natural selection might imply the evolution of high fertility when individuals have access to greater wealth. However, improvements in socio-economic status are instead negatively correlated with fertility (Borgerhoff Mulder, 1998; Bryant, 2007; Livi-Bacci, 1986). Due to this evolution, more than half of the global population now live in countries with below replacement fertilities. This can be thought of as demographic transition, as fertilities decreased with the shift from pre- to post-industrial societies (e.g. Borgerhoff Mulder, 1998; Boyd and Richerson, 1985; Bryant, 2007; Kaplan, 1996; Livi-Bacci, 1986; Mace, 1996). However, for the scope of this investigation, I explore

the transversal dimension of this evolution, investigating the within population heterogeneity that emerges with high socio-economic status individuals evolving to lower fertilities than their lower socio-economic status counterparts.

Investigating drivers of the evolution of low fertility is important in understanding population dynamics and comparing societies. Understanding the mechanisms of this shift may assist in managing ageing populations and drastically decreasing fertility levels. An integro-difference equation model is developed and sensitivity analysis performed to determine regions within which low fertility evolves at high socio-economic status, while allowing for strategic choice within the framework of cultural evolution where imitation from non-parents is informed by Darwinian evolution. In doing this I seek answers to the question: what are the mechanisms that drive the effects of maladaptive competition and lead those of higher socio-economic status to invest in lower fertilities? I investigate the effects of wealth distribution and social learning.

Throughout these studies, competitive strategies evolve despite the subsequent sacrifice in overall population fitness. In this thesis I will demonstrate the utility of mathematical modelling — and dynamical systems modelling in particular — in investigating these reproductive tradeoffs and in exploring possible evolutionary trajectories.

AN ORDINARY DIFFERENTIAL EQUATION MODEL OF MALE
REPRODUCTIVE STRATEGIES AND SEX RATIOS

Although we humans share many features with other members of the primate order, especially with the closest living members of our hominid family — members of genus *Pan* including chimpanzees — there are substantial differences between our lineage and that of other primates. These differences include larger brains, long post-menopausal life spans, shorter interbirth intervals, intergenerational care of offspring, and the habit of pair bonding. In this chapter, I consider this pair-bonding habit and explore the effects of changing sex ratios on the evolution of this observed social monogamy.

Persistent bonds between mating pairs are common in birds, but social monogamy is rare in mammals where females are committed to internal gestation and lactation. Those female commitments influence opportunities for fathering. Males may gain more paternities by outcompeting other males for multiple mates rather than remaining with one. Yet, unlike most mammals, including our closest primate cousins, humans regularly form pair bonds. The stability of these relationships varies widely both among and within human communities, but adults usually form pair bonds across the wide array of subsistence and social systems observed both historically and ethnographically.

To explain the origins of human pair bonding, evolutionary anthropologists use many lines of evidence. Two of them are especially influential: first, the archaeological record of human lineage that begins more than two million years ago with stone tools and the bones of large animals; and second, among living people who depend on wild foods, men usually hunt while women usually gather. This sexual division of labour is addressed in more detail Chapter 4. Our human species, let alone the homo genus, evolved before the origins of agriculture about 10-12 thousand years ago. So hunter-gatherers are especially useful windows into the ancient problems and solutions that contributed to the evolution of our lineage as was noted in the Introduction of this thesis. The earliest archaeology and foraging specialisations by sex seem consistent with the hunting hypothesis, which proposes that human pair bonding evolved when ancestral populations began to rely on hunting and ancestral females paired

with hunters who in turn provisioned their offspring. This long favoured hypothesis assumes that pair bonding arises from benefits for paternal investment in the survival of children (Lancaster and Lancaster, 1983; Washburn and Lancaster, 1968). However, others suggest that this reliance on paternal provisioning is insufficient, instead proposing that alternative mechanisms resulted in an evolutionary push towards pair bonds (Hawkes *et al.*, 1995; Lukas and Clutton-Brock, 2013; Marlowe, 2000; Marlowe and Berbesque, 2012).

The benefit of this paternal provisioning made nuclear families units of common economic and reproductive interest, resulting in the shorter interbirth intervals and higher survival of long-dependent juveniles that is characteristic of humans (Kaplan *et al.*, 2000; Lancaster and Lancaster, 1983; Washburn and Lancaster, 1968). However, paternal provisioning and pair bonding are absent in the non-human members of the great ape radiation, indicating that an alternate male strategy of multiple mating, with males competing for paternities of the offspring of all available females, is the likely ancestral condition of human lineage. When most males are seeking multiple mates, caring for dependent juveniles must not only trade off against the possibility of gaining more paternities elsewhere, but also risk supplying fitness benefits to competitors who secure the paternities of those dependants. This points to possible benefits for a third strategy. In addition to seeking multiple mates or devoting care to dependants, a male might invest his time and effort in guarding a mate to prevent competitors from gaining extra-pair paternities. Guarding is the action of protecting one's mate from successful mating with a competing male.

From this perspective, males are faced with a form of "the social dilemma" where increased production — in this case care that increases the survival of dependants — raises the payoff for theft (Hawkes *et al.*, 1995; Tullock, 1974). If those who mate with multiple females without paying the cost of paternal investment can appropriate the fitness benefits supplied by carers, caring strategies could not spread. This male's dilemma (Hawkes *et al.*, 1995) points to a benefit for males who allocate effort to guarding their females in order to raise their own probability of paternity. Mate guarding

increases the probability that the paternity of offspring born to a guarded female belongs to the guarding male rather than a multiple mater. With the male's dilemma in mind, mate guarding may be an especially important form of male competition and a possible avenue to pair bonding.

This simplification of payoffs identifies three mutually exclusive ways for males to earn reproductive benefits. Net gains from effort devoted to seeking additional mates, increasing dependant survival, or increasing paternity certainty are dependent on the strategies of the competing males.

Recent work increasingly challenges conventional arguments of paternal provisioning as the pathway for the evolution of pair bonds in humans. This includes quantitative observations of modern hunter-gatherers in which the daily failure risk of hunters, coupled with wide distribution of bonanzas when they are successful, challenges the view that hunting is paternal effort. The meat of big animals is not controlled by the successful hunter but treated as a common good with shares claimed widely and mostly consumed by those outside of his own nuclear family (Hawkes, 1993; Hawkes *et al.*, 2014; Wood and Marlowe, 2013). This wide sharing of resources is investigated in Chapter 4. Moreover, comparative analyses of the social systems of non-human mammals find that when paternal care does occur, it is a consequence rather than a cause of pair bonding or social monogamy (de Waal and Gavrilets, 2013; Lukas and Clutton-Brock, 2013).

The possibility that mate guarding has been an avenue to pair bonding deserves particular attention for the evolution of human lineage because humans are distinguished from the great apes by remarkable longevity which includes a long post-fertile life stage in women (Alberts *et al.*, 2013; Croft *et al.*, 2015; Levitis *et al.*, 2013). One hypothesis about the evolution of human life history proposes that the long postmenopausal life span evident in humans was driven by grandmothing (Hawkes *et al.*, 1998). Kim and colleagues' (Kim *et al.*, 2012, 2014) two-sex agent-based model of this hypothesis results in a male-biased shift in sex ratio in the fertile ages as grandmothing pro-

pels longevity past the end of female fertility, while males remain fertile to old age (Coxworth *et al.*, 2015). When the number of competitors rises relative to the availability and eligibility of fertile females, males gain fitness advantages by altering their strategies in response to the increase in competition (Clutton-Brock and Parker, 1992; Harts and Kokko, 2013; Marlowe and Berbesque, 2012). Because most organisms are fertile throughout adulthood, the sex ratio in the fertile ages is generally labelled the adult sex ratio (ASR). Coxworth *et al.* (2015) use the model developed by Kim *et al.* (2014) to track the evolution of changing ASRs with the evolution of a human-like grandmothering life history and propose that it was the human male-biased ASR that propelled the evolution of our pair-bonding habit.

A model of three male mating strategies (dependant care, multiple mating, and mate guarding) is developed in this chapter and the response of payoffs to changes in the sex ratio in the fertile ages, the ASR, are analysed. These strategies have been modelled in the literature in varying combinations and to varying degrees of success (Fromhage *et al.*, 2007; Grafen and Ridley, 1983; Gross, 2005; Kokko and Jennions, 2003; Kokko and Rankin, 2006; Kokko, 2008; Kokko and Jennions, 2008; Marlowe and Berbesque, 2012; Winkler, 1987).

I begin the investigation of these male reproductive strategies by detailing the recursion model developed by Schacht and Bell (2016) and critiquing some of the assumptions of their model. Following the lead of, but departing from, this recursion model developed by Schacht and Bell (2016), I develop an ordinary differential equation (ODE) model, adjust the method of obtaining the ASR and introduce parameters that allow for guarding inefficiency. Where Schacht and Bell (2016) adjust the ASR by assuming that guarding is perfect and eternal, permanently removing guarded females and their guards from the population and thus changing the ASR, the ODE model in this chapter parametrises the ASR and analyses its effect on long-term equilibrium strategies using bifurcation analysis. This one-sex model does not explicitly model the female population, instead parametrising female availability by the sex ratio. This differs from how Gavrilets (2012) addressed the male's dilemma by focusing on female

faithfulness and preference for carers. However, this focus on female preference ignores empirical evidence that hunter-gatherer males do not prioritise paternal provisioning. The introduction of parameters of guarding inefficiency also allow for the investigation of the effect of theft on guarding when paternity is slightly uncertain.

2.1 OUTLINE OF RECURSION MODEL BY SCHACHT AND BELL (2016)

The following section outlines the recursion model developed by Schacht and Bell (2016) in further mathematical detail than originally presented and proposes changes to the model which are then developed in Section 2.2. The model tracks the evolution of three male strategies as they respond to changes in the sex ratio. These strategies are defined as paternal care to dependants (PC), mate guarding (MG) and multiple mating (MM), and have respective frequencies p , q , and $1 - p - q$. Male mating success is frequency dependent on M_t/F_t , the ratio of all fertile non-guarding males to unguarded females at time t , which is defined on discrete fixed intervals. These intervals give one time step as the time taken from conception to independence, or sexual maturity. The fitness of each male strategy shifts in response to changes in this sex ratio as this indicates partner availability. Evolutionary dynamics of strategy frequencies are simulated by calculating equilibrium fitnesses of each strategy as the sex ratio changes. Figure 2.1 is a schematic chart of the recursive algorithm outlined in Schacht and Bell (2016).

2.1.1 *Adult sex ratio dynamics*

In Schacht and Bell (2016) the adult sex ratio, M_t/F_t , described does not strictly follow the standard definition of the ASR, which includes all fertile adults regardless of a female's present fertility status. Within their model, the adult sex ratio shifts as per-partner availability changes with the establishment of pair bonds. Adult sex ratio dynamics are defined as proportional to the change in the frequency of guarding

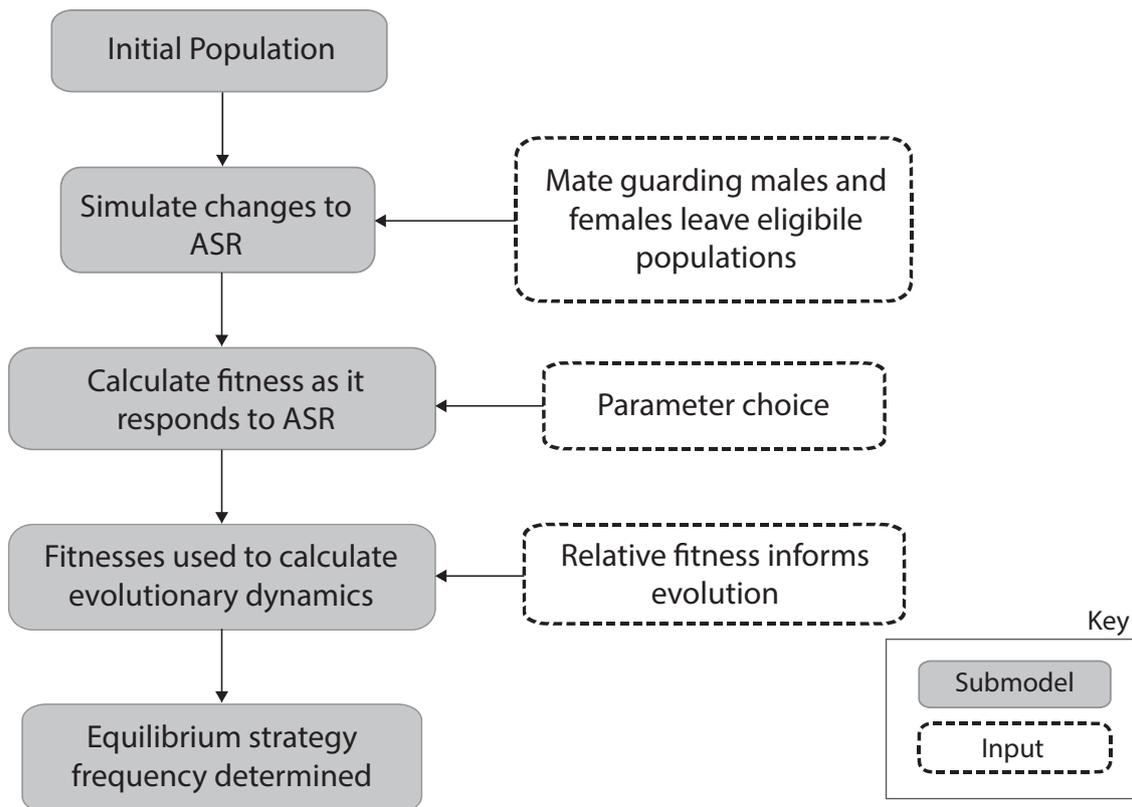


Figure 2.1: Schematic diagram of each time step within the recursion model developed by Schacht and Bell (2016).

males. Due to the assumption of perfectly successful mate guarding in the model, females who are guarded by guarding males and the males guarding them are removed from the mating pool. The sex ratio changes in response to this bond formation, as the overall number of eligible, unpaired mating males and females changes. This in turn affects the strategic choices of the remaining males. This construction reflects a sex ratio more akin to the definition of the operational sex ratio (OSR) — for example, as defined by Emlen and Oring (1977) and Mitani *et al.* (1996) — which conventionally includes only those eligible for conception, or the mating sex ratio. For example, in mammals, the OSR does not include females who are unable to conceive due to pregnancy or lactation. A review of the different definitions of the sex ratio is given by Ancona *et al.* (2017).

This inconsistency in definition of the sex ratio modelled makes it difficult to compare results with documented values obtained from demographic studies (Coxworth *et al.*, 2015). Correct definitions of the sex ratio are key to understanding populations and strategic choice, as was emphasised in Kokko and Jennions (2008).

In the recursion model in Schacht and Bell (2016), sex ratio dynamics are modelled separately for female-biased and male-biased populations. One time step represents the time taken for conception and upbringing to independence of one child; at each time step it is assumed that each female has one child, who then becomes a fertile adult. There is a steady flux of fertile adults.

For male-biased mating sex ratios, a greater number of males are competing for female mating opportunities. At any given time t , when $M_t > F_t$,

$$F_{t+1} = F_t(1 - q_t), \quad (2.1)$$

$$M_{t+1} = M_t - q_t F_t, \quad (2.2)$$

$$q_{t+1} = \frac{q_t M_t - q_t F_t}{M_t - q_t F_t}. \quad (2.3)$$

In this male-biased scenario, newly guarded females are removed from the eligible female population with probability q_t , the fraction of guarding males, at each time step. This assumes that all guarding males will necessarily find a female, and all females are guarded with perfect efficiency. The number of new females guarded by males at time t is $q_t F_t$.

Since only social monogamy is considered, this same number $q_t F_t$ of male guards are similarly removed from male eligibility. While general convention would not remove these males and females from the ASR and a female would not be removed from the OSR until she is pregnant, the complete removal of guarding males and the females they guard dictates the changes in the sex ratio in the mating pool, or the mating sex ratio.

The numerator in the proportion of guarding q_{t+1} given by Equation (2.3), represents the change in the population of guarding males or the remaining guarders, that is, the number of guarding males minus the number of guarding males with newly guarded females. Further, since q_t represents the proportion of guarding males out of the whole population M_t at a given time t , the denominator of Equation (2.3) represents the total number of males of any strategy still searching for mates.

For female-biased populations, $M_t \leq F_t$, where there is an excess of female partners available, it is assumed that males gain no benefit from mate guarding. This zero benefit causes the frequency of mate guarding, q , to automatically shift to zero. Protecting a mate from cuckoldry does not ensure an individual any more paternities than searching for a new mate through paternal care or multiple mating. Thus the frequency of guarding males, q , is 0. In other words, guarding males make no significant impact on the population and mutants are immediately taken over by paternal carers and multiple maters. Consequently, the population is constant and dependent only on initial conditions as no guarded pairs are removed from eligibility.

$$F_{t+1} = F_0 - q_0 M_0, \quad (2.4)$$

$$M_{t+1} = M_0(1 - q_0), \quad (2.5)$$

$$q_{t+1} = 0. \quad (2.6)$$

This formulation and the assumptions regarding the availability of guarded females may be a useful simplification, but it fails to capture the essence of the mate-guarding social dilemma. Males may choose strategies that increase their reproductive output and quality, but this increases the payoff for paternity theft. This is a male form of ‘the social dilemma’ (Hawkes *et al.*, 1995) in which those contributing to increased offspring production benefit free-riders who take the benefit without paying the cost.

By removing guarding males and the females they guard from the population as described above, guarding is assumed to be perfectly effective. Guarding males are not

subject to cuckoldry by multiple-mating males and their presence has no effect on the remaining males or their strategic choices. The mating males take only paternity opportunities from unguarded females, that is, only reducing the paternities of caring and other mating males. This complete removal of guarded pairs from the available mating pool restricts individuals from affecting or being affected by competition. With this perfectly effective guarding, there is no opportunity for paternity takeover by a mating male, and the question arises as to who the guarding males are guarding against.

From this perspective, the recursive set up in Schacht and Bell (2016) is a special case of perfect mate guarding where guarded females are equivalent to pregnant and lactating female mammals in conventional definitions of the OSR, yet the sex ratio analysed is of the form of the ASR. Guarded females are removed from eligibility. Further, paternities of females being guarded are impossible to obtain even if they are not yet pregnant and guarding males are themselves entirely immune to other paternity opportunities.

In the next section, fitnesses of each strategy are summarised and explained, further developments are suggested and more extensive analysis of equilibrium population frequencies is performed.

2.1.2 *Paternal-care strategy*

At each time step, caring males pair with females with a probability dependent on the availability of unguarded females, y_t . Caring males provide survival benefits to their mate's offspring with magnitude c and all males survive from one time step to the next with probability u , regardless of strategy. While paired with females, caring males are subject to paternity theft by multiple maters. This theft, referred to as cuckoldry in Schacht and Bell (2016), occurs at a given time t with probability h_t . The form of this probability is obtained by considering the limit of a transition probability matrix as

time progresses to infinity. It describes how a caring male divides his time between searching for available mates and caring for the offspring of his current mate, both his own and those of multiple-mating males who have stolen paternities from him. This transition between possible states is visualised in Figure 2.2.

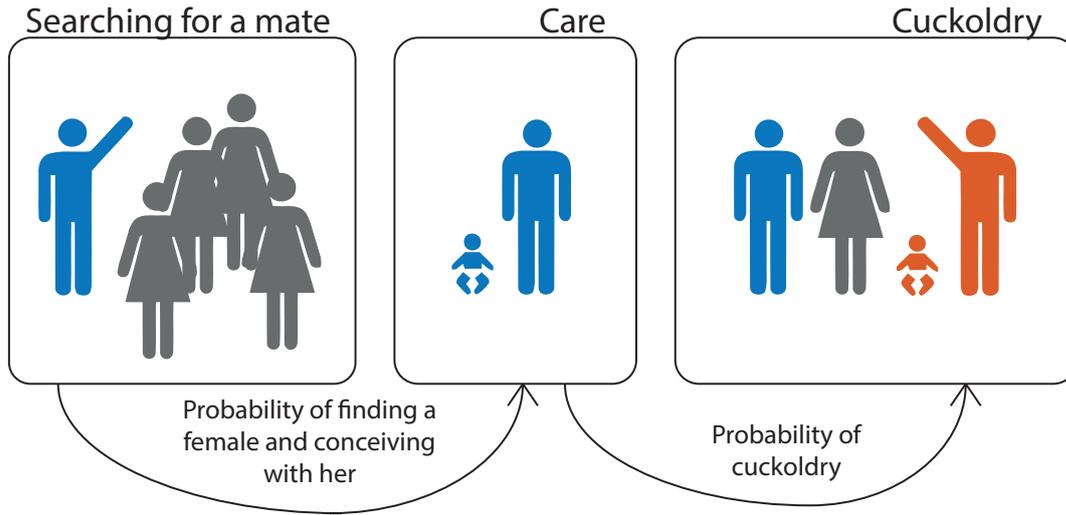


Figure 2.2: Paternally caring males transition between three states: searching for a mate, caring for their own offspring, or caring for the offspring of a MM male who has cuckolded him. The rates at which PC males transition between these states is determined by the transition matrix given in (2.7).

The following transition matrix represents this Markov process, wherein the term indexed by (i, j) in the transition matrix (2.7), represents the proportion of time a caring male who is in state $i \in [\text{Mate}, \text{Care}, \text{Cuckolded}]$ indicated by the rows, spends his time on activity $j \in [\text{Mate}, \text{Care}, \text{Cuckolded}]$ indicated by the columns. The transition matrix is given by

$$\begin{array}{c}
 \text{Mate} \\
 \text{Care} \\
 \text{Cuckolded}
 \end{array}
 \begin{array}{ccc}
 \text{Mate} & \text{Care} & \text{Cuckolded} \\
 \left(\begin{array}{ccc}
 (1-b)[(1-k)(1-(\alpha(1-p')b)+k)] & b & (1-b)(1-k)\alpha(1-p')b \\
 (1-\alpha) & \alpha & 0 \\
 (1-\alpha) & 0 & \alpha
 \end{array} \right) \cdot
 \end{array}
 \quad (2.7)$$

Here, b is the probability of a female producing offspring; k is the probability of protection from cuckoldry; a is the probability of finding a female; p' is the proportion of caring males out of all non-guarding males; and α is the proportion of time a caring male spends caring for either his own child or the child of a multiple mater who has cuckolded him. These and other parameters used are summarised in Table 2.1.

The term (Mate, Mate) gives the probability that an individual who has found a mate is continuing to mate with that female partner. To remain in this mating state, this female must not already be pregnant, either by the carer himself or another multiple-mating male. The term is given by the following probability

$$\underbrace{(1-b)}_{\text{Prob. of F not falling pregnant with PC}} \times \left[\underbrace{(1-k)}_{\text{Prob. of theft due to no protection}} \times \underbrace{(1-(a(1-p')b))}_{\text{Prob. that F not pregnant by MM male}} + \underbrace{k}_{\text{Protection of F from theft}} \right].$$

The probability that a caring male obtains the paternity of his mate's offspring and subsequently cares for that child is the probability of successful conception with that female. This is the intrinsic female probability of conception, b , in the term (Mate, Care) in the transition matrix (2.7).

The term (Mate, Cuckolded) represents the time spent caring for the offspring of a multiple-mating male who has cuckolded him. The probability that the paternity of offspring is that of a multiple mater is the probability that the female has not fallen pregnant with the carer, multiplied by the probability that a multiple mater is able to find that female and win that paternity, i.e., get her pregnant. This is given by the following expression

$$\underbrace{(1-b)}_{\text{Prob. of F not falling pregnant with PC}} \times \underbrace{(1-k)}_{\text{Prob. of theft due to no protection}} \times \underbrace{a}_{\text{Prob. of MM male finding F}} \times \underbrace{(1-p')}_{\text{Frequency of MM males}} \times \underbrace{b}_{\text{Prob. of conception with MM male}}.$$

Caring males who are currently caring for their own offspring, that is, they have not been cuckolded, divide their time between mating and care, at probabilities $(1 - \alpha)$ and α respectively. This is denoted in the second row of the transition matrix. Similarly, in the third row, males who are caring for the offspring of mating males from times when they were cuckolded spend their time mating and caring for these offspring at probabilities $(1 - \alpha)$ and α respectively.

Using these expressions, the probability that a male will be cuckolded is found. Assuming that a caring male will continue to search for a mate until his mate is pregnant, and that following this successful conception he will care for that offspring regardless of its paternity, the probability of being cuckolded is obtained by taking the infinite power of the transition matrix (2.7). Schacht and Bell (2016) make the simplifying assumption that $\alpha = 1$, and thus obtain the probability of cuckoldry, or paternity theft

$$h_t = \frac{(1 - b)(1 - k)a_t(1 - p')}{1 + (1 - b)(1 - k)a_t(1 - p')}. \quad (2.8)$$

As an alternative explanation to the transition matrix provided in Schacht and Bell (2016), consider that at each time step there is a set of females who have not yet conceived, F_{NP} . Within one time step, they are able to conceive with caring males with probability x , and mating males with probability y . If they do not conceive, the female remains in the 'not pregnant' set, F_{NP} . This continues until each female is pregnant, and the males are assigned paternities. Thus, the probability of a caring male obtaining paternities and then spending his time caring for his own offspring is $x/(x + y)$, and of a multiple-mating male obtaining the paternity and the caring male caring for these offspring is $y/(x + y)$.

Thus, if x is the probability of conception with unpaired females and if pairing with a caring male ensures paternity certainty, then $x = b$. If y is the probability of cuckoldry at any one instance, y is given by the term (Mate, Cuckolded) in transition matrix (2.7), i.e., $y = (1 - b)(1 - k)a(1 - p')b$. Combining these and rearranging gives h_t , the probability of cuckoldry, as given by Equation (2.8).

Further, the probability of a male of any strategy finding an available female is y_t . This is frequency dependent on the availability of females if the population is male-biased, or equivalent to 1 if the population is female-biased. Hence,

$$y_t = \min \left[\frac{F_t}{M_t}, 1 \right]. \quad (2.9)$$

Combining these terms gives the overall fitness of the caring strategy. This is given by the following deterministic equation for the lifetime fitness of a caring male:

$$\begin{aligned} w_p = & \underbrace{u^0}_{\text{Prob. of male survival to } t=0} \underbrace{y_0}_{\text{Prob. of finding female at } t=0} \underbrace{(1+c)}_{\text{Benefit from care}} \underbrace{(1-h_0)}_{\text{Prob. of not being cuckolded at } t=0} \\ & + \underbrace{u^1}_{\text{Prob. of male survival to } t=1} \underbrace{y_1}_{\text{Prob. of finding female at } t=1} \underbrace{(1+c)}_{\text{Benefit from care}} \underbrace{(1-h_1)}_{\text{Prob. of not being cuckolded at } t=1} + \dots \\ & = (1+c) \sum_{t=0}^{\infty} u^t y_t (1-h_t). \end{aligned} \quad (2.10)$$

2.1.3 Multiple-mating strategy

Multiple-mating males are able to mate with multiple females, and have the added benefit of also being able to steal paternities from caring males. These added paternity benefits from stealing are given by g_t , the expected number of theft events per multiple mater.

The fitness benefit, z_t , of mating with multiple available, unpaired females is given by the total number of these unpaired females shared amongst all multiple-mating males. This is given by

$$z_t = \frac{F_t - y_t M_t (p_t + q_t)}{M_t (1 - p_t - q_t)}. \quad (2.11)$$

The expected number of paternities stolen from carers by multiple-mating males, g_t , can be calculated by first finding the maximum possible number of paternities a multiple mater can gain through theft, f_t , and adjusting this by the probability of successful cuckoldry, h_t . The maximum possible number of paternities, f_t , is obtained by calculating the number of females paired with caring males available to be taken, $y_t p_t M_t$, and sharing those paternity opportunities between all multiple-mating males, $M_t(1 - p_t - q_t)$. Thus,

$$f_t = \frac{y_t p_t M_t}{M_t(1 - p_t - q_t)}. \quad (2.12)$$

Adjusting for the actual probability of theft, h_t , then gives

$$g_t = f_t h_t. \quad (2.13)$$

The overall fitness of multiple-mating males is given by the deterministic lifetime fitness expression:

$$\begin{aligned} w_m &= \underbrace{u^0}_{\text{Prob. of male survival to } t=0} \left[\underbrace{z_0}_{\text{Fitness benefit from shared paternity at } t=0} + \underbrace{g_0}_{\text{Expected no. of cuckold events}} \underbrace{(1+c)}_{\text{Benefit from care}} \right] \\ &= \sum_{t=0}^{\infty} u^t [z_t + g_t(1+c)]. \end{aligned} \quad (2.14)$$

2.1.4 *Mate-guarding strategy*

The fitness of mate guarding is solely dependent on the probability of finding a female, defined above as y_t , and the probability of subsequently guarding this female throughout the guarder's lifetime. This assumption models lifelong mate guarding and once guarded pairs are formed, both the male and female are removed from eligibility, as described in Section 2.1.1. This models eternal and perfect guarding.

The fitness of guarding males is given by

$$\begin{aligned}
 w_g = & \underbrace{u^0}_{\text{Prob. of male survival to } t=0} \underbrace{y_0}_{\text{Prob. of finding F at } t=0} + \underbrace{u^1}_{\text{Prob. of male survival to } t=1} \underbrace{y_0}_{\text{Prob. of finding F at } t=0} + \dots \\
 & + \underbrace{u^1}_{\text{Prob. of male survival to } t=1} \underbrace{(1-y_0)}_{\text{Prob. of not finding F at } t=0} \underbrace{y_1}_{\text{Prob. of finding F at } t=1} + \\
 & \underbrace{u^2}_{\text{Prob. of male survival to } t=2} \underbrace{(1-y_0)}_{\text{Prob. of not finding F at } t=0} \underbrace{y_1}_{\text{Prob. of finding F at } t=1} + \dots \\
 & + \underbrace{u^2}_{\text{Prob. of male survival to } t=2} \underbrace{(1-y_0)}_{\text{Prob. of not finding F at } t=0} \underbrace{(1-y_1)}_{\text{Prob. of not finding F at } t=1} \underbrace{y_2}_{\text{Prob. of finding F at } t=2} + \dots
 \end{aligned}$$

This geometric series simplifies to

$$\begin{aligned}
 w_g &= u^0 \frac{1}{1-u} + u^1 \frac{1}{1-u} y_1 (1-y_0) + u^2 \frac{1}{1-u} y_2 (1-y_1)(1-y_0) + \dots \\
 &= u^0 \frac{1}{1-u} + \sum_{t=1}^{\infty} u^t \frac{1}{1-u} y_t \prod_{j=0}^{t-1} (1-y_j). \tag{2.15}
 \end{aligned}$$

A summary of the parameters used is provided in Table 2.1.

2.1.5 Results

Following from the work of Schacht and Bell (2016), the model is recoded and simulated in MATLAB for efficiency. The model is simulated for a larger range of ASRs (M/F) than previously investigated to examine the dynamics of the system when females are extremely scarce. However, these values are still within the range of realistic ASR values of human hunter-gatherers, as given in Table 2.2.

Simulations are given in Figure 2.3 showing equilibrium strategy frequencies at changing ASRs. It can be seen that for all values of paternal-care benefit, c , and theft, k , mate guarding is the evolutionary equilibrium when females are extremely scarce. That is, as

Parameter	Interpretation	Value
a_t	Probability of a female encountering another caring or mating male	$\min[F_t/M_t, 1]$
b	Probability of conception per 'mating bout' for unguarded females	Between 0 and 1
k	Level of prevention from theft	Between 0 and 1
p'	Frequency of caring males out of non-guarding males	$p/(1 - q)$
u	Probability of male survival	Between 0 and 1
c	Added survival benefit to offspring of caring males	Between 0 and 1
y_t	Probability of finding a female	$\min[F_t/M_t, 1]$
h_t	Probability of cuckoldry	Equation (2.8)
z_t	Fitness benefit gained from shared paternity for mating	Equation (2.11)
f_t	Maximum paternities a multiple mater can gain through cuckoldry	Equation (2.12)
g_t	Expected number of cuckoldry events per time t	$f_t h_t$

Table 2.1: Summary of terms used to calculate the fitness of each strategy. The first section of the table corresponds to parameters relating to cuckoldry.

the sex ratio approaches 2 where fertile females are half as scarce as fertile males, mate guarding prevails even when the benefit of care is maximised, $c = 1$. Even for parameter combinations where paternal care outcompetes other strategies for a wide range of ASRs, mate guarding will eventually prevail when the sex ratio is large enough. This is evident in Figure 2.3(c) and (d). The switch behaviour points to the existence of a bifurcation that is dependent on sex ratio. This bifurcation is further considered in the development and analysis of an analogous ODE model presented in Section 2.2.

Population	ASR M/F
5 chimpanzee population averages	0.47
Kanyawara chimpanzees	0.70
!Kung	1.46
Ache	1.87
Hiwi	1.62
Hadza	1.60

Table 2.2: ASR values taken from specific assumptions about fertile ages (Coxworth *et al.*, 2015), and mortality profiles calculated for specific empirical populations. The first population is taken from a synthetic mortality schedule based on 5 different chimpanzee populations (Hill *et al.*, 2001). The second is a larger data set of one of these chimpanzee populations (Muller and Wrangham, 2014). The following populations are human hunter-gatherer populations as reported by Blurton Jones (2016); Hill and Hurtado (1996); Hill *et al.* (2007) and Howell (1979).

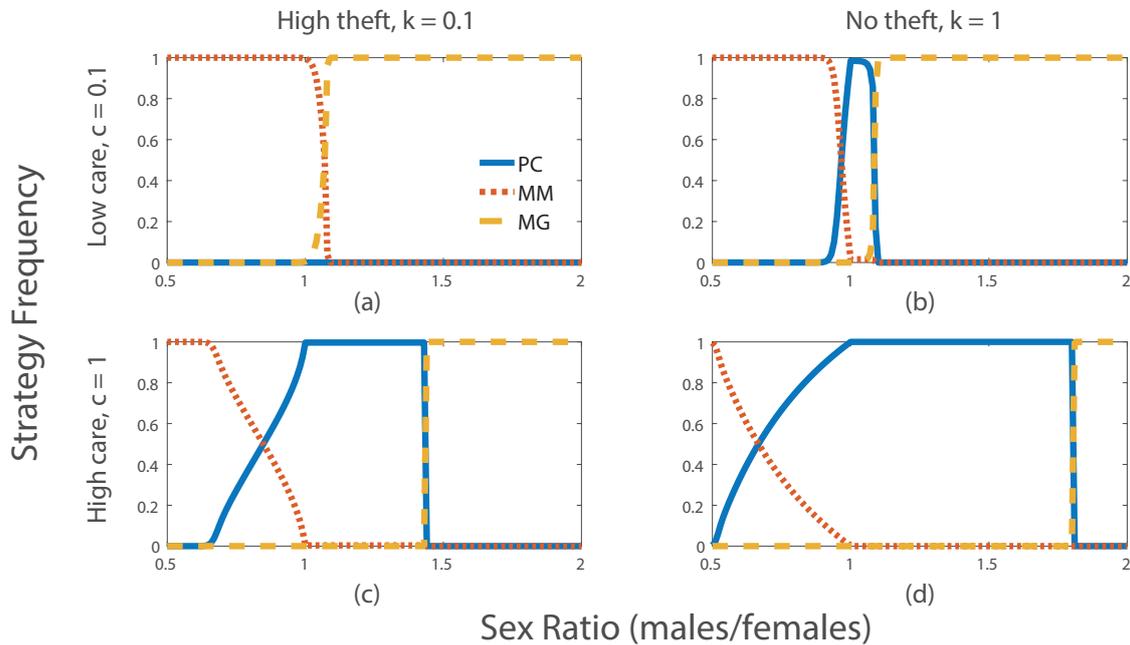


Figure 2.3: Effect of mating sex ratio on the frequency of strategies (PC, MM, and MG) at equilibrium given different parameters of care and cuckoldry. Initial conditions are $p_0 = q_0 = 0.005$, and parameters of probability of birth and probability of death are $b = 0.5$ and $u = 0.9$.

2.1.5.1 *Overall dynamics as parameters change*

If care increases offspring survival by less than 50%, i.e., $c < 0.5$, the frequency of strategies at equilibrium follows the equilibrium behaviour shown in Figure 2.3(a). Mate guarding begins to increase in the population as soon as there is a scarcity of females until guarding fully takes over other strategies, as was shown in Schacht and Bell (2016). For greater benefit of care, higher c , there is a region of strategy coexistence where the proportion of caring males increases, coexisting with multiple maters until the sex ratio is balanced and multiple mating is removed. Following this, as the ASR continues to increase, care persists until a threshold ASR value is reached and mate guarding once again takes over.

Differing values of protection from theft by caring males, k , determines the rate at which paternal care increases in frequency. Higher values of protection result in high frequencies of caring males for a greater range of ASR. This can be seen by comparing panel (c) with panel (d) in Figure 2.3. For example for $c = 1$, if $k = 0.1$ shown in Figure 2.3(c) caring males are in majority for $0.85 < \text{ASR} < 1.43$, while if $k = 1$ shown in Figure 2.3(d), caring males are at a high frequency for a larger range, $0.65 < \text{ASR} < 1.80$.

Further, the region in which multiple mating outcompetes other strategies changes as the likelihood of theft, k , changes, as given by Schacht and Bell (2016). Multiple mating wins at low sex ratios where it is difficult to find a female to guard, and shared paternities from multiple mating are more easily obtained than forming guarding or caring pairs.

2.1.5.2 *Coexistence of strategies*

By performing analyses on a wide range of values of care, c , and theft, k , a set of parameters within which mixed strategies occur emerges. In Figure 2.4(a) where $c = 0.6$ and $k = 0.01$, between sex ratios of 0.9 and 1.2, multiple-mating males prevail over caring and guarding strategies, but there is potential for paternal care to exist sim-

ultaneously. However, as the ASR increases to become more male biased, guarding overwhelms other strategies.

When the benefit of care, c , increases, caring males persist as the winning strategy for an increasingly wider range of ASRs. In Figure 2.4(b), paternal care reaches a maximum equilibrium frequency of 0.95 until a switch in strategies occurs at a sex ratio of approximately 1.3. Mate guarding once again overtakes care and multiple mating as the prevailing reproductive strategy when sex ratios are sufficiently male-biased.

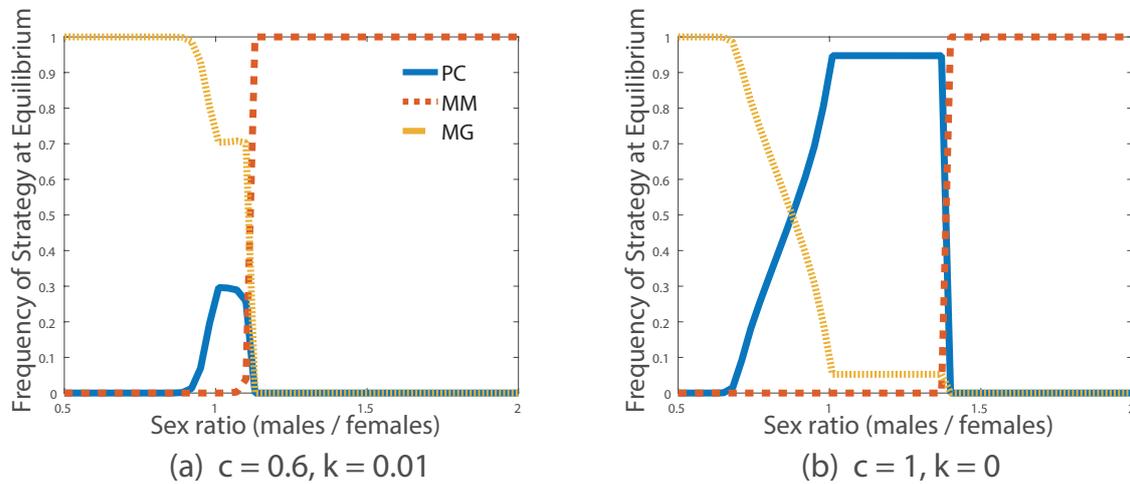


Figure 2.4: Effect of sex ratio on the frequency of strategies (caring, multiple mating and guarding) at equilibrium for two different combinations of c and k , demonstrating the coexistence of strategies. For (a) this occurs between an ASR of 0.9 and 1.2; for (b) this occurs between an ASR of 0.6 and 1.4. Other parameter values are defined as $p_0 = q_0 = 0.005$, $b = 0.5$ and $u = 0.9$.

2.1.5.3 Regions of different equilibria

To extend the results presented in Schacht and Bell (2016), a sensitivity analysis is performed to investigate equilibrium frequencies of mate guarding and paternal care as c and k change across all possible values. By simulating the model at two different, realistic sex ratios it is possible to find regions in the c - k parameter space where each strategy takes over. Of particular interest are sex ratios close to 1, where there is po-

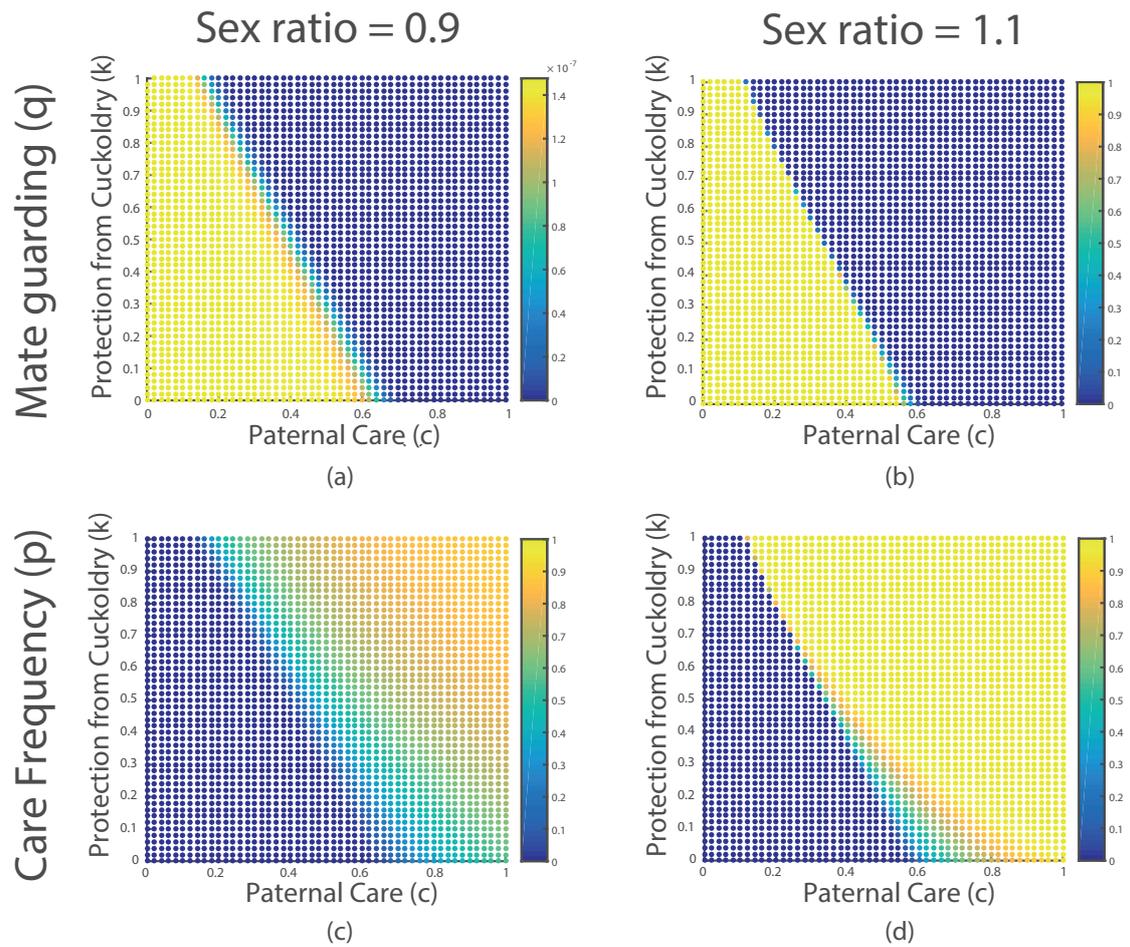


Figure 2.5: Equilibrium values of male strategies given two different initial sex ratios. Panels (a) and (b) present regions of mate-guarding density, q , as a function of parameters c and k . Panels (c) and (d) present regions of paternal-care density, p , as functions of c and k . Blue represents zero density of the corresponding strategy, and yellow represents a high density of the strategy. Specific density colours are given in the colour bars on the right of each plot. Sex ratio is 0.9 in panels (a) and (c), and 1.1 in panels (b) and (d).

tential for coexistence, and a boundary exists between equilibrium steady states. For this reason, in Figure 2.5, a slightly female-biased population (sex ratio of 0.9) and a slightly male-biased population (sex ratio of 1.1) are simulated and compared.

It is evident that a bifurcation exists in the c - k parameter space, across which the steady state switches between strategies. This is particularly evident in Figure 2.5(b). For $ASR = 1.1$, mate guarding takes over the population for $k < -2.125c + 0.26$. This

is obtained by fitting a line to the boundary in Figure 2.5(b) across which mate guarding prevails, i.e., $q = 1$. Density of the paternal-care strategy can also be observed in Figure 2.5(c) and 2.5(d). This shows coexistence with multiple mating where a range of colours can be seen.

Sensitivity analysis is also performed at chimpanzee-like and hunter-gatherer-like sex ratios given in Table 2.2. Results are compared for a sex ratio of 0.70, as is the documented mating sex ratio for Kanyawara chimpanzee population, with that of the Hadza, 1.60. However, a switch in the winning strategy only occurs when theft is unlikely and there is a large benefit to care, i.e., high k and high c . This can be seen at the Hadza hunter-gatherer ASR in Figure 2.6(b) and 2.6(d).

Thus, it can be seen that at male-biased hunter-gatherer-like ASRs, there is a large region of mate guarding seen in yellow in Figure 2.6(b). This can be compared to the Kanyawara chimpanzee, female-biased simulation where there is no mate guarding in Figure 2.6(a). Results from the agent-based model developed by Kim *et al.* (2014) showed that the male-biased sex ratio of hunter-gatherers emerged as a result of the grandmother hypothesis; there was a transition from female-biased to male-biased sex ratios as life histories evolved from a chimpanzee-like equilibrium to a hunter-gatherer-like equilibrium. This provides links between grandmothing and the evolution of male reproductive strategies. As the increase in longevity and postmenopausal female life span results in increasingly male-biased sex ratios, these male-biased sex ratios in turn drive changes in male reproductive strategies.

In the next section, this model is recast into an ODE model and analytic and numerical bifurcations are investigated further. In this way, it is possible to more accurately determine the dependence of long-term strategic equilibria on the sex ratio.

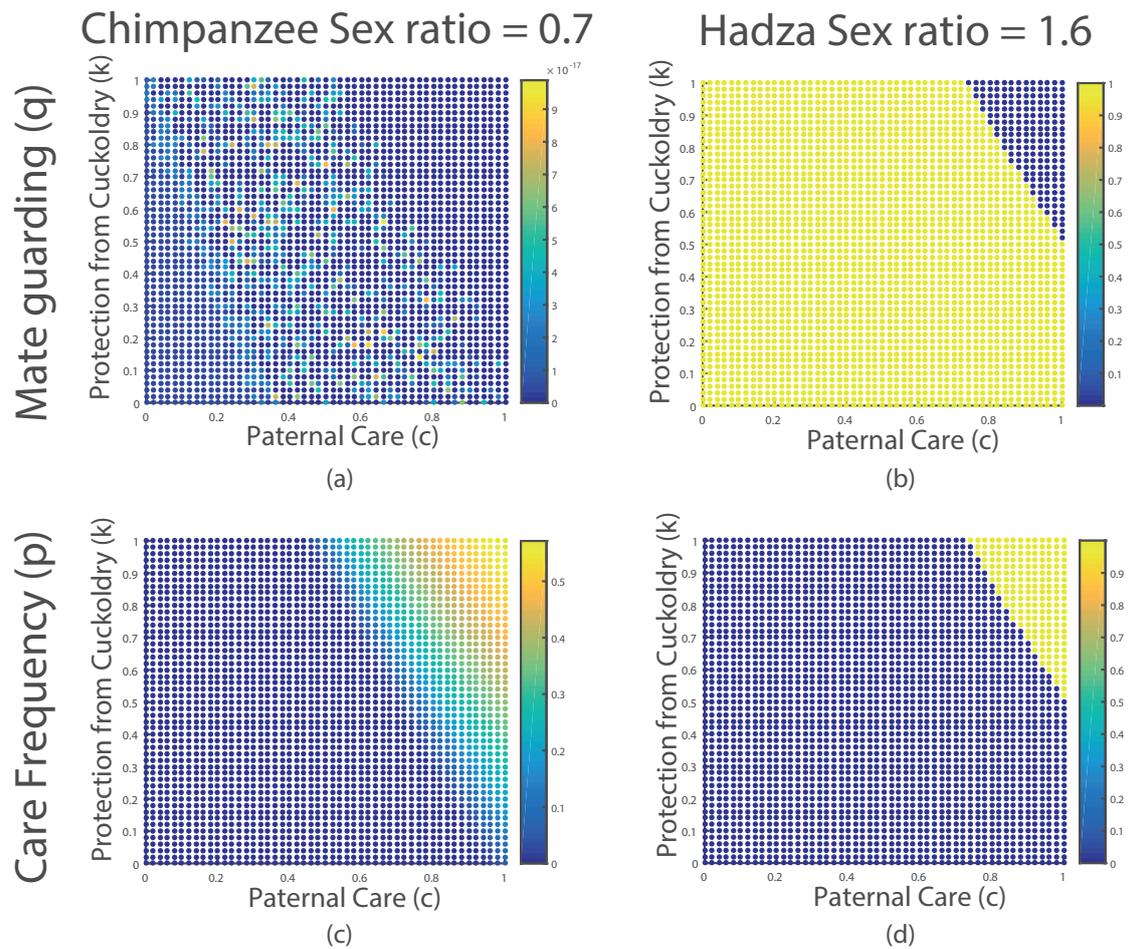


Figure 2.6: Equilibrium values of male strategies given two different initial sex ratios informed by documented demographic sex ratios. Panels (a) and (b) present regions of mate-guarding density, q , as a function of parameters c and k . Panels (c) and (d) present regions of paternal-care density, p , as functions of c and k . Blue represents zero density of the corresponding strategy, and yellow represents a high density of the strategy. Specific density colours are given in the colour bars on the right of each plot.

2.2 ORDINARY DIFFERENTIAL EQUATION MODEL

In this section an ODE model is developed, following the instrumental work of Hawkes *et al.* (1995) and Schacht and Bell (2016). Working in this continuous ODE framework allows for the investigation of long-term equilibrium strategies through bifurcation analysis. Of particular interest are parameters defining sex ratio and parameters of guarding efficiency.

The sensitivity of the model to assumptions regarding the effectiveness of guarding and the magnitude of the effect of male care on dependant survival is investigated. Where Schacht and Bell (2016) considered only perfectly effective guarding, I introduce a parameter that varies guarding efficiency. This allows some paternities of guarded females to be stolen by multiple-mating males. Schacht and Bell (2016) assumed that guarded females are completely removed from the eligible population and used their disappearance from eligibility to alter the sex ratio. As noted above, this models a form of the mating sex ratio, rather than the ASR. In the ODE model, both guarding males and guarded females are included in the ASR to remain consistent with the general usage of the ASR.

I further add the additional relaxing assumption of pair-bond breakup. Schacht and Bell (2016) assumed that guarding males remained paired until they left the population by death and females were assumed immortal and guarded until the end of the guarder's life. While a modelling convenience, it allows guarders a larger benefit than is likely to occur in real life. Instead, a constant proportion of pairs in this system are allowed to break up, moving guarding males back to the searching category and guarded females back to eligibility.

Four male compartments are defined with rates of growth dependent on their strategies and constant rate of death that is independent of strategic choice. These compartments are defined as caring males, P ; multiple-mating males, M ; and searching and guarding males, S and G respectively. The searching male population captures the behaviour of males adopting a guarding strategy but who are yet to find a female to guard due to female scarcity. The ODE model is defined for two cases. Where ρ is the ASR parameter, the model is defined separately for female-biased, $\rho \leq 1$, and male-biased, $\rho > 1$.

For female-biased populations, there is an excess of females available for conception relative to males. Therefore, a male need not spend time searching for a female — he is sure to find one immediately. Thus, searching and guarding compartments are col-

lapsed into one compartment: guarding males, G . Pair-bond breakup does not need to be modelled as guarders will find a new mate quickly after breakup with his prior mate. The three-compartment ODE system for female-biased populations is represented as

$$\begin{aligned}
 \frac{dP}{dt} &= \underbrace{b(1 - \hat{M})}_{\text{Logistic growth}} \underbrace{(1 + c)}_{\text{Care benefit}} \underbrace{k_P}_{\text{Paternities won by PC}} \underbrace{P}_{\text{Prob. of PC finding unpaired F}} - \underbrace{\mu P}_{\text{Death of PC}}, \\
 \frac{dM}{dt} &= \underbrace{b(1 - \hat{M})}_{\text{Logistic growth}} \underbrace{\Omega M}_{\text{Prob. of MM finding unpaired F}} + \underbrace{b(1 - \hat{M})(1 + c)(1 - k_P)P}_{\text{Gained paternities from theft of mates of PC}} \\
 &\quad + \underbrace{b(1 - \hat{M})(1 - k_G)G}_{\text{Gained paternities from theft from MG pairs}} - \underbrace{\mu P}_{\text{Death of MM}}, \\
 \frac{dG}{dt} &= \underbrace{b(1 - \hat{M})}_{\text{Logistic growth}} \underbrace{k_G G}_{\text{Paternities won by MG}} - \underbrace{\mu G}_{\text{Death of MG}}.
 \end{aligned} \tag{2.16}$$

The constant b is the intrinsic rate of birth; c is the benefit to offspring survival from caring males; $\hat{M} = (P + M + G)$ is the total population of males relative to the carrying capacity; k_i is the rate of conception with males from strategy i , with $(1 - k_i)$ being the rate of theft of paternities from those strategies by multiple maters; and $\Omega(t)$ is the number of available females per multiple-mating male at a given time. For simplicity I denote $\Omega(t)$ as simply Ω . The logistic growth rate employed here allows long-term behaviour to approach a finite equilibrium.

Multiple-mating males are characterised by investment in mating with all available females including the mates of caring males and, to a lesser extent, the mates of guarding males. By mating in this way, multiple maters are able to steal paternities from other males. Theft of paternities is simplified by explicitly assuming that females who fail to conceive with their mates will necessarily produce offspring with multiple maters. The proportion of paternities obtained by a caring male is defined as k_P and therefore, the corresponding proportion of paternities taken by multiple-mating males as $(1 - k_P)$. High values of k_P correspond to low rates of extra pair paternity, and vice versa.

Similarly, guarding inefficiency is introduced by allowing multiple-mating males some chance at paternities of the offspring of guarded females. Following the same logic as above, the rate of conception within guarded pairs is defined as k_G and the rate of paternities gained by multiple maters as $(1 - k_G)$. Guarded females are less available to multiple-mating males than other females because guards are devoted to guarding their mates from paternity theft. Thus, multiple maters obtain paternities from the mates of carers more readily than from guarders. Therefore, it is necessary to impose the restriction $k_G > k_P$.

The number of unpaired females multiple maters are able to find and with whom they will produce offspring is defined as Ω , i.e.,

$$\begin{aligned}\Omega &= \frac{\text{Unguarded females}}{\text{Non-guarding males}} \\ &= \frac{\frac{\hat{M}}{\rho} - G}{\hat{M} - G},\end{aligned}\tag{2.17}$$

where ρ is the sex ratio parameter defined as males over females, and \hat{M} is the population of males as given previously, or $\hat{M} = (P + M + S + G)$ in the male-biased case. Defining ρ in this way gives \hat{M}/ρ as the total number of females in the population.

For a male-biased population, $\rho > 1$, guarding males who are searching for a mate but unable to find one due to female scarcity do not produce offspring at that time.

These males are modelled by the searching compartment S. The four-compartment ODE system for male-biased populations is represented by

$$\begin{aligned}
\frac{dP}{dt} &= \underbrace{b(1 - \hat{M})}_{\text{Logistic growth}} \underbrace{(1 + c)}_{\text{Care benefit}} \underbrace{k_P}_{\text{Paternities won by PC}} \underbrace{\Omega P}_{\text{Prob. of PC finding unpaired F}} - \underbrace{\mu P}_{\text{Death of PC}}, \\
\frac{dM}{dt} &= \underbrace{b(1 - \hat{M})}_{\text{Logistic growth}} \underbrace{\Omega M}_{\text{Prob. of MM finding unpaired F}} + \underbrace{b(1 - \hat{M})(1 + c)(1 - k_P)\Omega P}_{\text{Gained paternities from theft of mates of PC}} \\
&\quad + \underbrace{b(1 - \hat{M})(1 - k_G)G}_{\text{Gained paternities from theft from MG pairs}} - \underbrace{\mu M}_{\text{Death of MM}}, \\
\frac{dS}{dt} &= \underbrace{b(1 - \hat{M})}_{\text{Logistic growth}} \underbrace{k_G G}_{\text{Paternities won by MG}} - \underbrace{\mu S}_{\text{Death of searching males}} - \underbrace{\phi S}_{\text{Rate of finding available F to guard}} + \underbrace{\beta G}_{\text{Pair-bond breakup}}, \\
\frac{dG}{dt} &= \underbrace{\phi S}_{\text{Rate of finding available F to guard}} - \underbrace{\mu G}_{\text{Death of guarding males}} - \underbrace{\beta G}_{\text{Pair-bond breakup}},
\end{aligned} \tag{2.18}$$

where parameters are defined as above; β is the rate of pair-bond breakup; $\hat{M} = (P + M + S + G)$ is the total population of males relative to the carrying capacity; and ϕ is the rate at which searching males find an available female and transition to the guarding population.

In this male-biased system, $\Omega < 1$ and can therefore be interpreted as the probability of finding a female. Thus, the rate of transition from searching to guarding, ϕ , can be found by assuming a Poisson process and using the convention that the transition probability is found by

$$\text{Probability} = 1 - \exp(-\text{Rate} \times \Delta t).$$

Therefore, the rate of transition from searching to guarding is given by

$$\phi = -\ln(1 - \Omega), \tag{2.19}$$

where it is assumed that the time step $\Delta t = 1$. As the population moves from male biased to female biased, i.e., as Ω approaches 1, ϕ approaches infinity and searching males instantaneously find mates and become guarding males. As a result, there are no searching males and the compartments S and G in the male system given by the last two equations in (2.18) reduce to the equation for G in the system (2.16). Therefore, these two systems are consistent at equal sex ratio.

A summary of the parameters used in the ODE system is given in Table 2.3.

Parameter	Interpretation	Value
b	Birth rate	1
β	Rate of pair-bond breakup	0.05
c	Benefit to children of the mates of caring males	0.8
k_P	Rate of conception with caring males	0.7
k_G	Rate of conception in guarded pairs	0.9
Ω	Number of females available in female-biased system, or probability of finding an available female in one time step Δt	Equation (2.17)
ϕ	Rate of finding a female	Equation (2.19)
μ	Death rate	0.05
ρ	Sex ratio (\hat{M}/F)	Female biased: 0.7, Male biased: 1.4

Table 2.3: Summary of parameters within the ODE system of male strategies. The third column provides values of parameters used for simulations of stability and equilibrium.

2.2.1 Results

The model is simulated to determine long-term equilibria given a variety of parameter sets, starting with the simple case where there is no theft from guarded pairs and

no pair-bond breakup, $k_G = 1$, $\beta = 0$. This models perfectly efficient guarding, as is assumed by Schacht and Bell (2016). Then, I introduce imperfect guarding by setting $k_G < 1$ and $\beta > 0$. Bifurcation analyses are performed on the system using AUTO07 to identify the specific effect of ASR and guarding efficiency k_G on the system. AUTO07 is a software for the continuation of solutions of ODE systems under given initial conditions.

These results are then interpreted and compared with ASRs from ethnographic studies of hunter-gatherer and chimpanzee populations (Blurton Jones, 2016; Hill and Hurtado, 1996; Hill *et al.*, 2001, 2007; Howell, 1979; Muller and Wrangham, 2014) as calculated by Coxworth *et al.* (2015).

First, the effect of care, c , and probability of theft from carers, k_P , is investigated for the case where guarding is perfect, before considering the case where guarding is imperfect. Figure 2.7 shows the equilibrium behaviour of the system at different ASRs when guarding is perfectly effective. As the system moves from female- to male-biased sex ratios, a switch between long-term equilibrium strategies occurs. In general, in female-biased populations multiple mating wins over competing strategies, and guarding wins in very male-biased populations. However, in Figure 2.7(b) and (d) where theft from paternal carers is not allowed, $k_P = 1$, there is a region within which care can persist within the population, represented by blue. If any theft is introduced, the guarding strategy outcompetes multiple mating and care for all male-biased ASRs, seen in the left hand side panels (a) and (c) with $k_P = 0.1$. The larger the survival benefit of care, c , the greater the ASR region within which care outperforms other strategies. The region of care persistence pushes in to the female-biased region where otherwise multiple mating would prevail. This can be seen by comparing panel (b) with panel (d).

Introducing guarding inefficiencies then allows a selective benefit for the coexistence of multiple mating and guarding even when populations are very male-biased. This can be seen in Figure 2.8, where some paternities are available to multiple maters, $k_G = 0.9$, and pair bonds are allowed to breakup, $\beta = 0.1$. Using the same parameters

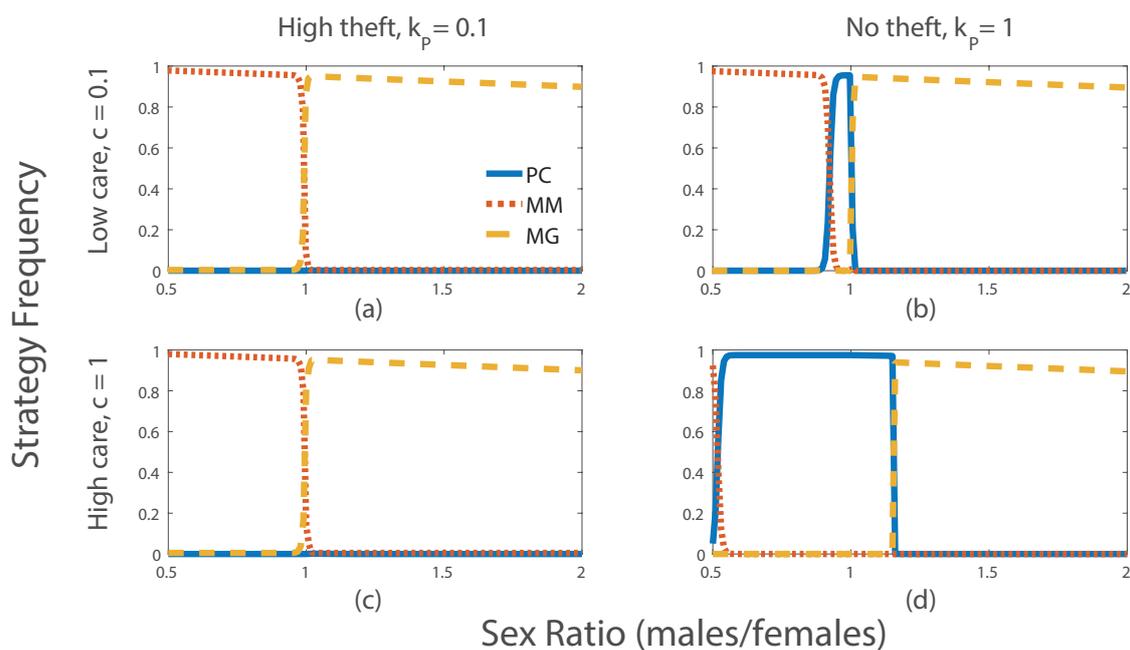


Figure 2.7: Equilibrium frequencies of each strategy given specific adult sex ratio, ρ , at high and low care, $c = 1$ and $c = 0.1$, and high and low proportion of theft from caring males, $k_p = 0.1$ and $k_p = 1$. Other parameters used for simulation are: $k_G = 1$, $\beta = 0$, $\mu = 0.05$. This models perfect guarding. Panels (a) and (c) demonstrate high proportions of theft. In these cases, multiple mating wins at female-biased sex ratios, and guarding takes over at male-biased ones. Panels (b) and (d) show a region of sex ratios where care takes over the population. The size of the region within which care wins increases as the survival benefit of care increases. At very male-biased sex ratios, guarding still takes over the population, and at very female-biased sex ratios, multiple mating still wins.

of care, c and k_p , as in Figure 2.7, the equilibrium behaviour of the caring population remains qualitatively similar. However, where there is no theft from carers, $k_p = 1$, and the benefit of care is at a maximum, $c = 1$, the region of care persistence is much larger, stretching into a region of male-biased sex ratios, where $ASR = 1.4$. However, I point out that in this case theft from carers is less likely than theft from guarders $k_p > k_G$, subsequently failing to capture the male's dilemma. This highlights the importance of guarding behaviours as limiting theft from carers smuggles in a form of guarding where carers can be certain of paternities. As the sex ratio increases to very male-biased, guarding coexists with a small proportion of multiple mating.

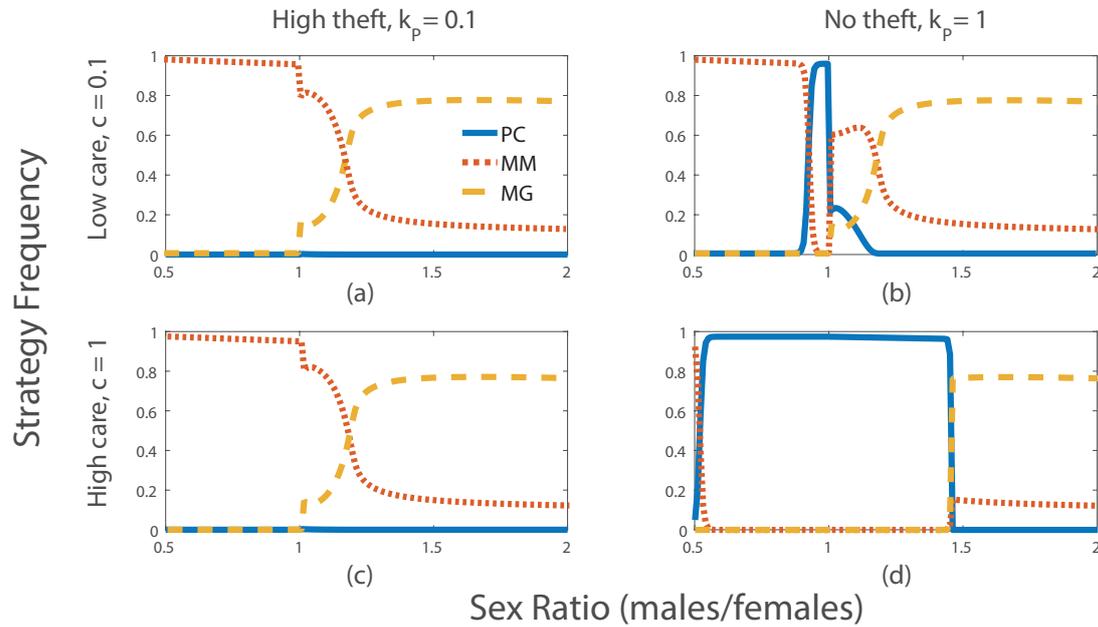


Figure 2.8: Equilibrium frequencies of each strategy given specific adult sex ratio, ρ , at high and low care, $c = 1$ and $c = 0.1$, and high and low proportion of theft from caring males, $k_p = 0.1$ and $k_p = 1$. Other parameters used for simulation are: $k_G = 0.9$, $\beta = 0.1$, $\mu = 0.05$, modelling imperfect guarding. Panels (a) and (c) demonstrate high proportions of theft. In these cases, multiple mating wins at female-biased sex ratios, and guarding and multiple mating coexist at male-biased sex ratios. Panels (b) and (d) show a region of sex ratios where care takes over the population, with guarding and multiple mating coexisting when populations are male-biased, though guarding still outperforms multiple mating.

Long-term equilibrium strategies are then compared at the ASRs calculated for chimpanzee and human populations in Table 2.2. In cases of limited care benefit (panels (a) and (b) in Figure 2.7 and 2.8), multiple mating wins at all female-biased sex ratios, meaning that for chimpanzee-like ASRs, multiple mating outperforms competing strategies. At male-biased sex ratios, when the benefit of care is low, guarding outperforms other strategies at all ASRs in human hunter-gatherer populations as given in Table 2.2, e.g. at the Hadza ASR of 1.60 (as calculated by Coxworth *et al.* (2015) from life tables in Blurton Jones (2016)). However, Figure 2.8 shows the possibility of coexistence with multiple maters at these male-biased ASRs, pointing to scope for cheaters to remain in the population.

However, when there is limited or no theft from carers, i.e., larger k_P , care can take over the population at some female-biased sex ratios and some male-biased sex ratios when $c = 1$. For example, at an ASR similar to that of the Kanyawara chimpanzees (0.70) care takes over the population when care benefit is high. Though this region of care encompasses a large range of ASRs, such a situation where $k_P > k_G$ is an inaccurate representation of the payoffs to guarding. The region of care persistence highlights the sensitivity of the model to variation in parameters of care and theft.

Mate guarding outperforms other strategies at all very male-biased populations even in the extreme case when care corresponds to juvenile immortality, i.e., $c = 1$. Further, the guarding strategy can coexist with multiple mating when guarding is not perfectly efficient. Assuming that all human populations have ASRs greater than 1.4, guarding males perform better than other strategies. However, if a population is only slightly male-biased, it is possible for care to win.

2.2.2 Sensitivity analysis

To investigate long-term equilibria in further detail and for cases that include theft from guarded pairs, sensitivity analysis is performed by finding bifurcations in the sex ratio, ρ .

Bifurcation diagrams for the male-biased and female-biased systems are presented. Constant parameters of death and birth are assumed: intrinsic rate of birth per female, b , is assumed to be 1 year^{-1} , where time in the model is given in years; and death rate, μ , is chosen as constant, and equivalent to 0.05 per year. Parameters used are summarised in Table 2.3.

2.2.2.1 Female-biased population

In the three-compartment female-biased system given by Equation (2.16), analytic steady states can be found. I also provide examples of numerical solutions for given parameter sets. Two steady states exist for this system, corresponding to the overwhelming persistence of multiple mating, and the coexistence of both care and multiple mating. Guarding vanishes in both steady states. The steady states for (P, M, G) are given by

$$\text{SS multiple mating} \quad \left(0, \frac{b - \mu\rho}{b}, 0 \right), \quad (2.20)$$

$$\text{SS coexistence} \quad \left(\frac{(k_P(1+c)\rho - 1)(bk_P(1+c) - \mu)}{bk_P(1+c)(\rho + c\rho - 1)}, \frac{(1 - k_P)(bk_P(1+c) - \mu)}{bk_P(1+c - 1/\rho)}, 0 \right). \quad (2.21)$$

Mate guarding does not take over the population when the sex ratio is female-biased. The proportion of theft allowed for guarding males, k_G , does not factor in to the steady states in these female-biased systems as guarding does not persist in any form.

The steady state where care and guarding go extinct and multiple mating persists (SS multiple mating) is stable under the conditions

$$k_P(1+c) < \frac{1}{\rho} \quad \text{and} \quad \mu < \frac{1}{\rho}b.$$

Given that $\mu < 1$ and $\rho < 1$ for female-biased sex ratios, and with the estimate that $b = 1$, the second condition is upheld in all cases of this female-biased system. Thus, provided that the first condition holds, multiple mating outperforms all other strategies and care goes extinct.

For care to persist in the population with multiple mating, i.e., the steady state given by Equation (2.21) to be stable, the following three conditions must hold

$$k_P(1+c) > 1, \quad \mu < \rho k_P(1+c), \quad \text{and} \quad \mu < b k_P(1+c).$$

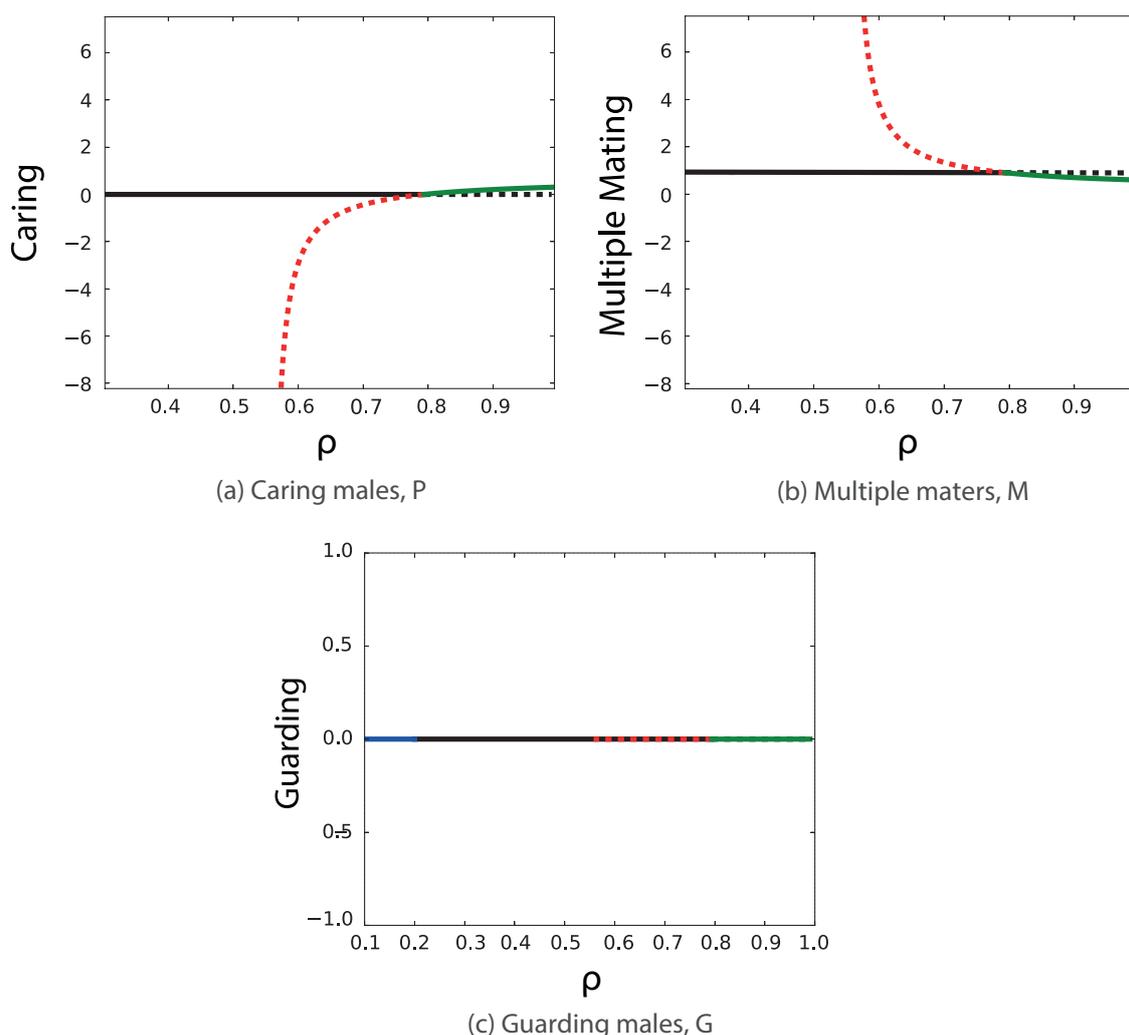


Figure 2.9: Bifurcations of the female-biased ODE system (Equation (2.16)), where sex ratio is less than 1, i.e. $\rho < 1$. Dashed lines correspond to unstable steady states, and solid lines to stable steady states. Steady states are given in red, green and black, corresponding to equivalent steady states across panels (a), (b) and (c). The green steady state corresponds to Equation (2.20), and red and black to Equation (2.21). The red dashed, unstable steady state is negative in the caring strategy and is therefore biologically unrealistic. Other parameters are low care, $c = 0.8$, and low theft, $k_P = 0.7$.

One-parameter bifurcations in the sex ratio, ρ , given high care, $c = 0.8$, and low theft, $k_P = 0.7$, are given in Figure 2.9. At very low sex ratios, the zero-care steady state is stable, meaning that all care dies out, and multiple mating takes over. This corresponds to the steady state given by Equation (2.20), and the black steady state in Figure 2.9. However, for $\rho > 0.79$, the stable steady state switches to Equation (2.21), where care and multiple mating coexist. This is given by the green steady state of Figure 2.9.

An example steady state obtained through numerical analysis given the parameter estimates in Table 2.3, and where $\rho = 0.7$, can be calculated using the analytic expressions of the steady states presented above. The steady states in the form (P, M, G) , the corresponding eigenvalues, and the subsequent stability of each solution given these parameter values are

Steady-State Solution with (P, M, G)	Eigenvalues	Stability
$(0, 0.9650, 0)$	$(0.0067, -0.0151, -1.3786)$	Unstable
$(0.4995, 0.4697, 0)$	$(-1.5700, -0.0191, -0.0059)$	Stable

2.2.2.2 Male-biased population

Due to the transfer term, ϕ , between searching and guarding, analytic steady-state solutions cannot be easily obtained for male-biased populations. The effect of the sex ratio ρ on the steady-state solutions is investigated numerically. The number and nature of the steady states is also determined by the proportion of paternities of guarded females that are stolen by multiple-mating males, k_G . One-parameter bifurcations in k_G are given in Figure 2.10, and in ρ in Figure 2.11. This analysis of k_G is also evident in comparing Figure 2.7 with Figure 2.8.

The bifurcation in Figure 2.10, for $\rho = 1.2$ and other parameters as given in Table 2.3, shows that care is never stable, and multiple mating is unstable at high guarding efficiency (high k_G). When guarding is highly efficient (high k_G), only the guarding strategy persists, labelled A. However, once guarding inefficiency is introduced and the paternities of guards can be stolen by multiple maters, i.e., k_G is anything other than 1, coexistence of multiple mating and guarding results, as is evident in the red steady state in Figure 2.10 and labelled as B.

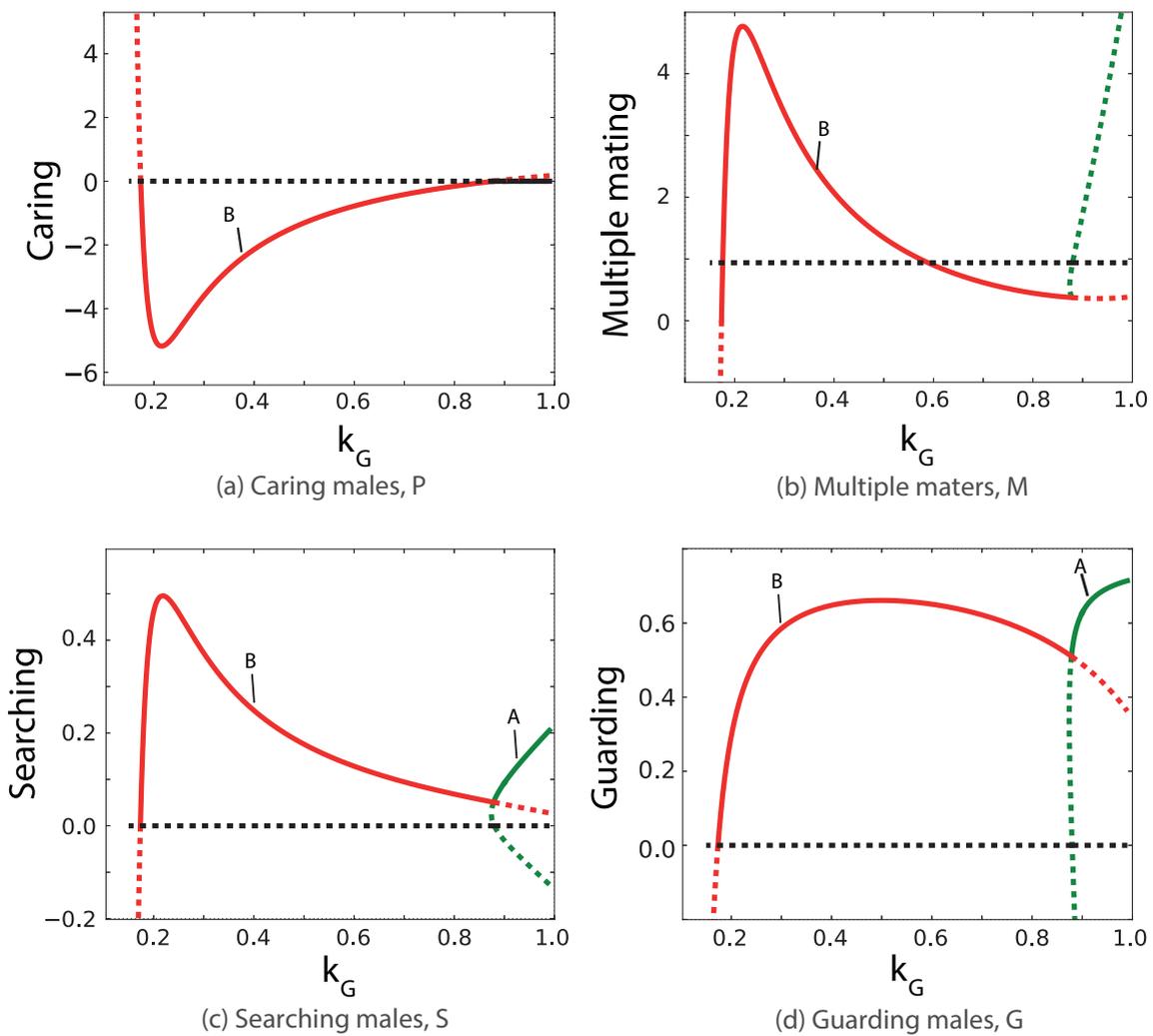


Figure 2.10: Bifurcation diagrams of the ODE system as guarding efficiency, k_G , changes. Dashed lines correspond to unstable steady states, and solid lines to stable steady states. Steady states are given in red, green and black, corresponding to equivalent steady states. A corresponds to guarding takeover, and B to coexistence of multiple mating and guarding strategies.

Further, bifurcation analysis on the effect of the sex ratio ρ is given in Figure 2.11. When the sex ratio is close to equal, the caring steady state can still be stable. This is shown in red and labelled A in the figure. At these low male-biased sex ratios, guarding is eliminated. Instead multiple mating coexists with care. This steady state continues until $\rho > 1.47$ (for the given parameters of care and theft used for Figure 2.11). At this point, the red steady state becomes unstable, and the solution instead approaches the stable steady state corresponding to guarding persistence with a small proportion

of multiple maters coexisting, labelled B and shown in black. There is a small region of bistability for multiple maters and carers (between $\rho \in [1.2, 1.47]$) where the stable steady-state is dependent on the initial conditions of these populations. The green steady state here corresponds to negative values for searching and guarding and are therefore unrealistic solutions, labelled C.

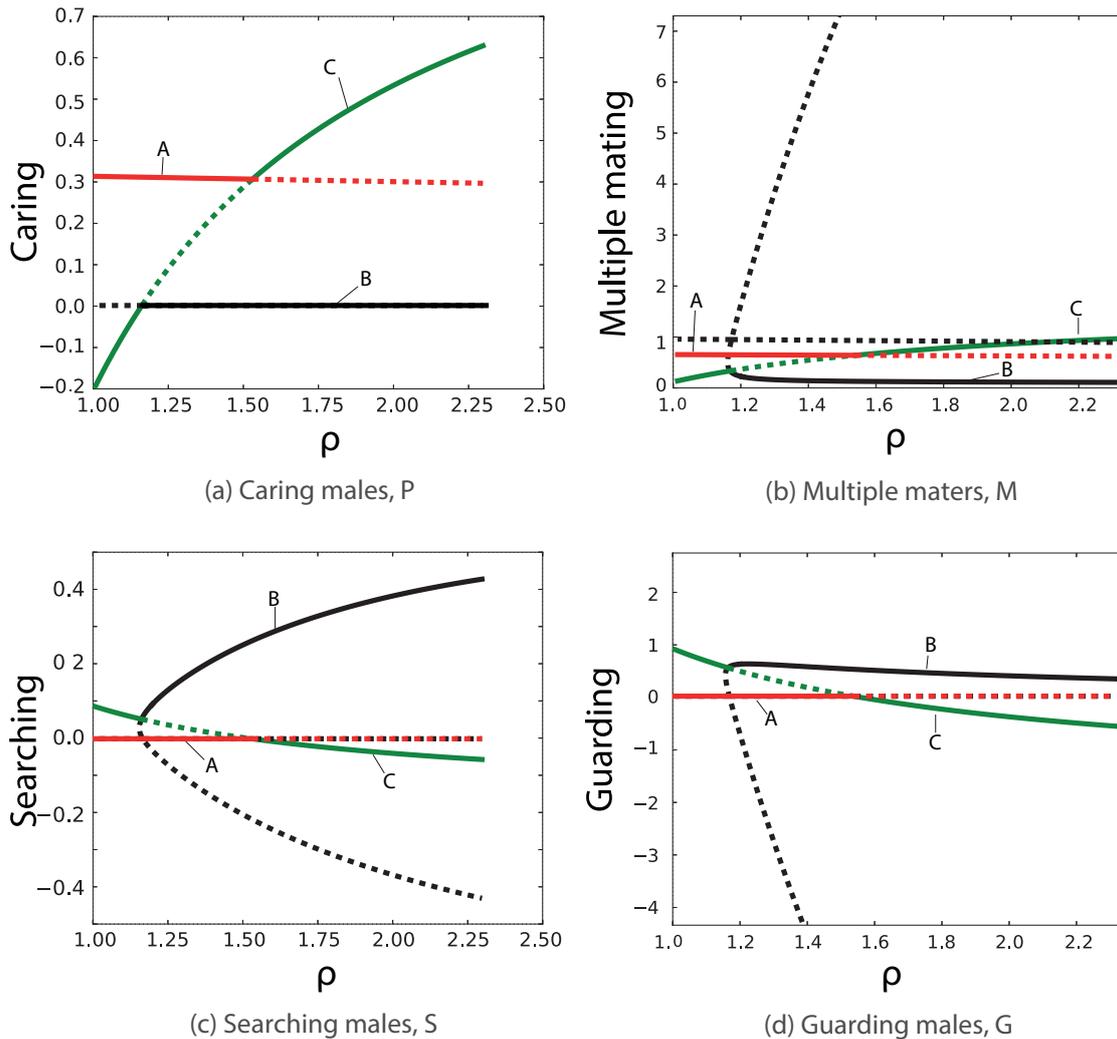


Figure 2.11: Bifurcation diagrams of the ODE system as the sex ratio, ρ , changes. Dashed lines correspond to unstable steady states, and solid lines to stable steady states. Steady states are given in red, green and black, corresponding to equivalent steady states. The steady state labelled A corresponds to care persistence at low male-biased sex ratios; B corresponds to guarding persistence with a small proportion of multiple maters coexisting; C corresponds to a negative solution and is therefore disregarded.

As in the female-biased case, I present an example steady state obtained through numerical simulation. I use parameter values given in Table 2.3 for a male-biased sex ratio $\rho = 1.4$. While analytic solutions for male-biased populations cannot be determined, numerical simulations show the existence of one equilibrium point at a large P value of 0.74, and another stable state corresponding to extinction of the paternal-care strategy. Three numerical solutions of the three steady states are given below.

Steady-State Solution with (P, M, S, G)	Eigenvalues	Stability
(0, 0, 0.2947, 0.6320)	(-0.0379, -0.0425, -0.5815, -1.2577)	Stable
(0.4877, 0.1416, 0.017, 0.3007)	(0.0094, -0.0191, -0.8570, -1.0410)	Unstable
(0.7416, 0.2153, 0, 0)	(-0.0082, -0.1914, -1.1091, -1.3487)	Stable

2.3 DISCUSSION

The ODE model presented allows for further investigation of the sensitivity of male mating strategies to the sex ratio in the fertile ages. Along with other studies of both human and non-human species (Coxworth *et al.*, 2015; Fromhage *et al.*, 2005, 2007; Marlowe, 2000; Marlowe and Berbesque, 2012; Schacht and Bell, 2016), the model provides further evidence for the proposal that pair bonding becomes advantageous to males as populations shift towards male-biased ASRs. The ODE model has shown that where there is an excess of available females, multiple mating and/or paternal care take over the population. Care performs better than multiple mating when theft of paternities from carers is low (high k_P). This may be a result of implicitly assuming that care incorporates guarding and its benefits. Alternatively, when available females are scarce, searching and guarding take over the male population, though, depending on the effectiveness of guarding, multiple maters can coexist with guarders.

Dependant care, and the risk of paternity theft, poses a form of the social dilemma as proposed by Tullock (1974). If effort devoted to care cannot be devoted to deterring other males from stealing this paternity, then paternity is not certain. Allowing a pro-

portion of paternities, k_P , to be certainly that of a carer, is a form of guarding. Care only triumphs in a range of ASRs close to 1, and when k_P is anything other than 0, further emphasising the importance of guarding strategies.

Across sexual reproducers, male gametes are smaller and more abundant, but the number of possible conceptions can be no more than the number of female gametes, which are larger and fewer in number (the Fisher Condition, Fisher, 1930). This defining difference between the sexes, anisogamy, is enough to make traits that increase success at mating competition evolve more easily in males than in females (Lehtonen *et al.*, 2016). Further differences between the sexes that evolved in our mammalian lineage, including internal gestation and lactation in females, add to the differential benefits to males for multiple mating.

The human habit of pair bonding is among the striking contrasts between us and most other mammals including our closest living relatives in genus *Pan* (Chapais, 2009). The origins of this pair-bonding habit have long been attributed to fitness benefits from paternal care (e.g. Lancaster and Lancaster, 1983), but explanations that attribute the origins of pairing to such benefits are increasingly found to be unsatisfactory (e.g. Lukas and Clutton-Brock, 2013). Attention to mate guarding instead (e.g. Hawkes *et al.*, 1995), especially to the important effects of mating sex ratios on the relative success of alternative male strategies (e.g. Blurton Jones *et al.*, 2000; Coxworth *et al.*, 2015; Schacht *et al.*, 2014; Schacht and Bell, 2016), appears an especially promising approach.

Initial contributions to understanding how male strategies vary with competitive context considered searching versus guarding (Grafen and Ridley, 1983; Parker and Stuart, 1976). Many subsequent models then ignore mate guarding as a strategic choice and focus only on the alternative strategies of multiple mating or paternal care (Gross, 2005; Kokko and Jennions, 2003; Kokko and Rankin, 2006; Kokko, 2008; Winkler, 1987). Schacht and Bell (2016) propose that a male bias in mating sex ratios favoured mate guarding as the pathway by which human pair bonding evolved. Following from work on the grandmother hypothesis in Kim *et al.* (2014), Coxworth *et al.* (2015, p.11810)

focused on this shift to male-biased mating sex ratios that accompanied the evolution of our grandmothering life history, and emphasised the importance of "this mate-guarding hypothesis [as] an alternative to long favoured arguments that pairing evolved in our lineage as a consequence of the benefits of cooperative parenting".

The ODE model developed here provides further evidence of this promise, hence demonstrating the effectiveness of mate guarding as a pathway to pair bonding in situations where multiple maters can easily claim paternities from the mates of their caring counterparts, and to a lesser extent, a fraction of paternities from guarded females. It also shows the potential for multiple maters to survive on the paternities of offspring from guarded pairs when guarding is not perfectly effective. When guarders cannot ensure the paternities of their mates with complete certainty, a small proportion of multiple maters can coexist with guarders. This supports the results of Schacht and Bell (2016) and adds the insight that guarding efficiency is important in determining winning strategies.

The magnitude of the change in sex ratio entailed in the evolution of human life history as proposed in the grandmother hypothesis (Coxworth *et al.*, 2015) is more than sufficient to allow mate guarding to take over populations, provided that guarding is close to fully efficient.

Developing this analogous ODE allows for a more thorough analysis of parameter regions within which each distinctive strategy persists. In particular, this allows for the investigation of the effect of sex ratio on steady states. As the sex ratio increases from a female-biased ape-like ASR, the benefits of mate guarding increase. The chance of obtaining a paternity through non-guarding strategies decreases with growing scarcity of fertile females.

The critical region of ρ where a transcritical bifurcation exists is around the sex ratio of modern day hunter-gatherers and is therefore especially significant. Thus, the results of our ODE model are consistent with the hypothesis that pair bonding is a

consequence of mate guarding given that it increases a male's probability of paternity in the presence of a particularly male-biased sex ratio. However, it has also shown that multiple maters can survive in the population. An alternative model of these male reproductive strategies is developed and analysed in Chapter 3.

A DIFFERENCE EQUATION MODEL OF MALE REPRODUCTIVE
STRATEGIES AND SEX RATIOS, WITH AN INVESTIGATION OF
INEFFECTIVE GUARDING

3.1 INTRODUCTION

As noted in Chapter 2, male mating strategies have been modelled within the literature (Fromhage *et al.*, 2007; Grafen and Ridley, 1983; Gross, 2005; Kokko and Jennions, 2003; Kokko and Rankin, 2006; Kokko, 2008; Kokko and Jennions, 2008; Marlowe and Berbesque, 2012; Winkler, 1987). This chapter presents a difference equation model of the three strategies considered in Chapter 2: multiple mating, paternal care and mate guarding. By employing a difference equation model, I develop a system in which the assumptions are more aligned with anthropological and ethnographic observations and hypotheses. I re-examine the assumptions implicit in the ODE and recursion models (Loo *et al.*, 2017b; Schacht and Bell, 2016) and explicitly define events that can occur in each mating period to further investigate the effect of adult sex ratio and guarding effectiveness on male mating strategies.

Definitions of both pair bonding and social monogamy vary throughout the literature (Komers and Brotherton, 1997; Lukas and Clutton-Brock, 2013). Some researchers restrict the category of pairing species to cases where pairs or families are not embedded in larger social groups. For simplicity, this chapter presents a model that ignores these issues and considers pairs existing within larger populations. Even with these simplifications that reduce the strength of guarding, it is shown that guarding still outcompetes other male strategies when sex ratios are sufficiently male-biased.

Variation in the success of male mating strategies depends on the number of competitors (Parker, 1974; Parker and Stuart, 1976). Evolutionary biologists have focused their attention on the importance of the sex ratio in the fertile ages which are conventionally labelled as the adult sex ratio (ASR) since most animals are fertile throughout adulthood (Coxworth *et al.*, 2015; Kokko and Jennions, 2008; Marlowe and Berbesque, 2012; Schacht and Borgerhoff Mulder, 2015; Schacht and Bell, 2016). But such lifelong fertility is not the case for human females whose fertility ends at about the same age that fertility ends in other great ape females. However, other great ape females display geriatric impairments while they are still fertile and usually die before reaching meno-

pause (Thompson *et al.*, 2007). In contrast, as outlined in Chapter 2, women can remain healthy and productive well beyond their fertile years even in the higher mortality regimes experienced by hunter-gatherers (Blurton Jones *et al.*, 2002; Hawkes, 2003).

I again highlight the links between sex ratio and male reproductive strategies, informed by changes that emerged out of investigations of postmenopausal longevity. The grandmother hypothesis (Hawkes *et al.*, 1998; Hawkes, 2003) proposes that postmenopausal longevity evolved in human lineage when habitats in ancient Africa became more open and ancestral populations did not follow receding forests. Savanna foods offered high return rates, but not to youngsters who were too small to handle these foods effectively. This could have resulted in higher costs to mothers, but as older females whose own fertility was declining continued to acquire and process these foods, their subsidies allowed mothers to produce more offspring sooner. According to the hypothesis, grandmothers that were ageing more slowly could subsidise more. Consequently, they left more descendants and longevity increased in subsequent generations. As longevity increased in both sexes, the physiology of sperm production carried fertility to older ages in males.

Simulations of a mathematical model of the grandmother hypothesis (Kim *et al.*, 2012, 2014) track sex ratios in the fertile ages (ASR) as grandmothing subsidies drive model populations from a great ape-like life history to a human-like one (Coxworth *et al.*, 2015). Across the transition, ASRs shift from female to male-biased. This is consistent with the notion (Coxworth *et al.*, 2015, p.11806) that "our distinctive life history... supplies previously unrecognised support for a mate-guarding hypothesis for the evolution of human pair bonds."

In this chapter, a difference equation model is developed to (i) investigate how the ASR affects the long-term equilibrium male strategy, and, (ii) explore the sensitivity of the resulting equilibrium to assumptions about the effectiveness of guarding and the magnitude of the effect of male care on dependant survival. Following and adding to the assumptions found in Schacht and Bell (2016) and the model in Chapter 2, a

discrete difference equation model is developed to explore the effects of mate guarding, the benefits of male care for dependant survival, extra-pair paternity and partner availability on the evolution of three male strategies where offspring are assumed to fully inherit the strategy of their father. Assumptions of frequency-dependent mating success follow those of Schacht and Bell (2016) and the strategies under consideration are similar to those investigated in Hawkes *et al.* (1995).

However, by employing a difference equation model, I break apart implicit assumptions made in previous models (Hawkes *et al.*, 1995; Schacht and Bell, 2016) in order to add parameters of guarding efficiencies. While these such parameters were included in Chapter 2, this difference equation model construction allows for clear, logical explanations of the assumptions. Assumptions are made explicit. Whereas Schacht and Bell (2016) only considered perfectly effective guarding, the model presented in this chapter has limits on guarding effectiveness that lead to less than perfect paternity certainty to investigate the importance of this issue in a world that is likely to include some extra-pair paternities. This is essential as the size and number of male gametes necessitate a degree of paternity uncertainty.

Since the aim of this chapter is to explore the relative payoffs of these strategies under different sex ratios in the fertile ages, the simplifying assumption of mutual exclusivity of strategies is employed. This is to ensure that effort devoted to competing for new mates cannot also be devoted to guarding a current one, nor can effort devoted to guarding a current mate be devoted to caring for her offspring. This follows from Tullock's first argument about the social dilemma (Tullock, 1974, p.9). Noting that "theft is the oldest labour saving device," Tullock invites readers to "... consider a society in which theft is completely unrestricted, i.e., no resources of any sort are devoted to preventing theft. ... under these circumstances, it is almost always true that the most highly profitable "investment" of resources is to take something from your neighbour". In addition to assuming mutual exclusion, the possibility of strategy switching is ignored to investigate the relative pay-offs of static, pure strategies depending on the ASR. The steps of the model are outlined below.

3.2 MODEL

A difference equation model is employed to explore the effects of pair bonding, mate stealing, and partner availability on male reproductive strategies. In particular, I explore the effect of guarding efficiency on equilibrium behaviours. The compartments of different male strategies follow that of Chapter 2 and are dependant care, P ; multiple mating, M ; and mate guarding, separated into two compartments — those who are actively searching for a female to guard, S , and those who are currently guarding a female, G . This allows the tracking of the number of guarded pairs and the number of actively searching males, who directly compete with multiple maters and caring males for paternities. Searching males, S , do not produce offspring at a given time, while guarding males, G , either produce offspring with their pairs or transition back to searching if pairs break up. The population of available unguarded females is denoted by F and, since only social monogamy is modelled, G also represents the number of guarded females.

The full difference equation system is given by

$$\begin{aligned}
 P(t + \Delta t) &= (1 - \mu_{A,m})P(t) + \frac{b}{2}(1 - \mu_{C,m})^{1-c}(1 - \mu_{A,f})B_P(\mathbf{X})(1 - k_P), \\
 M(t + \Delta t) &= (1 - \mu_{A,m})M(t) + \frac{b}{2}(1 - \mu_{C,m})(1 - \mu_{A,f}) [B_M(\mathbf{X}) + B_S(\mathbf{X})k_G] \\
 &\quad + \frac{b}{2}(1 - \mu_{C,m})^{1-c}(1 - \mu_{A,f})B_P(\mathbf{X})k_P, \\
 S(t + \Delta t) &= (1 - \mu_{A,m}) [S(t) + \beta G(t) - B_S(\mathbf{X})] + \mu_{A,f}(1 - \mu_{A,m}) [G(t) - \beta G(t) + B_S(\mathbf{X})] \\
 &\quad + \frac{b}{2}(1 - \mu_{C,m})(1 - \mu_{A,f}) [G(t) - \beta G(t) + B_S(\mathbf{X})], \\
 G(t + \Delta t) &= (1 - \mu_{A,m})(1 - \mu_{A,f}) [G(t) - \beta G(t) + B_S(\mathbf{X})], \\
 F(t + \Delta t) &= (1 - \mu_{A,f}) [F(t) + \beta G(t) - B_S(\mathbf{X})] + \mu_{A,m}(1 - \mu_{A,f}) [G(t) - \beta G(t) + B_S(\mathbf{X})] \\
 &\quad + \frac{b}{2} \{ (1 - \mu_{C,f})(1 - \mu_{A,f}) [G(t) - \beta G(t) + B_S(\mathbf{X}) + B_M(\mathbf{X})] \\
 &\quad + (1 - \mu_{C,f})^{1-c}(1 - \mu_{A,f})B_P(\mathbf{X}) \},
 \end{aligned}$$

where $B_a(\mathbf{X})$ represents the birth function of each searching strategy $a = P, S, M$ and

$\mathbf{X} = (P, M, S, G, F)$ is the vector of all population groups. The constant b is the birth rate per year and is a measure of female fecundity. The care benefit to survival, c , applies to the offspring of carers. The proportion of paternities stolen from strategies P and G by multiple maters are given by k_P and k_G respectively. The probability of death, $\mu_{i,j}$, is defined separately for age class $i = A, C$ adults or children, of sex $j = m, f$ males or females. This allows for sex-specific removal rates to drive biases in sex ratio. Pair-bond breakup is also allowed at a constant proportion β . These parameters are summarised in Table 3.1.

Parameter	Interpretation	Value
r_A	Adult mortality rate	0.02
r_C	Immature mortality rate	0.03
σ	Removal rate ratio	Between 0 and 2
$\mu_{A,f}$	Probability of female adult mortality/removal	$(1 - \exp[-r_A \sigma \Delta t])$
$\mu_{A,m}$	Probability of male adult mortality/removal	$(1 - \exp[-r_A \Delta t])$
μ_C	Probability of immature mortality	$(1 - \exp[-r_C \Delta t])$
b	Birth rate	1
c	Extent of care benefit to survival	Between 0 and 1
β	Proportion of random pair-bond breakup	Between 0 and 1
ϵ_P	Availability of cared offspring to theft	Between 0 and 1
k_P	Proportion of cared paternities stolen	$\frac{\epsilon_P M}{1 + \epsilon_P M}$
ϵ_G	Ineffectiveness of guarding against extra-pair paternities	$\epsilon_G \leq \epsilon_P$ and between 0 and 1
k_G	Proportion of guarded paternities stolen	$\frac{\epsilon_G}{1 + \epsilon_G M}$
Δt	Time-step	10

Table 3.1: Summary of parameters used within the difference equation model, their interpretation and baseline values, or corresponding equations.

Within the difference equation system, a series of events occur at each time step, Δt . Let X_n be the population size of a given compartment X at a certain time $t = n\Delta t$. To determine the dynamics at each time step, let $X_{n,i}$ be the population size of X at each sub-step $i = 1, 2, 3, 4$ during Δt where each sub-step is ordered sequentially as shown below:

1. Breaking pair bonds,
2. Mating events,
3. Death,
4. Offspring become adults.

In order to transition from $t = n\Delta t$ to $t = (n + 1)\Delta t$, sub-steps occur in order with the final sub-step, $i = 4$, corresponding to the next time step $t = (n + 1)\Delta t$. I note that the order of the system is the most sensible order of events. Proceeding through the system in an alternate order defines a different model to the system above, resulting in perturbations in the results. However, the qualitative effect of ASR remains unchanged. The difference equations for each sub-step are described in detail as follows.

3.2.1 *Pair-bond breakup*

I assume that a constant proportion of pair-bond breakup occurs at sub-step $i = 1$. As a result of this breakup, guarding males return to the searching compartment and females return to eligibility. Multiple-mating and caring populations remain unchanged. Thus,

$$P_{n,1} = P_n,$$

$$M_{n,1} = M_n,$$

$$S_{n,1} = S_n + \beta G_n,$$

$$G_{n,1} = G_n - \beta G_n,$$

$$F_{n,1} = F_n + \beta G_n.$$

Breakup occurs due to random effects parametrised by the constant β . This can be interpreted in terms of a male deciding to search for a different female, or a female choosing to leave. However, following from Hawkes *et al.* (1995) I emphasise the interpretation of male-male competition, such that pairs may break up when males defer to their higher status counterparts.

3.2.2 Mating

At each sub-step $i = 2$ males search for potential mates. Guarding males not in a pair search for a female to guard, while multiple-mating males and paternal carers search for females continually. The number of females found by a male of strategy α is defined by a birth function $B_\alpha(\mathbf{X})$ and $\mathbf{X} = (P, M, S, G, F)$ is the population vector. This is defined separately for male-biased and female-biased populations.

Firstly, for female-biased populations, I assume that caring and guarding males have priority over multiple-mating males in securing mates. Since only social monogamy is considered, once carers and guarders have successfully paired with females, the remaining females are then assigned to multiple maters. The birth functions in the female-biased case are then given by

$$B_P(\mathbf{X}) = P,$$

$$B_S(\mathbf{X}) = S,$$

$$B_M(\mathbf{X}) = F - P - S.$$

Birth function, $B_a(\mathbf{X})$	Value when female-biased	Value when male-biased
$B_P(\mathbf{X})$	P	$F \frac{P}{\hat{M}}$
$B_S(\mathbf{X})$	S	$F \frac{S}{\hat{M}}$
$B_M(\mathbf{X})$	$F - P - S$	$F \frac{M}{\hat{M}}$

Table 3.2: Birth function used, constructed with different frequency-dependent paternity payoffs, where $\hat{M} = P + S + M$ is the total population of actively searching males.

In male-biased populations, where females are scarce, paternities are assigned proportionally to each of the searching male strategies, P , M and S . This is given by

$$\begin{aligned} B_P(\mathbf{X}) &= F \frac{P}{\hat{M}}, \\ B_S(\mathbf{X}) &= F \frac{S}{\hat{M}}, \\ B_M(\mathbf{X}) &= F \frac{M}{\hat{M}}. \end{aligned}$$

These approximations of the birth function are summarised in Table 3.2.

During this mating sub-step, searching and guarding adult populations are adjusted based on the number of new pairs formed in this time step. When searching males find a female with whom to pair, they move to the guarding population and the female is removed from the eligible female population $F_{n,1}$. Thus, the recursion for adults in this sub-step is

$$\begin{aligned} P_{n,2} &= P_{n,1}, \\ M_{n,2} &= M_{n,1}, \\ S_{n,2} &= S_{n,1} - B_S(\mathbf{X}), \\ G_{n,2} &= G_{n,1} + B_S(\mathbf{X}), \\ F_{n,2} &= F_{n,1} - B_S(\mathbf{X}). \end{aligned}$$

During this mating sub-step, dependants are then born to each strategy. These offspring populations are defined by $C_{n,2}^j$, where $j = P, M, G$ is the strategy of the father,

taking the simplifying assumption of patrilineal inheritance. Offspring are born based on $B_\alpha(\mathbf{X})$, the number of females found by males of the given strategy α , and the availability of paternities to being stolen by multiple maters. A proportion k_α of paternities are stolen by multiple maters from males of strategy α . Thus, the offspring of carers is given by

$$C_{n,2}^P = bB_P(\mathbf{X}_{n,1})(1 - k_P),$$

where b is the probability that a female gives birth in this time step and k_P is the proportion of paternities stolen from paternal carers by multiple maters.

The paternities belonging to guarders is similarly given by

$$C_{n,2}^G = bG_{n,2}(1 - k_G),$$

where k_G is the proportion of paternities stolen from guarders due to imperfect guarding.

The offspring of multiple maters are broken down into $C_{n,2}^{M,P}$ and $C_{n,2}^{M,G/M}$, which denote paternities stolen from carers and thus subject to the benefit of care, and offspring born to unpaired multiple maters or stolen from guarding pairs and thus receiving no care benefit, respectively. The offspring born to multiple maters are given by

$$\begin{aligned} C_{n,2}^{M,P} &= bB_P(\mathbf{X}_{n,1})k_P, \\ C_{n,2}^{M,G/M} &= bB_M(\mathbf{X}_{n,1}) + bG_{n,2}k_G, \end{aligned}$$

where b , k_P and k_G are defined as above.

In order to determine the proportion k_α of paternities stolen from males of given strategy α , I define $\epsilon_\alpha \in [0, 1]$ as the relative availability of females to being taken by multiple maters over their partners from strategy α . The paternities of the offspring of a given female are fully susceptible to theft when $\epsilon_\alpha = 1$, meaning multiple maters

have the same chance of mating with a particular female as her partner, and completely unavailable when $\epsilon_a = 0$. Thus, the proportion of paternities k_a stolen from males of strategy a is given by

$$k_a = \frac{\epsilon_a M}{1 + \epsilon_a M}. \quad (3.1)$$

This is a simplification of the cuckoldry term used in Schacht and Bell (2016) that was described in detail in Chapter 2, Equation (2.8).

An alternative interpretation of the availability of the paternities of guarded females to being stolen by multiple maters, ϵ_G , is that it indicates guarding efficiency. If ϵ_G is high, this corresponds to low guarding efficiency, and therefore, larger proportions of paternity theft. The term $(1 - \epsilon_G)$, therefore, can be interpreted as guarding effectiveness.

3.2.3 *Death (or removal)*

Death occurs at sub-step $i = 3$. Paternal-caring and multiple-mating populations are updated by

$$\begin{aligned} P_{n,3} &= (1 - \mu_{A,m})P_{n,2}, \\ M_{n,3} &= (1 - \mu_{A,m})M_{n,2}, \end{aligned}$$

where the constant $\mu_{A,m}$ corresponds to the adult male probability of death, and thus, survival is given by $(1 - \mu_{A,m})$.

In the case of searching and guarding males, in addition to considering individual survival, it is also necessary to consider what happens if one's mate dies. If the female mate of a guarder dies, the male returns to searching for a new mate and, similarly, if

the guarder dies, his mate returns to eligibility. Searching, guarding and eligible female populations are therefore updated by

$$\begin{aligned}
 S_{n,3} &= \underbrace{(1 - \mu_{A,m})}_{\text{Surviving searchers}} S_{n,2} + \underbrace{\mu_{A,f}}_{\text{Guarded female dies}} \underbrace{(1 - \mu_{A,m})}_{\text{Guarding male survives}} G_{n,2}, \\
 G_{n,3} &= \underbrace{(1 - \mu_{A,m})}_{\text{Guarding male survives}} \underbrace{(1 - \mu_{A,f})}_{\text{Guarded female survives}} G_{n,2}, \\
 F_{n,3} &= \underbrace{(1 - \mu_{A,f})}_{\text{Eligible female survives}} F_{n,2} + \underbrace{(1 - \mu_{A,f})}_{\text{Guarded female survives}} \underbrace{\mu_{A,m}}_{\text{Guarding male dies}} G_{n,2}.
 \end{aligned}$$

For the searching population, the first term corresponds to the surviving fraction of searching males, and the second term to surviving guarding males whose females have died and who therefore return to the searching compartment. For the guarding population, the survival of both the guarding male and the guarded female are accounted for. Further, for the female population, the first term calculates the surviving fraction of eligible and unpaired females, and the second term reintroduces surviving females whose guards have died.

The terms defining the probability of death $\mu_{i,j}$ for age class $i = A, C$, adults or children, and of sex $j = m, f$, male or female, are obtained by assuming an exponential distribution based on mortality rates r_A for adults and r_C for offspring.

To obtain variable sex ratios other than equal, I vary the removal rate of adult females. This removal rate could be a result of higher or lower mortality than males, or females reaching the end of fertility. The difference between $\mu_{A,m}$ and $\mu_{A,f}$ determines the extent of bias in the equilibrium adult sex ratio. The probabilities of removal in time step Δt are given by

$$\begin{aligned}
 \mu_{A,m} &= 1 - \exp[-r_A \Delta t], \\
 \mu_{A,f} &= 1 - \exp[-r_A \sigma \Delta t],
 \end{aligned}$$

where σ is the removal rate ratio. The adult male probability of removal or death, $\mu_{A,m}$ is given as constant, and the female removal is adjusted by the ratio σ . With these sex-specific mortalities, the ASR at equilibrium can take values other than 1. Figure 3.1 shows the dependence of the ASR at equilibrium on the removal rate ratio, σ . For $\sigma = 1$, the equilibrium ASR is balanced at $1/2$, and as σ increases or decreases, the ASR shifts from male-biased to female-biased, respectively. As σ approaches 0, the female population increases to infinity. At this strength of female-bias, the benefit of multiple mating far outweighs other strategies. Due to the overwhelming excess of females and the assumption that multiple maters will be able to mate with all available females, the population is maintained at an ASR around 0.35. Thus, as can be seen in Figure 3.1, as σ approaches 0, the equilibrium ASR does not similarly go to 0.

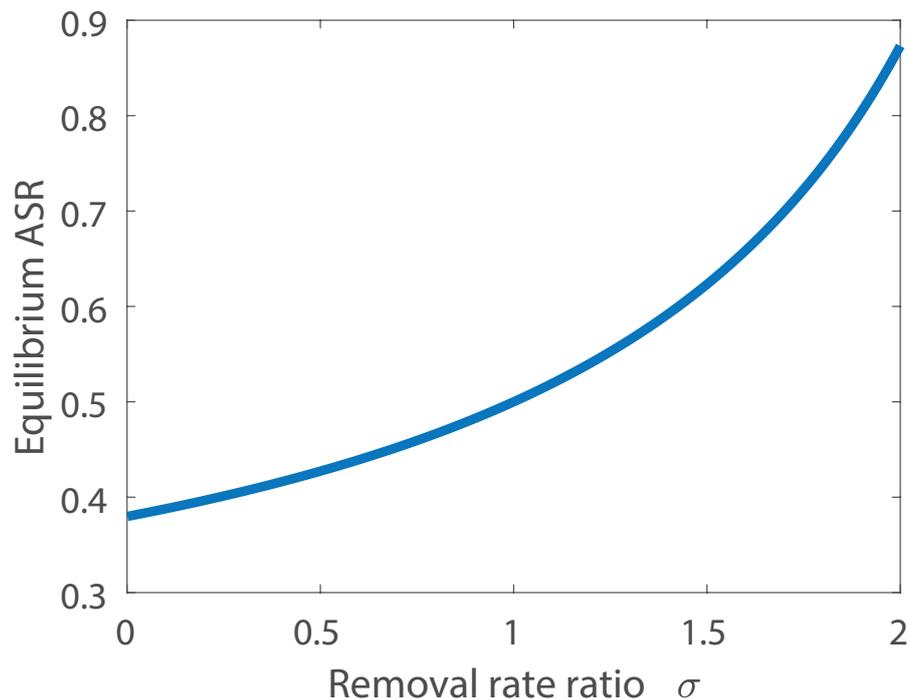


Figure 3.1: The effect of the removal rate ratio σ on the ASR at equilibrium.

Juveniles are subject to offspring mortality rates and their survival is further dependent on the survival of their mother. If a dependant's mother dies, the dependant also dies. Juvenile populations are given by

$$\begin{aligned}
 C_{n,3}^G &= \underbrace{(1 - \mu_C)}_{\text{Offspring survives}} \underbrace{(1 - \mu_{A,f})}_{\text{Mother survives}} C_{n,2}^G, \\
 C_{n,3}^P &= \underbrace{(1 - \mu_{PC})}_{\text{Offspring survives with care benefit}} \underbrace{(1 - \mu_{A,f})}_{\text{Mother survives}} C_{n,2}^P, \\
 C_{n,3}^M &= \underbrace{(1 - \mu_C)}_{\text{Offspring survives}} \underbrace{(1 - \mu_{A,f})}_{\text{Mother survives}} C_{n,2}^{M,G/M} + \underbrace{(1 - \mu_{PC})}_{\text{Offspring survives with care benefit}} \underbrace{(1 - \mu_{A,f})}_{\text{Mother survives}} C_{n,2}^{M,P}.
 \end{aligned}$$

The term $(1 - \mu_{A,f})$ is the survival fraction of adult females, ensuring that dependants only survive provided their mother survives. The constant μ_C is the baseline probability of death of offspring, which applies to the offspring of guarding pairs and multiple maters, who do not receive any care benefit. The constant μ_{PC} defines the probability of death of the dependants of carers. This term adjusts baseline mortality μ_C by a parameter of care benefit, $c \in [0, 1]$. Here, I define c such that $c = 0$ corresponds to equal survival of the offspring of caring males with the offspring of guarding and multiple-mating males, and $c = 1$ to the juvenile immortality of the dependants of carers. The benefit of care is restricted to the juvenile years. Investment in paternal care alters the removal rate r_C by a factor of $(1 - c)$. The survival probability of those who obtain survival benefits from care can be described in terms of μ_C by the following:

$$\begin{aligned}
 \text{Survival probability with care benefit} &= 1 - \mu_{PC} \\
 &= 1 - (1 - \exp[-r_{PC}\Delta t]) \\
 &= \exp[-r_c(1 - c)\Delta t] \\
 &= (\exp[-r_c\Delta t])^{1-c} \\
 &= (1 - \mu_C)^{1-c}.
 \end{aligned}$$

3.2.4 Offspring become eligible

This sub-step corresponds to children maturing to become eligible adults. Half of each child compartment surviving at sub-step $i = 3$ move to adult male compartments, and the other half become adult females to ensure equal sex ratio at birth, since juvenile mortality is not sex-specific. Full strategy inheritance is assumed, which means that offspring follow the strategy of their paternal fathers. The difference equations are

$$\begin{aligned} P_{n+1} &= P_{n,3} + \frac{1}{2}C_{n,3}^P, \\ M_{n+1} &= M_{n,3} + \frac{1}{2}\left(C_{n,3}^{M,P} + C_{n,3}^{M,G/M}\right), \\ S_{n+1} &= S_{n,3} + \frac{1}{2}C_{n,3}^G, \\ G_{n+1} &= G_{n,3}, \\ F_{n+1} &= F_{n,3} + \frac{1}{2}\left(C_{n,3}^P + C_{n,3}^{M,P} + C_{n,3}^{M,G/M} + C_{n,3}^G\right), \end{aligned}$$

which become the population values of the next time step.

Differences between this model, the recursion model presented in Schacht and Bell (2016) and the ODE described in Chapter 2 are outlined in Table 3.3.

3.2.5 Parameter estimates

Simulations are run with a time step of 10 years, $\Delta t = 10$ years, in order to capture an average of one offspring per female per time step. This takes into account weaning time and child dependency and allows offspring to mature sexually before entering eligibility. This time step follows the implicit choice of time step given in Schacht and Bell (2016), where females produce one offspring per time step, unless cared for, where they can produce up to $(1 + c)$ offspring. A continuous model will remove problems that arise from this lengthy time step, but requires a more complicated age structure that is beyond the scope of this chapter. Further, birth rate, b , is defined as 1 offspring

per time step. Mortality rates are chosen as adult mortality rate, $r_A = 0.02$, which is adjusted by sex to impose variations in ASR, and immature mortality rate, $r_C = 0.03$, which is adjusted by care.

Figure 3.2 illustrates the processes in the model described above, and Table 3.1 lists the parameters used. Dynamics are simulated in MATLAB and the resulting frequencies of equilibrium strategies for populations compared. An extensive numerical sensitivity analysis is presented in Appendix B, however I summarise these results in the following sections.

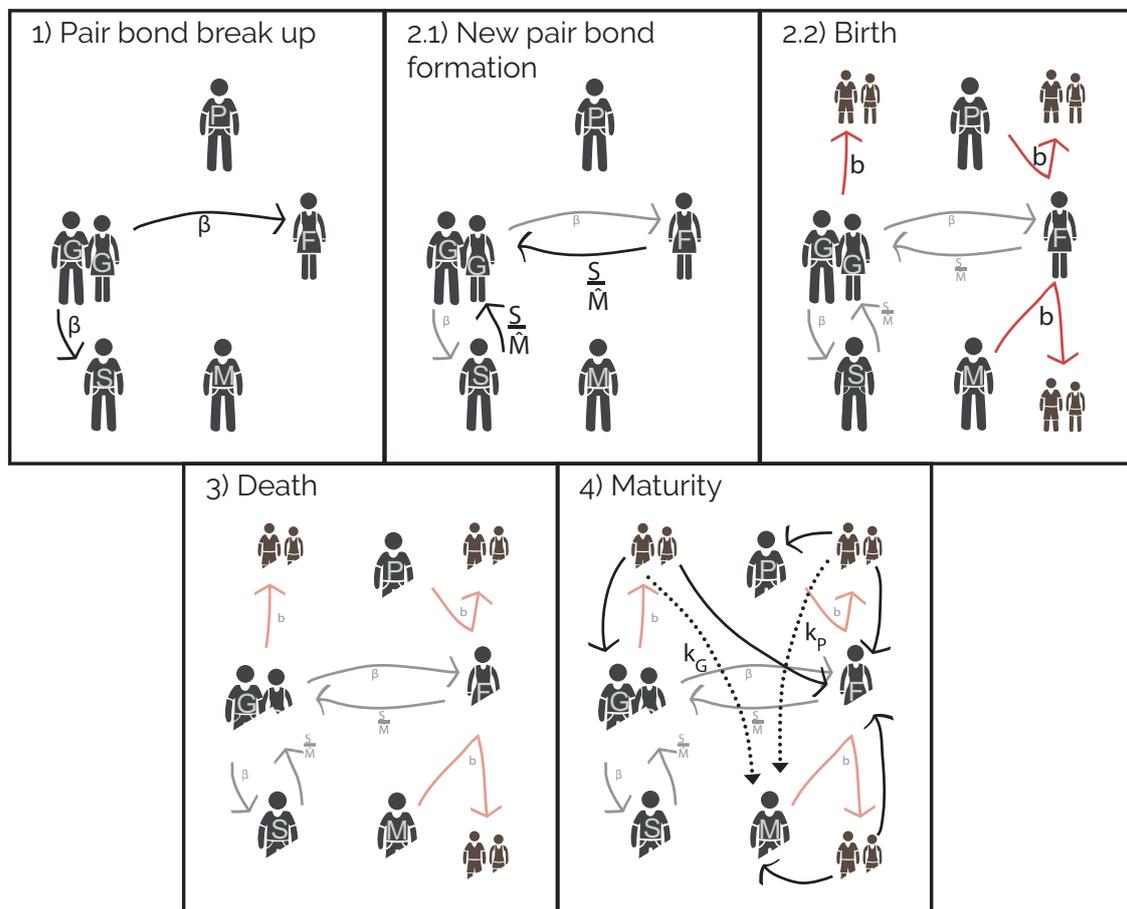


Figure 3.2: Flow chart outlining the steps of the difference equation model described in Section 3.2.

Parameter	Assumption		
	Schacht and Bell (2016) recursion model	Chapter 2 ODE model	Difference equation model
Care, c	Care increases the birth rate of females, resulting in a greater number of surviving offspring. Females can have one to two surviving offspring per time step.	Care benefits juvenile survival. Females have a maximum of b offspring per time step and survival is dependent on her mate's strategy.	Care benefits juvenile survival. Females have a maximum of b offspring per time step and survival is dependent on her mate's strategy.
Theft of paternities from caring males, k , k_P or ϵ_P	Cuckoldry, k , of the paternities of only paternally caring males by multiple-mating males.	k_P is the rate of conception with caring males; $(1 - k_P)$ is the proportion of the offspring of carers sired by multiple maters.	ϵ_P defines relative female availability of paternities to theft by multiple maters, with k_P defining the proportion of the offspring of carers sired by multiple maters.
Theft of paternities from guarding males, ϵ_G or k_G	No theft. Guarding provides eternal pairs, and paternity certainty.	k_G is the rate of conception with guarding males; $(1 - k_G)$ is the proportion of the offspring of guarders sired by multiple maters. $k_G > k_P$	ϵ_G defines relative female availability of paternities to theft by multiple maters, with k_G defining the proportion of the offspring of carers sired by multiple maters. $\epsilon_G < \epsilon_P$.
Pair-bond breakup, β	Pairs remain together until death.	Guarding pairs break up at a constant rate.	Guarding pairs break up at a constant rate.
Survival	Offspring survival not explicitly modelled. Adult mortality equal for males and females, u .	Offspring survival adjusted by care. All other baseline mortalities equal.	Offspring survival adjusted by care. Male and female removal adjusted by sex ratio.

Table 3.3: Table summarising and comparing assumptions and parameters used within the recursion developed by Schacht and Bell (2016), the ODE model in Chapter 2 and the difference equation model developed here.

3.3 EFFECT OF CHANGING ASR ON THE FREQUENCY OF MALE STRATEGIES

As noted in Section 3.1, a shift in ASRs from female- to male-biased accompanies the transition from a great ape-like life history to a human-like one. Thus, it is of special interest to consider the effect of ASRs within this range on male reproductive strategies. In particular, I investigate equilibrium behaviours at great ape-like and human-like sex ratios, taking these values from Coxworth *et al.* (2015). In this way, I again consider the links between male reproductive strategies and the grandmother hypothesis.

Population	ASR $M/(M + F)$	ASR M/F
5 chimpanzee population averages	0.32	0.47
Kanyawara chimpanzees	0.41	0.70
!Kung	0.59	1.46
Ache	0.65	1.87
Hiwi	0.62	1.62
Hadza	0.62	1.60

Table 3.4: ASR values taken from specific assumptions about fertile ages (Coxworth *et al.*, 2015), and mortality profiles calculated for specific empirical populations (see the text for further specifics). The first population is taken from a synthetic mortality schedule based on 5 different chimpanzee populations (Hill *et al.*, 2001). The second is a later, larger (although still very small) data set from one of these chimpanzee populations (Muller and Wrangham, 2014). Fertile ages include all males older than 15 years, and females between 10 and 45 years. The following populations are human hunter-gatherers as reported by (Blurton Jones, 2016; Hill and Hurtado, 1996; Hill *et al.*, 2007; Howell, 1979). Fertile ages include males 20 to 65, and females from 20 to 40. These estimates of the ASR differ from others reported (e.g. Kramer *et al.*, 2017; Schacht *et al.*, 2014); see Discussion. For the chimpanzee estimates, fertile ages "included males older than 15 years and females between ages 10 and 45 years" (Coxworth *et al.* (2015, p.11808), citing Thompson *et al.* (2007) here).

Here, in Table 3.4, ASRs are given as the proportion of males in the total fertile population as suggested by Ancona *et al.* (2017) (a ratio calculated by Coxworth *et al.* (2015), and appearing in the second column of their Tables 1 and 2), and in the third column as the more widely used ratio of fertile males to fertile females, M/F . They

(Coxworth *et al.*, 2015, p. 11808) used life tables from the sources cited and, assuming stationary populations, calculated the ASR by modelling age structure using "probability of survival to each age in the published life tables, summing the calculated number of survivors for males and females to each of the fertile ages, then dividing the sum for each sex by their combined total to get the fraction of fertile adults by sex." For chimpanzees they assumed (Coxworth *et al.*, 2015, p.11808) that fertile ages "included males older than 15 years and females between ages 10 and 45 years" (citing ref Thompson *et al.*, 2007, here). For non-humans, ASR calculation can be met with some challenges (Ancona *et al.*, 2017), but is relatively straightforward as all adult males and females can be counted as eligible for conception. For humans, fertile ages "included men from 20 and 65 years based on reported age ranges of fertilities from the ethnographers and those reported by Tuljapurkar *et al.*" (citing ref Tuljapurkar *et al.*, 2007, here). "Women from 20 to 40 years are included based on average ages of first and last birth" (citing ref Robson *et al.*, 2006, here). Issues around calculating human ASRs and alternative estimates are considered in the Discussion in this chapter.

Figure 3.3 displays the long-term equilibrium strategies of the model at a range of ASRs including representative ASRs given in Table 3.4. The four panels in Figure 3.3 show that at a chimpanzee-like female-biased ASR of 0.41 or less, multiple mating takes over the population. In fact, this is the case for all female-biased sex ratios ($ASR < 0.5$). Based on the frequency-dependent birth function (see Table 3.2) the benefit of gaining the extra paternities at such a female-biased ASR, once guarding and caring males have obtained their mates, is large enough to push the long-term equilibrium strategy to favour multiple-mating males.

Now consider a human-like male-biased ASR of 0.62, following ethnographically based estimates of the ASR of the Hadza in particular, as given in Table 3.4. In panels (a) and (b) of Figure 3.3, the guarding strategy is favoured, while in panel (c) and (d), the case of high pair-bond break and inefficient guarding, caring persists in the population. While this points to paternal care outperforming mate guarding, I note that this only occurs where pair-bond break is high, and the availability of caring is close to that

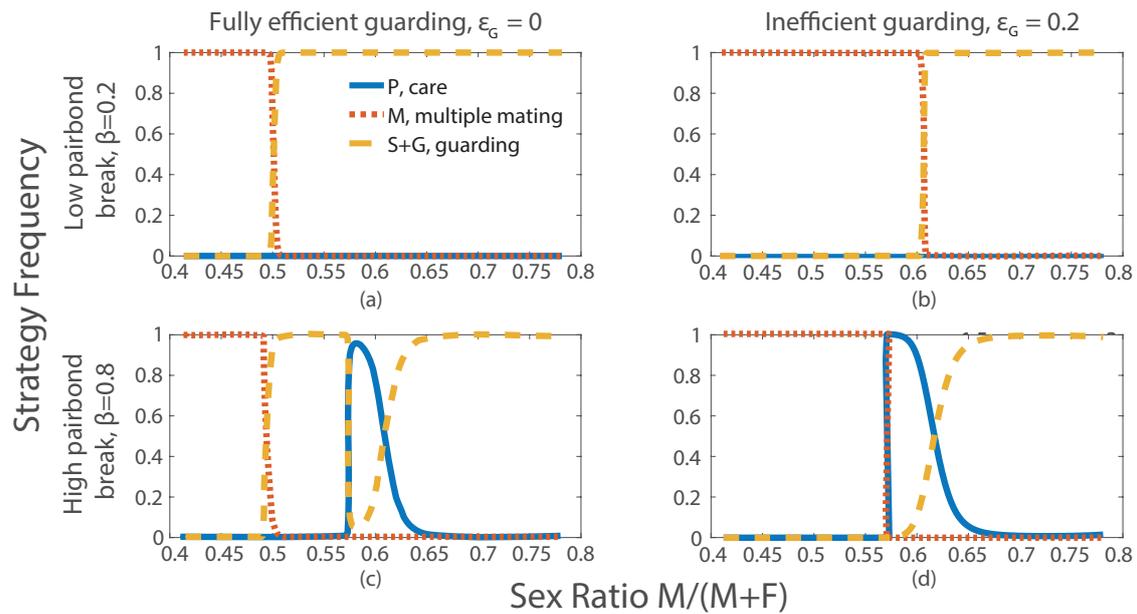


Figure 3.3: Simulations showing changes to the equilibrium strategic frequency given changes to the sex ratio, for different parameter sets, in particular showing the qualitative effect of changes in guarding efficiency, ϵ_G , and pair-bond breakup, β . Other parameters used are $c = 0.2$ (a care benefit raising juvenile survival by 20%) and $\epsilon_P = 0.2$.

of the availability of guarding. In Figure 3.3, the paternities of carers are only slightly available to theft, $\epsilon_P = 0.2$. At more male-biased ASRs, guarding still outperforms other strategies. Changes to the value of the guarding efficiency parameter define regions within which different equilibrium stable strategies can result. This is explored in Section 3.4. Overall, mate guarding takes over the population at very male-biased ASRs.

3.4 EFFECT OF LIKELIHOOD OF EXTRA-PAIR PATERNITIES

Investigating the changing frequency of strategies as parameters change reveals the sensitivity of the system to changes in the efficiency of guarding, ϵ_G . If ϵ_G is perturbed above 0, the ASR at which the population switches from multiple mating to guarding increases. This puts the ASR at which the switch occurs between 0.5 and

0.62, a range that is especially relevant when considering issues of human evolution since it includes the ASRs of human hunter-gatherer populations as shown in Table 3.4. If guarding is highly inefficient (ϵ_G close to 1) then it is possible for a population with a human-like ASR (less than 0.62) to be overtaken by multiple maters.

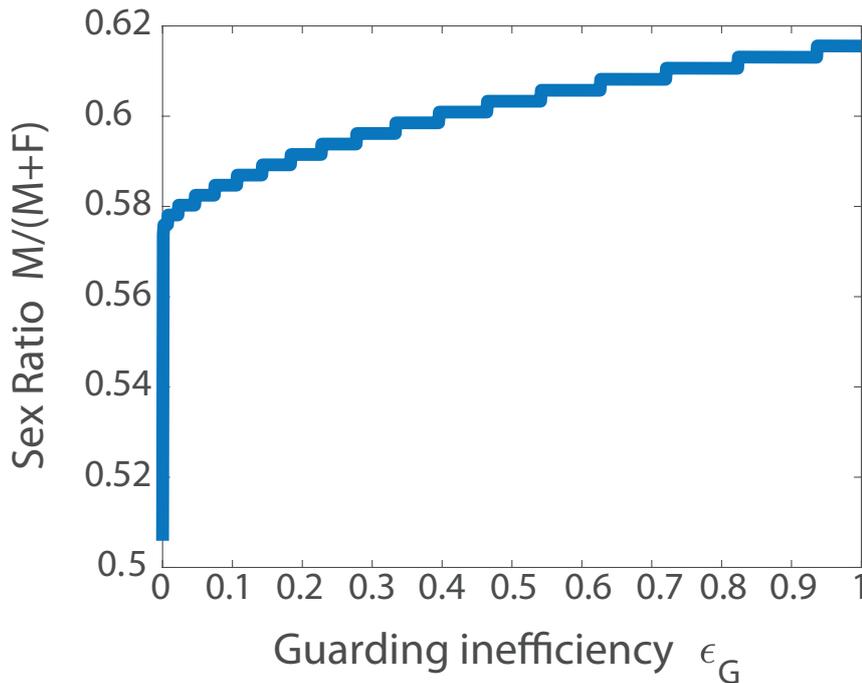


Figure 3.4: Effect of changing guarding inefficiency, ϵ_G , on the ASR at which the dominant strategy switches from multiple mating to guarding, i.e., when guarding begins to take over the population. When ϵ_G is just greater than zero, so that guarding is slightly less than perfectly effective, the ASR required for guarding to take over from multiple mating rises immediately from 0.5 to 0.57 and the takeover threshold ASR for guarding increases, becoming more male biased with decreasing effectiveness of guarding. Other parameters used are $\beta = 0.8$, $c = 0.2$ and $\epsilon_P = 1$. When $\epsilon_G = 1$, all guarded females' offspring are susceptible to extra-pair paternities by multiple-mating males, and the sex ratio at which guarding begins to take over is 0.62.

Figure 3.4 shows the effect of guarding inefficiency, ϵ_G , on the ASR at which guarding takes over the population when care, c , is low, stealing from cared mates, ϵ_P , is high, and pair-bond break, β , is high. When the paternities of the offspring of guarded females are unavailable to multiple maters, $\epsilon_G = 0$, guarders begin to take over the

population at an equal ASR, i.e., fertile $M/(M + F) = 0.5$. When ϵ_G is anything other than 0, such that guarding is anything less than perfectly effective, the ASR at which guarding takes over competing strategies is pushed to $ASR > 0.57$. As ϵ_G continues to increase and guarding becomes less effective, the ASR at which guarding takes over continues to increase. As the paternities of the offspring of guarded females become more available to multiple maters, multiple maters are able to subsidise their relatively lower chance of finding available females with their ability to steal from guarders. Thus, multiple maters can outperform other strategies at some male-biased sex ratios given that guarding is inefficient. When $\epsilon_G = 1$ the point of switch is at $ASR = 0.62$.

In the hunter-gatherer sample presented in Table 3.4 ASRs range between 0.58 and 0.65. This is the region where winning strategies depends strongly on the efficiency of guarding. Therefore, it is possible for multiple mating to persist in populations with human-like mating sex ratios as long as guarding is not perfectly effective. This shift in the point at which mate guarding takes over shows the importance of guarding efficiency in determining the winning strategy.

3.5 EFFECT OF BENEFITS TO CARE

A care benefit of $c = 0.2$ is assumed in Figure 3.3 where carers do not succeed against multiple maters or guarders. Simulations show that care only persists in the population where multiple maters get no extra-pair paternities from the offspring of the mates of carers, i.e., $\epsilon_P = 0$, and at near equal sex ratios. This can be seen in Figure 3.5(a) and (b). When multiple maters are unable to steal paternities from carers, the strategy of care outperforms other strategies at a range of ASRs. The larger the survival benefit of care (comparing panels (b) with (a) in Figure 3.5), the greater the range of ASR values at which care overcomes both multiple mating and guarding. However, once the male's dilemma is recognised and extra-pair paternities can occur, this region of care disappears. This is evident in panels (c) and (d) of Figure 3.5. Note that if no theft of paternity from carers can occur, caring effort effectively includes perfectly comprehens-

ive guarding. Otherwise, extra-pair paternity of the offspring of carers' mates should be at least possible. When there is any chance of theft, even if care results in immortal offspring, caring does not persist in the population.

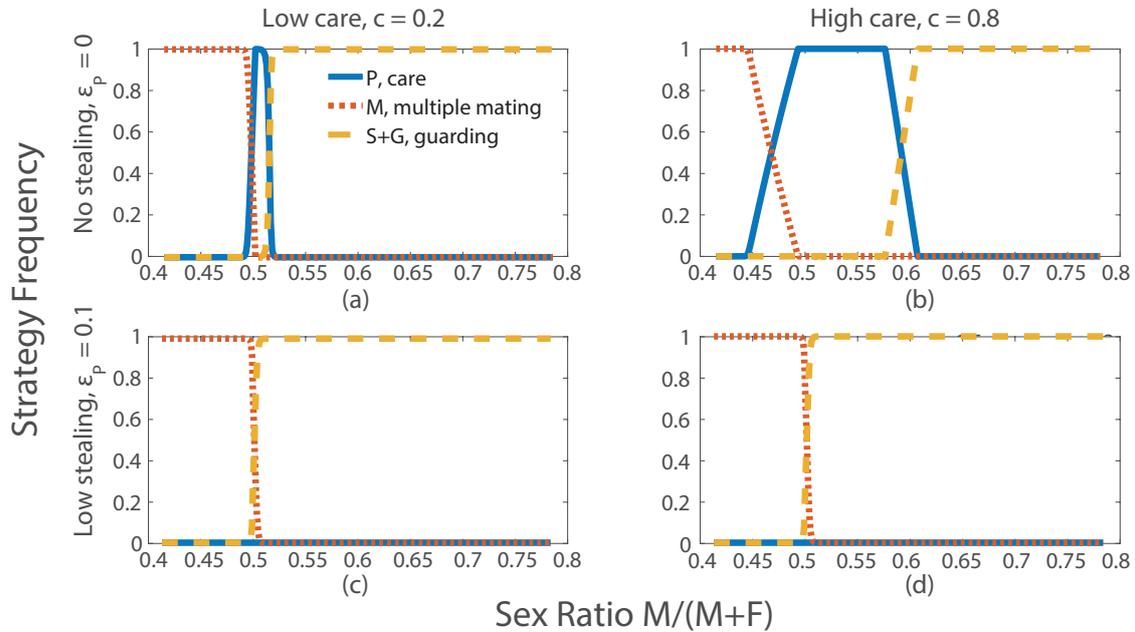


Figure 3.5: The effect of care on the equilibrium strategies given different ASRs. When there is no benefit to multiple mating, that is, when $\epsilon_P = 0$ and $\epsilon_G = 0$ in panels (a) and (b), the strategy of care can overcome other strategies, for a small range of ASRs. Once extra-pair paternity is possible, this region where care survives disappears, and even if offspring are immortal, $c = 1$, multiple mating wins at female-biased ASRs and guarding wins at male-biased ASRs. Parameters used are low pair-bond breakup, $\beta = 0.2$; and no paternities lost by guarders, $\epsilon_G = 0$. This models fully efficient guarding, as assumed by Schacht and Bell (2016).

3.6 DISCUSSION

Various mathematical models have shown paternal care to be an insufficient basis for the evolution of pair bonding (Loo *et al.*, 2017b; Schacht and Bell, 2016). Regardless of the magnitude of care benefit for dependant survival (even to the point of near-immortality, as shown in Figure 3.5), as long as paternity is less than certain, male care is not a sufficient explanation for the evolution of social monogamy or pair bonding as

a male mating strategy. While there are parameter sets within which care *is* the long-term equilibrium strategy, this occurs only when carers have certain paternity. Certain paternity further implies that guarding is required for the evolution of pair bonding. Moreover, guarding is only favoured when ASRs are male biased, which highlights the importance of likely links between the male-biased ASRs that accompanied the evolution of our grandmothering life history on one hand and the evolution of pair bonding in our lineage on the other (Coxworth *et al.*, 2015). The results of the model concur with Schacht and Bell (2016) who used alternative assumptions and a different modeling approach. By breaking down the model assumptions implicit in Schacht and Bell (2016) I was able to further emphasise that care does not evolve under realistic hunter-gatherer-like parameters and also demonstrate the importance of guarding efficiency on the evolution of male reproductive strategies.

Comparing these results to those of Schacht and Bell (2016) shows that the inefficiency parameter produces similar results to reducing the probability of male survival from one period to the next, their u , described in Chapter 2. However, while the effect is similar, the interpretation is not. If a male does not survive, he will not produce offspring. This is different from a male being cuckolded, or failing to produce offspring at that time step. Further, the parameter u (in Schacht and Bell, 2016) limits the scope of both caring *and* guarding strategies. In the model presented here, parameters β and ϵ_G are used to target variation in just the mate-guarding strategy. By doing so, the high sensitivity of the model to guarding inefficiencies becomes evident. Even with reduced benefits, guarding still has overwhelming success at very male-biased sex ratios.

Previous exploration of the relative payoffs to the male strategies considered here (Hawkes *et al.*, 1995) paralleled the treatment of the social dilemma in Hirshleifer (1991), and equilibrium allocations showed very little care. Even with reduced marginal gains for additional guarding effort, Hawkes *et al.* (1995) found high allocation to guarding throughout a wide range of parameter values. The question then arises: if mate guarding is so successful in such a general model, why is it so rare in mammals? Here I show the fundamental importance of a variable Hawkes *et al.* (1995) did not con-

sider: the ASR. I found that in contrast to their results, multiple mating does not only dominate female-biased ASRs, but when guarding is even slightly inefficient, multiple mating continues to dominate in some male-biased sex ratios. This was echoed in the investigation in Chapter 2. This is a key discovery.

The results above are also different from those obtained by Gavrilets (2012), who introduced heterogeneity in males, female choice for provisioning mates, and female faithfulness to solve the male's dilemma. In his constructions, guarding disappeared early as a possible alternative. Gavrilets' conclusion about what is required in order for pair bonding to evolve differs from the results shown here of the overwhelming persistence of multiple mating even in some male-biased populations, where the paternity of carers is less than perfectly certain, as well as the likely success of guarding as a strategy at human-like mating sex ratios.

The ASR estimates used to represent humans show a substantial contrast between the female-bias in great apes and male-bias in humans. Their life table calculations are explained above (Section 3.3). Comparing those ASRs to other reports, Coxworth *et al.* (2015, p. 11809) note that, "Figure 2 in Schacht *et al.* (2014, p.217) is the most serious challenge to our characterisation of mating sex ratios as male-biased . . . [because] eight of these [fifteen] societies — more than half — have female-biased ASRs, a pattern that our model and arguments suggest is "not human." Why do the ASRs reported by Schacht *et al.* (2014) differ so much from those calculated by Coxworth *et al.* (2015) ?

Schacht *et al.* (2014, p.3-4) explain that they accumulated reports "from both published sources and personal communication. . . determined from the ethnographers' data on the number of individuals of mating age in their population. . .". Coxworth *et al.* (2015) addressed the difference by enumerating reasons that numbers of fertile males could be underestimated by ethnographers, including frequent travelling of young men that results in under-counting them, and classic cases where unmarried men were not included. They emphasise another important problem that arises in counting fertile men (or males in general) but not fertile women. This is a difficulty

implied by Darwin (1871, p.258) when, in elaborating his theory of sexual selection, he noted that "unarmed, unadorned, or unattractive males would succeed equally well in the battle for life and in leaving a numerous progeny, if better endowed males were not present."

If the measure of male fertility is realised paternities, then males that fail to win them may not be counted as competitors, even when the competitive threat they pose is an important driver of selection (e.g. the bachelor threat for equids Rubenstein (1986); Rubenstein and Hack (2004), and primates Kirkpatrick and Grueter (2010)). When old men get no more paternities because younger men out-compete them, and when unmarried men are not counted — including physiologically fertile sub adults because local conventions deem them still ineligible to marry — dynamics that play major roles in constructing and maintaining social institutions are obscured (see Rodseth (2012) and references therein).

Coxworth *et al.* (2015) fell prey to this problem when they used age-specific fertilities to exclude men under 20 from the fertile ages. So the high human sex ratios used here are still underestimates. On the other hand, Coxworth *et al.* (2015) also note that the hunter-gatherer populations investigated are all growing, which means that the stationary population assumption they used to calculate sex ratios from life tables overestimates older age classes.

Kramer *et al.* (2017) investigate a longitudinal data set for another population of hunter-gatherers to show that the stochasticity of birth sex ratios has an enormous effect on ASRs in very small populations. Pume first births are relatively early compared to other foragers. Kramer *et al.* (2017) use birth records to calculate both a beginning and end to fertilities that are notably earlier than the estimates used by Coxworth *et al.* (2015) for other foragers. The longitudinal Pume data and modelling of the year-to-year shifts in age structure incorporate attention to individual heterogeneity and show extreme annual variation. Of special interest here, it is evident that the annual ASRs range from 0.43 to 0.67, which encompasses the entire range of ASRs in our Table 3.4 from

calculations for both chimpanzees and human foragers in Coxworth *et al.* (2015). Not only does this further underscore questions about how to appraise and compare ASRs, it also raises questions about the time scale of ASR effects on behavioural strategies that are beyond the scope of this investigation.

The model and its results given in this chapter follow that of Schacht and Bell (2016) in showing that the payoffs for male strategies change with the sex ratio in the fertile ages and, as expected, that male strategies would evolve in response to the changing availability of females. Partner scarcity can make the payoff rise for protecting one's mate from competing males and, depending on its effectiveness, mate guarding can become the winning strategy. Guarding effectiveness is an important addition to the model, as it has a significant effect on the equilibrium winning strategy within the range of documented hunter-gatherer ASRs. This is of special interest for the evolution of our own lineage. Human populations everywhere include large fractions of women who are past their fertile years (Blurton Jones *et al.*, 2002; Blurton Jones, 2016; Hill and Hurtado, 1996; Howell, 1979), resulting in notably male-biased human ASRs. Such a male bias is rare among mammals and distinguishes us from our closest living relatives, the great apes, where females become frail and usually die during their fertile years (Hill *et al.*, 2001). The modelling in this chapter aligns with other work that shows pair bonds are unlikely to evolve due to the benefits of paternal care, while strengthening the hypothesis that the evolution of human grandmothing life history made pairing advantageous in the evolution of the human lineage.

APPENDIX B: FURTHER SENSITIVITY ANALYSES

Benefit of care and potential of theft from caring males

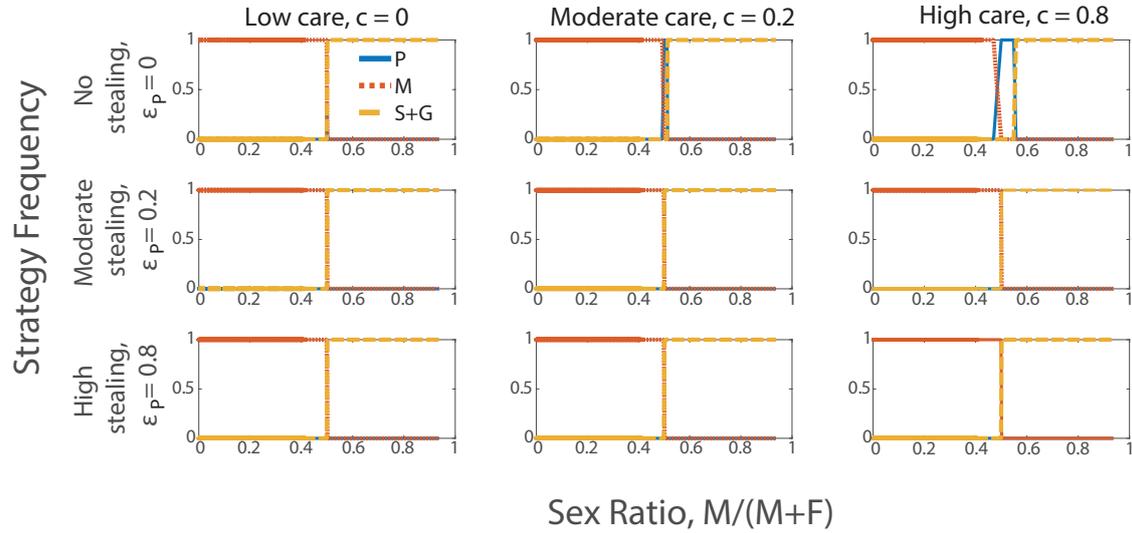


Figure B.1: The effect of different parameters of the benefit of care on the equilibrium strategies given different sex ratios, and given fully efficient guarding, $\epsilon_G = 0$, and low pair-bond breakup, $\beta = 0.1$. In the top right panel, care persists in a small region of ASRs around an equal sex ratio. In all other parameter sets, multiple mating persists at female-biased sex ratios ($ASR < 0.5$), and guarding wins at all male-biased sex ratios ($ASR \geq 0.5$).

As highlighted in the main text, care only persists in populations at near equal sex ratios, and where carers have certain paternity, stealing of paternities does not occur, i.e. $\epsilon_P = 0$. This can be seen in the top right panel of Figure B.1, where $\epsilon_P = 0$ and care persists around a near equal sex ratio. Once theft is introduced, $\epsilon_P = 0.2$ in the panel below it, this region disappears.

If inefficient guarding is introduced, comparing Figure B.1 to Figure B.2, I note that care can win at lower survival benefits than in the case of fully efficient guarding, and also in very male-biased populations. This can be seen in comparing the top row of Figure B.1 with the top row of Figure B.2. Care wins for larger regions in Figure B.2 than in the top row of Figure B.1. However, as was described in the main text, I note that

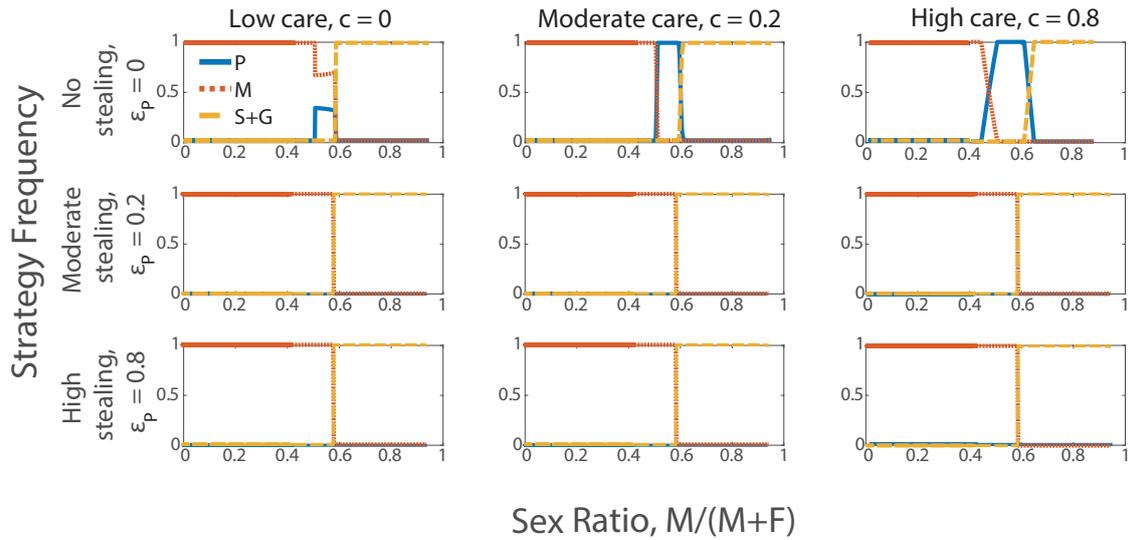


Figure B.2: The effect of different parameters of the benefit of care on the equilibrium strategies given different sex ratios, and given inefficient guarding, $\epsilon_G = 0.1$, and low pair-bond breakup, $\beta = 0.1$. Here, where theft from guarders occurs, the benefit to guarding is smaller than in Figure B.1 and thus, care persists in all cases where theft from carers does not occur ($\epsilon_P = 0$, in the top row).

the first row represents an unrealistic case, where $\epsilon_G > \epsilon_P$, meaning that the mates of guarding males are more available than that of caring males. In these cases, care wins as it mimics the effects of guarding.

Theft by multiple-mating males

Further investigation demonstrates the influential effect of varying the availability of paternities to theft by multiple-mating males. Qualitative behaviour is similar for both low and high levels of care benefit, seen in Figure B.3 and B.4 respectively. The first column of Figure B.3 shows that care persists only where $\epsilon_G \geq \epsilon_P$; the paternities of guarded females are as available or more available to theft than that of caring males. Again, this smuggles effects of guarding into care, as described in the main text and in the definition of parameters given in the model description. The left column of Figure

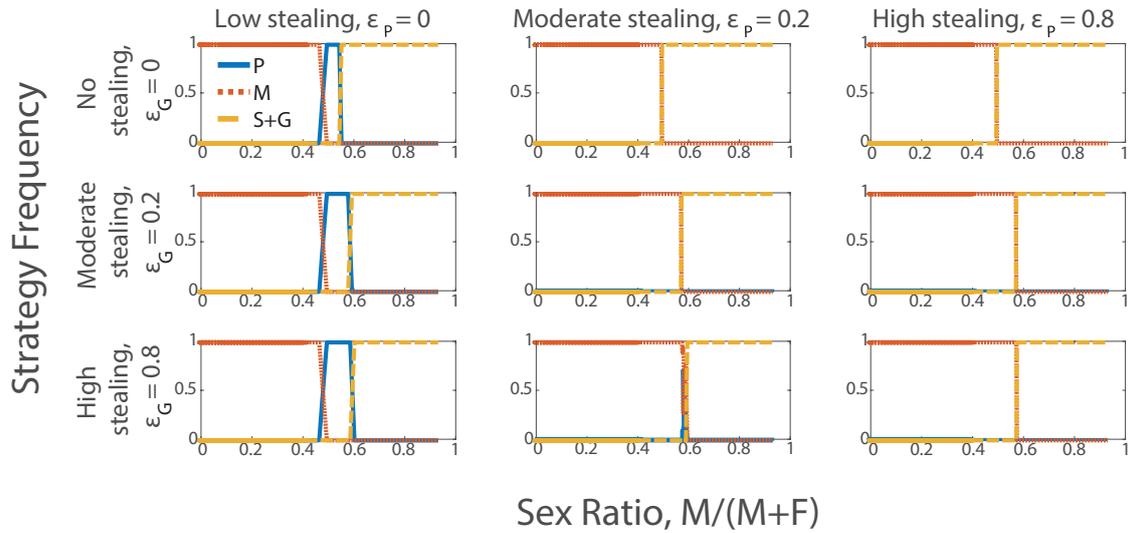


Figure B.3: The effect of the availability of the paternities of females to theft by multiple-mating males. High, moderate and low availabilities, ϵ_P and ϵ_G , are presented. Other parameters are that of $c = 0.8$ (or high survival benefit to care) and low pair-bond breakup, $\beta = 0.1$. The left panels show persistence of care, where theft from carers does not occur, $\epsilon_P = 0$. In the other panels, multiple mating wins in female-biased populations, and guarding wins at male-biased. The ASR at which the switch between these winning strategies occurs is dependent on how available the paternities of offspring of mates of guarding males are to theft by multiple maters, ϵ_G .

B.4 also demonstrates this. If caring supplies higher paternity assurance than guarding, i.e., $\epsilon_G \geq \epsilon_P$, then care can persist in a close to equal sex ratio.

Guarding inefficiencies

For parameter sets exploring the effect of guarding inefficiencies, β and ϵ_G , multiple mating is the persistent strategy at female-biased sex ratios, and guarding is the persistent strategy at very male-biased sex ratios. This can be seen in Figures B.5 and B.6, where I set $\epsilon_P = 0.8$. The panels on the right of Figure B.5 show care persisting at very male-biased populations, but further exploration of these long-term equilibria show that these populations are extinct. When the size of the total population is close to 0, care is a winning strategy as it produces surviving juveniles, when levels of care

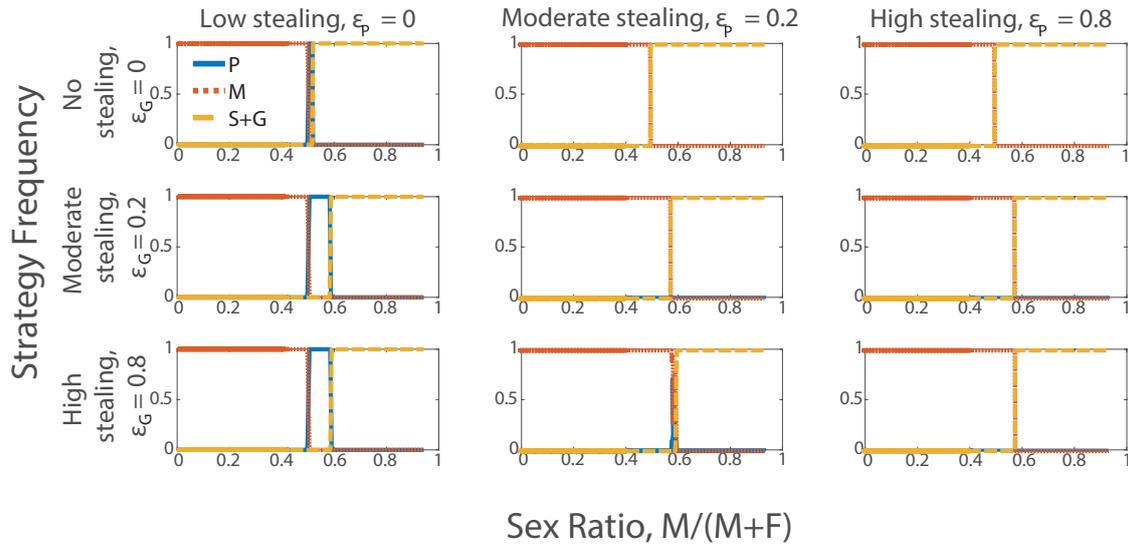


Figure B.4: The effect of availability of paternities to theft by multiple maters. Different combinations of high, moderate and low availabilities, ϵ_P and ϵ_G , are presented. Other parameters are low care benefit, $c = 0.1$, and low pair-bond breakup, $\beta = 0.1$. Where care here is low, the region within which care persists in the left column, is smaller than that of Figure B.3. Again, in the other panels, multiple mating wins in female-biased populations, and guarding wins at male-biased. The ASR at which the switch between these winning strategies occurs is dependent on how available the paternities of offspring of mates of guarding males are to theft by multiple maters, ϵ_G .

benefit are high, as is the case of Figure B.5, but not Figure B.6 (comparing the right column of Figure B.5, where care is high, $c = 0.8$, with that of Figure B.6, where care is low, $c = 0.2$).

Further, the higher the availability of the paternities of guarders' mates' offspring to theft by multiple maters, the higher the ASR at which guarding takes over the population. This is further explored in Figure 3.3 of the main text.

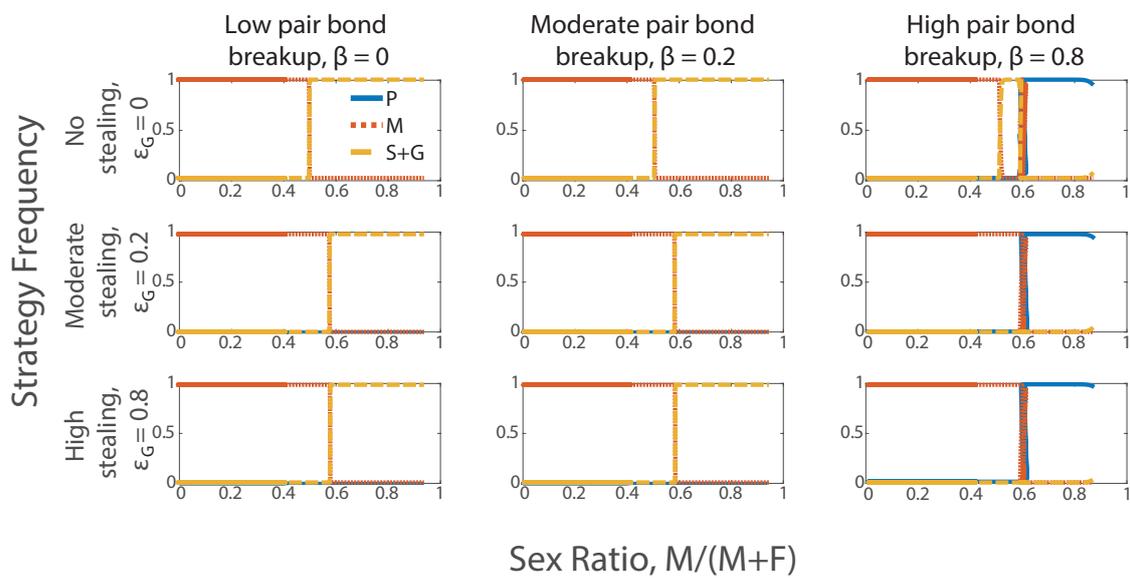


Figure B.5: The effect of changes to parameters of guarding inefficiency, at high care benefit, $c = 0.8$ and where $\epsilon_P = 0.8$. Different combinations of parameters quantifying pair-bond breakup, β , and theft of paternities from guarders, ϵ_G , are presented. The right column shows care persisting at male-biased ASRs, but further investigation into the populations show extinction. For other combinations of parameter regions, multiple mating wins when female-biased, and guarding persists when male-biased.

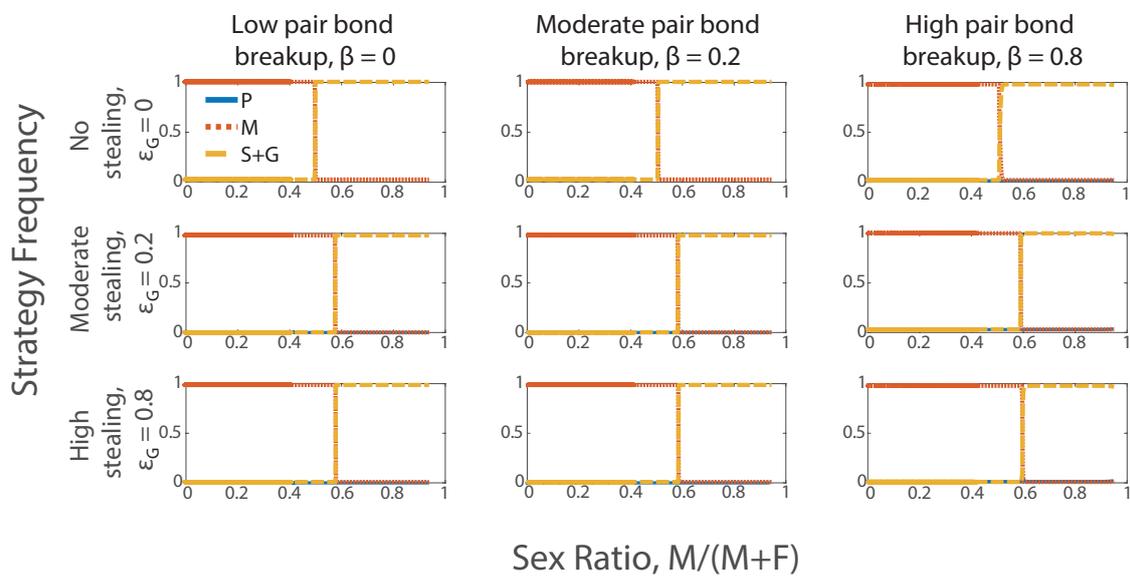


Figure B.6: The effect of changes to parameters of guarding inefficiency, at low care benefit, $c = 0.2$ and where $\epsilon_P = 0.8$. Different combinations of parameters quantifying pair-bond breakup, β , and theft of paternities from guarders, ϵ_G , are presented. Where care is lower and theft of the paternities of carers' mates' offspring is high, multiple mating persists in female-biased populations, and guarding in most male-biased populations.

WHY MALES COMPETE RATHER THAN CARE, WITH AN
APPLICATION TO SUPPLYING COLLECTIVE GOODS

4.1 INTRODUCTION

Males and females demonstrate stark differences across a vast majority of animal species. Differences in gamete size and number, or anisogamy, define the two sexes. Males possess numerous but small gametes (sperm) relative to females' few but large gametes (eggs) (Lehtonen and Parker, 2014; Parker *et al.*, 1972; Parker and Lehtonen, 2014). This biological difference is established from initial fertilisation and this gametic dimorphism plays a significant role in sex-role divergence (Lehtonen *et al.*, 2016; Parker and Lehtonen, 2014).

Offspring production through sexual reproduction requires the fertilisation of female eggs by male sperm. Maximising one's reproductive success is then dependent on choices in reproductive behaviours or sex roles. One such path is parental care, which ensures the differential survivorship of current offspring. A separate path, mating, invests in the production of additional offspring. Both males and females are then faced with an allocation problem: does one invest reproductive effort into either parental care or mating (Houston *et al.*, 2005; Klug *et al.*, 2012; McNamara *et al.*, 2000; Parker *et al.*, 2002; Trivers, 1972)? Traits that guide this distinction in allocation of reproductive effort are evident in many taxa. There are clear differences in reproductive behaviour that go beyond anisogamy (Janicke *et al.*, 2016; Parker and Pizzari, 2015; Schärer *et al.*, 2012); there are differences in traits that improve offspring survival (Clutton-Brock, 1991; Queller, 1997; Trivers, 1972) and traits that improve paternity chances and mating success (Andersson, 1994).

Darwin (1859, 1871) and other early commentators (Bateman, 1948; Fisher, 1915; Trivers, 1972) noted that throughout many taxa, males tend more towards competing for fertilisation opportunities than females (see Dewsbury, 2005, for historical review). This contrasts with females who tend to allocate more effort to parental care (Balshine, 2012; Clutton-Brock, 1991; Cockburn, 2006; Kokko *et al.*, 2012). Accounting for these trends in post-copulatory behaviours in terms of pre-copulatory asymmetries like anisogamy remains an outstanding evolutionary problem. While both males and females

are faced with the option to care for their offspring, why do males compete more readily than care?

Trivers (1972) made the assumption that females' larger, scarcer gametes meant that they had more to lose from the start, which constrained them to continue investing more in those offspring. While that was based on a fallacy (Dawkins and Carlisle, 1976), subsequent resolutions to this problem follow from closer examination of how anisogamy, by definition, constrains the payoffs for both paternal care and mating competition.

Lehtonen *et al.* (2016) links these payoffs with anisogamy through two decisive results. First of these is that females who invest in mating competition necessarily reduce their number of eggs available for fertilisation. Thus, these females have fewer offspring relative to their frugal counterparts. This removes scope for positive selection on mating competition amongst females. The second result follows from the sheer relative number of gametes produced by males, such that not every sperm may be fertilised. Thus, males stand to profit from sacrificing a fraction of their gametes by allocating reproductive effort into mating competition if the result is increased probability of fertilisation with a comparatively rare female egg relative to other competing males. Those males who are outcompeted will fertilise fewer eggs, while competitive males secure more fertilisations. This implies positive selection for male mating strategies, echoing the notion expressed in Darwin (1859, p.88) regarding the definition of "sexual selection. . . depend[ing] not on a struggle for existence, but on a struggle between the males for possession of the females. . . the result [of which] is not death to the unsuccessful competitor, but few or no offspring." It is one's relative reproductive success that determines strategic persistence.

Thus, it is evident that anisogamy, a pre-copulatory distinguisher, promotes mating competition in males. The sex that invests less in parental care is necessarily more likely to invest in competition (Kokko *et al.*, 2012). This is because, due to the increase in mating success obtained from competing, those investing in competition are able to suffer

the cost of maintaining the fitness-reducing trait that increases their competitiveness. This tradeoff between parental care and mating indicates that males are incentivised to reduce their effort into care (Clutton-Brock and Parker, 1992; Parker and Pizzari, 2015).

Other modelling efforts along this vein have demonstrated that reduced male mortality and the ability of males to differentially impact brood survival may have evolved in tandem to reduce the proportion of a male's life that is spent mating (Kokko *et al.*, 2012). In these cases, selection on competition reduces while selection for more paternally caring and better caring males increases (Fromhage and Jennions, 2016; Jennions and Fromhage, 2017; Kokko *et al.*, 2012; McNamara and Wolf, 2015). Each of the models cited shows parental care trading off against mating competition. Male gains through paternal care must necessarily come through differential offspring survivorship, taken at an opportunity cost of accruing the reproductive advantages of mating.

However, I concede that assuming an a priori tradeoff between mating and parenting effort is not always appropriate (Stiver and Alonzo, 2009). Effort allocated into parenting and mating yield different immediate marginal payoffs. This differentiation therefore informs our choice of ordinary differential equations to model these payoffs. Within the differential equation model, I define distinct reproductive payoffs for allocation of effort into either parenting or mating and investigate the long-term behaviour of the subsequent system of ODEs. Stability analysis of the model then describes conditions under which natural selection will act more strongly on either the parenting or mating advantages of a behaviour, that may initially profit both the survival of a male's offspring and a male's competitive mating ability. If a trait produces advantages to offspring survival and competitive mating ability alike, which of these avenues offers the payoffs upon which natural selection operates to maintain the trait in the population?

This chapter introduces an ODE model to compare the strategies of competition and care in males, and demonstrates the persistence of competition over care in a wide range of increasingly realistic scenarios. The model is easily generalised and I present extensions to the model of increasing complexity. These extensions include the

addition of paternity uncertainty and an extension of the two-strategy model to a multi-mixed-strategy model where reproductive effort can be divided between competition and paternal care. This mixed-strategy model also explores varying competition curves and considers the interpretations of these curves and their results. Finally, the model will show that in a range of situations, despite small competitive benefits relative to potential survival benefits, competition can outweigh and overcome paternal care.

4.1.1 *Hunter-gatherer large-game hunting*

As a specific example pertinent to our species, I apply the model to an example of male hunter-gatherer large-game hunting behaviours. Observations of hunting behaviours in hunter-gatherer communities has led to the common perception that paternal investment is a unique human behaviour compared to other primates (Lancaster and Lancaster, 1983). This has been a key aspect of human life history evolution with foragers and hunters investing their energy and resources into feeding themselves and their families (Washburn and Lancaster, 1968).

However, as argued by Hawkes (1993), the acquisition of large-game by modern hunter-gatherers fails to show correlation between hunter's acquisition rates and the consumption rates of their families. This evidence is contrary to claims that large-game hunting evolved as a response to the need to care for one's family. It is instead observed that large-game is shared widely amongst others with no direct benefit or bias towards spouses and offspring. Why would males invest in acquisition of large game, instead of the more consistent supply of small game which can be directed to one's family, if they were aiming to produce greater provisions for their direct offspring?

Hawkes (1993) propose that this widely shared resource returns to the community as a public good. Acquired meat can be supplied by any member and produces a consumable good to all. There is no consumption advantage to the supplier. This notion comes from economic theory where consumers include those who have not paid the cost of acquisition. This falls into the problem of "the tragedy of the commons"

(Hardin, 1998). The common good will not be supplied by agents unless the behaviour is alternatively incentivised by a benefit other than direct consumption. Hawkes (1993, p.341) hypothesised that "the incentive for providing widely shared goods is favourable attention from other group members." Hawkes and Bliege Bird (2002) connected this hypothesis of the "show-off hypothesis" with Zahavi's handicap principle (Zahavi, 1975, 1977, 1991, 1995).

Zahavi (1975) established the handicap principle by suggesting that handicaps established due to the development and persistence of certain wasteful characteristics may have developed through mate preferences and selection. These handicaps act as signals of quality to a mate or rival and are necessarily honest (Zahavi, 1977). Further, Zahavi (1991) emphasised the importance of signalling systems and the evolution of extravagance. In his later comment Zahavi (1995) applies concepts of handicaps to altruism to show that previous models of kin selection (Hamilton, 1964) and reciprocal altruism (Trivers, 1971) are insufficient explanations of altruistic behaviours in observations where those behaviours are not reciprocated. Alternatively, as similarly described in the observations of Hadza hunter-gatherers (Hawkes, 1993), those 'helping' by engaging in altruistic behaviours were increasing their paternity chances. These were indeed selfish behaviours.

The show-off hypothesis outlines that investment in the acquisition of large-game acts as a costly signal where large-game hunting is too costly to fake and is necessarily honest. Therefore, the audience receives information about qualities that make the signaller a desirable ally and formidable competitor. This arena of signalling is of special interest to the audience because they receive consumption benefits in addition to this information. Hawkes and Bliege Bird (2002, p.59) explain that "men's contribution to subsistence may have evolved and may persist because men establish and maintain their relative social standing by showing off their hunting prowess."

Observational evidence from the Ache people in Paraguay further supports this argument. Ache hunters have better reproductive success and resource sharing, without

any bias to the hunter's family, is well documented (Hill and Hurtado, 1996). Similarly, in the Hadza community in northern Tanzania, hunters specialise in large-game where acquired meat is again shared widely. In this case better hunters are more often married to harder-working wives and are therefore able to obtain more surviving paternities in this way (Hawkes, 1991; Hawkes *et al.*, 1991, 2001; O'Connell *et al.*, 1988). Blurton Jones (2016) also shows that better hunters have higher reproductive success not because their offspring have higher survival, but because they have more of them.

However, despite this evidence, large-game hunting as subsistence provisioning by paternal carers is still widely accepted. I would instead argue that these hypotheses on the persistence of large-game hunting as familial subsistence provisioning are insufficient explanations of wasteful behaviour where acquired large-game meat is shared.

4.2 MODEL OF PATERNAL CARE AND MATING COMPETITION

4.2.1 *Populations*

I first formulate a simple ODE model, starting with a population comprising of males and females. To investigate the tradeoff between paternal care and mating competition, I compare two pure strategies: males who invest all of their time and effort in paternal care, and those who invest in mating competition. Mating competition can be manifest in a variety of forms, such as contests, mate choice, or scrambles. For the sake of simplicity and generalisation this compartment is defined as males with any competitive trait leading to increased likelihood of paternity. These strategies are defined by the variables C for paternal carers and M for competing males. The female population is denoted by the variable F . All populations are considered to be adult, fertile populations.

4.2.2 Ordinary differential equation system

To determine the equilibrium behaviours of each strategy and the winning strategy given different parameters, a system of ODEs is formulated for the three populations, C, M and F. This system is given by

$$\text{Carers } \frac{dC}{dt} = \underbrace{\frac{b}{2} \exp(-\tau(1-c)\mu) F \frac{C}{C+\alpha M}}_{\text{Birth term}} - \underbrace{(\mu + \epsilon T)C}_{\text{Density-dependent death rate}}, \quad (4.1)$$

$$\text{Competers } \frac{dM}{dt} = \underbrace{\frac{b}{2} \exp(-\tau\mu) F \frac{\alpha M}{C+\alpha M}}_{\text{Birth term}} - \underbrace{(\mu + \epsilon T)M}_{\text{Density-dependent death rate}}, \quad (4.2)$$

$$\text{Females } \frac{dF}{dt} = \underbrace{\frac{b}{2} \frac{C \exp(-\tau(1-c)\mu) + \alpha M \exp(-\tau\mu)}{C+\alpha M} F}_{\text{Birth term}} - \underbrace{(\mu + \epsilon T)F}_{\text{Density-dependent death rate}}. \quad (4.3)$$

These equations represent the birth and death of each population and implicitly model the transition from childhood to maturity. Within the birth terms, b is the intrinsic birth rate per female taking into account birth and weaning time, τ is the age of maturity to fertile adulthood, and μ is the baseline mortality rate. The constant c represents the offspring survival benefit to carers, and α is the advantage of increased likelihood of paternities given to competing males. This balance between competition (investment in α) and care (investment in survival benefit c) represents how males may partition their reproductive effort. The marginal advantages of each of these potential reproductive strategies are modelled and sensitivity analysis on these parameters is given to highlight regions where natural selection acts most strongly on either strategy.

The survival benefit provided to the offspring of carers is parametrised by c , representing a decrease in baseline mortality, μ . The mortality rate of the offspring of carers is $(1-c)\mu$. This models the payoff of paternal care by increasing the fraction of surviving offspring. Upon reaching sexual maturity, adult mortality becomes equivalent to that of females and competing males. The juvenile population is implicitly modelled by as-

suming that the offspring of carers survive to age τ at probability $\exp(-\tau(1-c)\mu)$. This models the surviving fraction of children that reach adulthood, given a defined mortality rate. The proportion of paternities obtained by the caring population is $\frac{C}{C+\alpha M}$, where the denominator is the sum of males weighted by their competitive standing.

The birth term for the mating competition population follows a similar form. Here, offspring mortality is given by the baseline mortality, μ , without any benefit from care. This corresponds to an offspring survival fraction of $\exp(-\tau\mu)$. The parameter α defines the paternity benefit of competition such that the proportion of paternities obtained by competing males is given by $\frac{\alpha M}{C+\alpha M}$. In this way, the competitive benefit can be controlled and the sensitivity of the model to this parameter can be analysed. Since mating competition increases paternity chances, the strategic benefit of competition is quantified and restricted to $\alpha \geq 1$. For example, if $\alpha = 2$, each competing male is twice as likely to obtain a paternity than one of his caring counterparts. The weighting parameter α can theoretically be any value greater than 1; however, to consider realistic values I investigate $1 \leq \alpha \leq 3$, so that the weighting advantage does not exceed 3-to-1.

The difference between the offspring survival fractions of each strategy determines the reproductive advantage to caring fathers. This pays off through a greater proportion of offspring surviving to adulthood. Increased offspring survivorship is an immediate reproductive advantage of caring. In contrast to this, given that $\alpha > 1$, competing males obtain an immediate marginal advantage in offspring production by winning a greater relative number of paternities. Defining benefits in this way remains consistent with Darwin's definition of sexual selection by capturing the notion that advantages of mating accrue through immediate marginal gains in current offspring production. This distinction is crucial for males; the relative offspring production advantage α would be an inappropriate formalisation of the payoff to mating effort in females.

Density-dependent adult mortality for each population is given by $\mu + \epsilon T$, where $T = F + C + M$ is the total population size, and ϵ is small. This density-dependent term causes the population to settle at a finite equilibrium.

Furthermore, it is assumed that half of the offspring are male and half are female, so all birth terms are multiplied by a factor of $1/2$.

Given initial conditions such that the population has equal sex ratio, i.e., $F_0 = C_0 + M_0$, the sex ratio remains equal for any given time, i.e., $F = C + M$, for all t . Under this assumption, the differential equation for the rate of change of the female population, Equation (4.3), can be disregarded and Equations (4.1) and (4.2) can be rewritten as expressions of C and M only. The simplified two-dimensional model is given by

$$\begin{aligned}\frac{dC}{dt} &= \frac{b}{2} \exp(-\tau(1-c)\mu) (C+M) \frac{C}{C+\alpha M} - (\mu + \epsilon T)C, \\ \frac{dM}{dt} &= \frac{b}{2} \exp(-\tau\mu) (C+M) \frac{\alpha M}{C+\alpha M} - (\mu + \epsilon T)M,\end{aligned}\tag{4.4}$$

with parameters defined as above, and where $T = F + C + M = 2(C + M)$.

In this ODE model, mortality for the offspring of carers is adjusted by a constant adjustment factor c . When $c = 1$, mortality of the offspring of carers is 0, meaning that all offspring survive to maturity, and when $c = 0$, mortality is equivalent to that of the offspring of competing males, μ . With this constant offspring mortality adjustment, analytic steady states can be calculated and sensitivity analysis of these steady states performed. This analysis highlights the parameter regions within which each strategy outperforms the other, giving regions where natural selection will act more strongly on traits that increase payoffs to either mating competition or parental care.

The simplified two-dimensional model of male populations given by Equations (4.4) has steady-state solutions given by

$$\begin{aligned}\text{SS Care} & & (C_1, M_1) &= \left(\frac{b \exp(-\tau(1-c)\mu) - 2\mu}{4\epsilon}, 0 \right), \\ \text{SS Competition} & & (C_2, M_2) &= \left(0, \frac{b \exp(-\tau\mu) - 2\mu}{4\epsilon} \right).\end{aligned}$$

These steady states correspond to equilibria where either the strategy of caring wins (SS Care) or where mating competition wins (SS Competition). There is an additional non-realistic steady state of coexistence occurring at $M = -C$. However, the population is non-viable here and dies out, and as such I ignore this equilibrium. There is no realistic coexistence at equilibrium. Performing stability analysis gives that the steady state where care persists (SS Care) is stable only when the following two conditions hold

$$\exp(-\tau(1-c)\mu) > \frac{2\mu}{b}, \quad (4.5)$$

$$\alpha < \exp(-\tau\mu)^{-c}. \quad (4.6)$$

Conversely, the steady state where male competitive behaviours persist (SS Competition) is stable when the following conditions hold

$$\exp(-\tau\mu) > \frac{2\mu}{b}, \quad (4.7)$$

$$\alpha > \exp(-\tau\mu)^{-c}. \quad (4.8)$$

Note that the stability conditions given by inequalities (4.6) and (4.8) are the converse of each other and therefore, as life history parameters change, the equilibrium solution of the ODE system will jump from one steady state to the other. Thus, it is evident that stability is dependent on life history parameters, μ , τ , and b .

Considering human life history, and the evolution of competition and care in our human lineage, I investigate the bifurcation and regions of stability for baseline hunter-gatherer life history parameters, $b = 0.3$, $\tau = 18$ and $\mu = 1/40$. This female birth rate, $b = 0.3$, corresponds to birth intervals of approximately $1/0.3 \sim 3$ years. This includes an approximate 1 year for female conception and delivery, with an additional 2 years for weaning (Kim *et al.*, 2012, 2014; Sear and Mace, 2008). Further, my approximations for the age of maturity, τ , and mortality rate, μ , are informed by Kim *et al.* (2014), who scale their life history parameters by life expectancy and who are themselves informed

by demographic data from great apes and humans (Gurven and Kaplan, 2007; Knott, 2001; Robbins *et al.*, 2006; Robson *et al.*, 2006; Sellen, 2007). This scaling originally established in Kim *et al.* (2012) corresponds to $\mu = 1/L$ and $\tau = L/2.5 + \tau_0$, where L is life expectancy and τ_0 is a constant age of weaning. For these values, stability conditions given by Equations (4.5) and (4.7) hold true. Thus, stability is determined by the values of α and c as given by Equations (4.6) and (4.8). For this human hunter-gatherer example, the bifurcation in the α - c plane is shown in Figure 4.1.

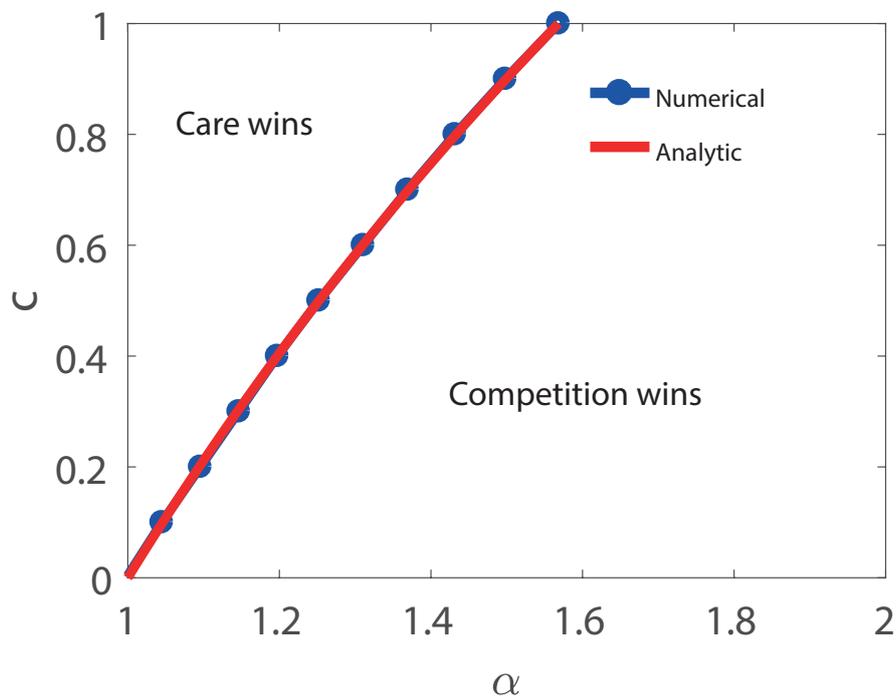


Figure 4.1: Bifurcation obtained from the analytic solution and steady state, in parameters of competition, α , and care, c . On the right of the line, mating competition outperforms the caring strategy, and on the left of the line, care persists over mating competition.

To the left of the bifurcation in Figure 4.1 the caring strategy wins, while to the right hand side of the bifurcation mating competition wins, overcoming the caring population. When males have increased relative paternity benefits from competition investment, i.e., α is slightly greater than 1, mating competition will outperform paternal care even at low levels of care. For these low values of c the benefit of mating competition need only result in marginally greater reproductive benefits (just greater

than 1) in order to outperform caring. For example, when $c = 0.25$, mating competition outperforms care when $\alpha > 1.12$. In the extreme and unrealistic case where the benefit of paternal care is maximised, $c = 1$, and all the offspring of carers reach maturity, the relative reproductive benefit need only be $\alpha > 1.6$ in order for mating competition to outperform care. That is, if mating competition causes competitors to be 1.6 times as likely to obtain paternities as paternal carers, despite care resulting in the survival of all offspring to adulthood, competition still outperforms care.

Additionally, I simulate the model numerically without population mitigation, i.e., $\epsilon = 0$, and plot the α and c at which the equilibrium winning strategy switches from care to competition. This numerical simulation is shown in Figure 4.1 in blue. Thus, restricting population growth has no effect on the overall dynamics of the system.

Parameter	Interpretation	Value
b	Birth rate	0.3 year^{-1}
c	Benefit to offspring of caring males	$0 < c < 1$
μ	Baseline mortality rate	$1/40$
τ	Age of independence and transition to fertility	18
α	Marginal reproductive benefit of mating competition	$\alpha \geq 1$

Table 4.1: Summary of baseline parameter estimates used in analysing and simulating the ODE system. Simulations and analysis use these baseline parameters, based on human hunter-gatherers (Gurven and Kaplan, 2007; Kim *et al.*, 2012, 2014; Robson *et al.*, 2006; Sear and Mace, 2008; Sellen, 2007), unless otherwise stated.

4.3 UNCERTAINTY OF PATERNITY

Paternity certainty and its effect on the evolution of male strategies is highly influential, particularly as is relevant to reproduction and competition (Loo *et al.*, 2017a,b). However, the model described above assumes full paternity certainty. Paternal carers are certain that their caring effort is directly benefiting their progeny. However, this

ignores the possibility of paternity uncertainty and theft. To investigate the effect of paternity uncertainty on the payoffs to care and competition, an uncertainty parameter λ is introduced to describe the proportion of offspring who are born to competing males and inherit the strategy of competition, but who remain in the care of paternal carers and thus gain the survival benefit from paternal care. I assume that λ is a constant proportion and investigate the effect of this uncertainty on the equilibrium winning strategy.

Assuming all other mechanisms and interactions remain the same as in Section 4.2, the ODE system is given by

$$\begin{aligned}\frac{dC}{dt} &= \frac{b}{2}(1-\lambda)\exp(-\tau(1-c)\mu)(C+M)\frac{C}{C+\alpha M} - (\mu + \epsilon T)C, \\ \frac{dM}{dt} &= \frac{b}{2}\exp(-\tau\mu)(C+H)\frac{\alpha M}{C+\alpha M} + \frac{b}{2}\lambda\exp(-\tau(1-c)\mu)(C+M)\frac{C}{C+\alpha M} \\ &\quad - (\mu + \epsilon T)M.\end{aligned}\quad (4.9)$$

I again investigate the effect of the parameters of care, c , and competition, α , and additionally explore the effect of paternity uncertainty, λ , on the equilibrium winning strategy of the system. When uncertainty is introduced, that is, $\lambda > 0$, the region within which paternal care overcomes mating competition shrinks. The benefit of care must render offspring close to immortal, with a high paternity certainty in order for paternal care to persist in the population, i.e., high c and low λ . As uncertainty increases, mating competition fully overcomes paternal care. This can be seen in Figure 4.2. Even under the unrealistic circumstance that $c = 1$ and the offspring of carers are immortal, λ need only be slightly larger than 0.2 in order for mating competition to completely overwhelm the population. This can be seen in Figure 4.2, where in panel (b) for $\lambda = 0.2$ which corresponds to 20% of paternities being stolen by competing males, the strategy of paternal care is almost entirely eliminated. While this may be interpreted as a relatively large proportion of theft, I highlight that even for the case where $\lambda = 0.1$ in Figure 4.2(a), the region of care is significantly reduced compared to the case of certain paternity.

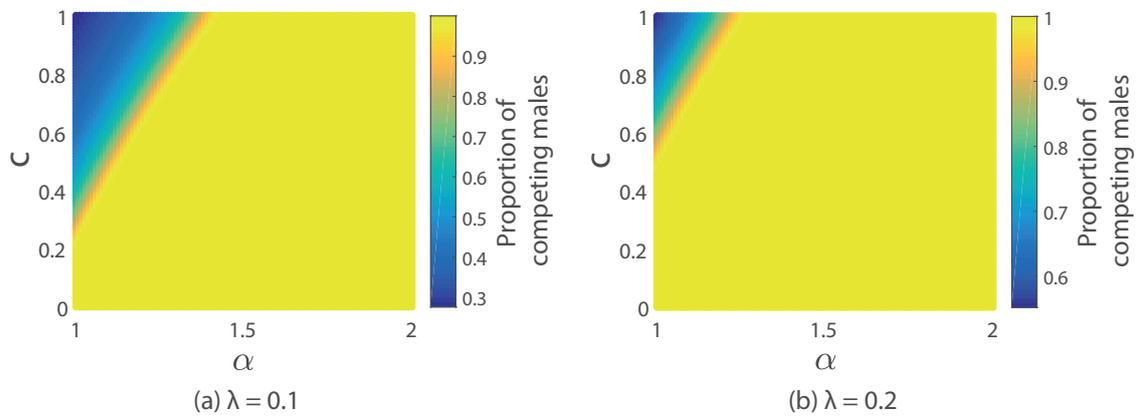


Figure 4.2: Equilibrium strategies for model with paternity uncertainty, λ , at two values of λ . Behaviour is investigated for varying values of paternal care survival benefit, c , and competition, α . Blue corresponds to the persistence of paternal care, and yellow to mating competition. Note that there is a region at low α where coexistence may occur.

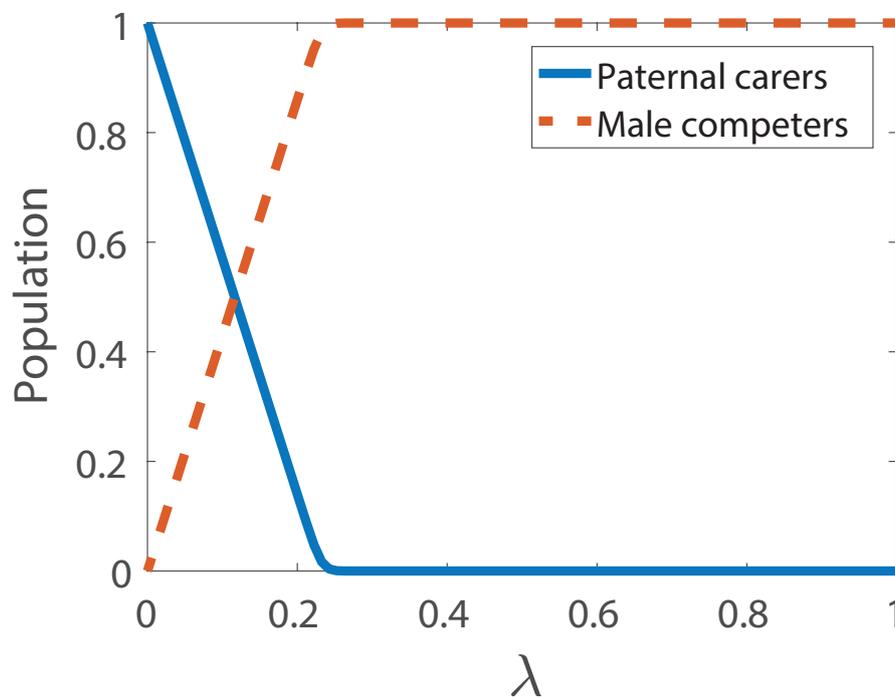


Figure 4.3: Effect of paternity uncertainty, λ , on the frequencies of care and competition. Other parameters used are $c = 0.8$, and $\alpha = 1.1$.

For a given payoff structure, i.e., c and α are constant, I further investigate the strategic frequency of the strategies as the proportion of paternities stolen by competing males, λ , varies. Where offspring survival benefit of care is high, $c = 0.8$, and competitive benefit is reasonably low, $\alpha = 1.1$, I plot the equilibrium male strategy frequency of competing males, M , and carers, C , as λ varies between 0 and 1 in Figure 4.3. For these values of competition and care benefit where, previously, care outperformed competition in Section 4.2, increased proportions of theft and paternity uncertainty drive the removal of paternal care from the population. That is, as λ increases, competition overtakes care as the equilibrium winning strategy. Mating competition overcomes the population when $\lambda > 0.14$. Between $0 < \lambda < 0.14$, the populations may coexist. At $\lambda = 0.07$, the proportion of competing males in the population becomes larger than that of paternal carers, before full takeover at $\lambda = 0.14$, and care is eliminated.

4.4 MIXED STRATEGY ODE SYSTEM

The previous model considers pure strategies of paternal care and mating competition. Individuals either invest fully into the survival of their offspring or their likelihood of obtaining paternities through competition. This section introduces mixed strategies and investigates the mechanisms that drive individuals of different mixed strategies to outcompete others at equilibrium.

To set up the model, let n be the number of strategies modelled such that for $i = [0 : n - 1]$, the proportion of mating effort invested in competitive mating is given by $h_i = i/(n - 1)$. Male strategies are defined by M_{h_i} , where $h_i \in [0, 1]$ is the competitive mating effort and a corresponding $p_i = 1 - h_i$ is invested in paternal care. This follows the simplifying assumption that time or effort not assigned to mating is alternatively assigned to paternal care and therefore diverted to the increased survival of offspring. Strategic populations are defined such that the case where $n = 2$ is equivalent to the model in Section 4.2, i.e., M_0 and M_1 correspond to populations C and M

from Section 4.2 respectively. Further, mating competition effort is defined such that if $h_i = 0.2$, a male in strategy M_{h_i} invests 20% of his time into a behaviour that increases his competitive standing amongst his peers and a corresponding 80% into the care of his offspring.

The system of ordinary differential equations is given by

$$\frac{dM_{h_i}}{dt} = \frac{b}{2} \exp(-\tau\mu(h_i)) F \frac{\alpha(h_i)M_{h_i}}{N} - \tilde{\mu}M_{h_i}, \quad \text{for } i = 0, 1, \dots, n-1, \quad (4.10)$$

$$\frac{dF}{dt} = \frac{b}{2} \left(\sum_{i=0}^{n-1} \exp(-\tau\mu(h_i)) \alpha(h_i)M_{h_i} \right) F \frac{1}{N} - \tilde{\mu}F. \quad (4.11)$$

The term $\tilde{\mu} = \mu + \epsilon T$ is the population density-dependent death rate as before where $T = F + \sum_i M_{h_i}$ is the total population. The constant b is the intrinsic female birth rate; $\alpha(h_i)$ is the competitive benefit of a given strategy M_{h_i} ; $\mu(h_i)$ is the mortality rate of offspring fathered by a male of strategy h_i ; and N is defined as the weighted sum given by

$$N = \sum_{i=0}^{n-1} \alpha(h_i)M_{h_i}.$$

Investment into paternal care adjusts offspring mortality. I assume that this benefit increases linearly with effort into care, taking the interpretation that, for example, resource provision provides proportional benefits to offspring; resource provision does not increase exponentially with increasing effort. For the spectrum of mixed strategies, h_i , offspring mortality is given by

$$\mu(h_i) = (1 - h_i c) \mu,$$

where c is the constant benefit of care and μ is baseline offspring mortality as before. In the case of two pure strategies, $n = 2$, this expression simplifies to offspring mortality as given in Section 4.2.

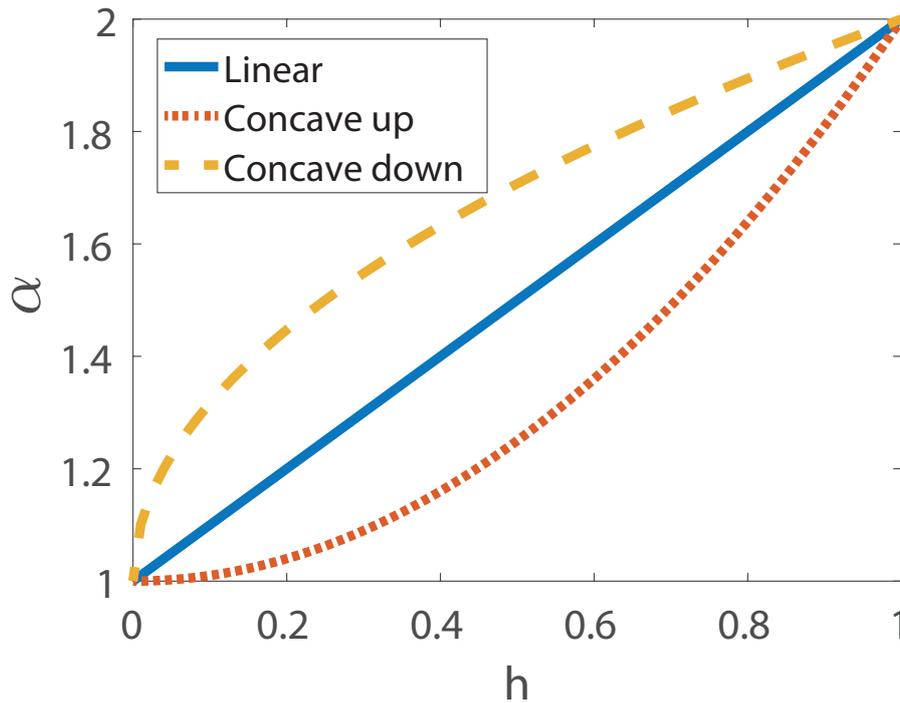


Figure 4.4: Different competition curves defining the advantage of mating competition, given different values of γ . These are investigated in the mixed strategy ODE system, using Equation (4.12). Functions considered take $\gamma = 1$ (linear), $\gamma = 2$ (concave up), and $\gamma = 1/2$ (concave down), and $\alpha_{\max} = 2$.

Investment in mating competition pays off by way of increased relative likelihood of obtaining paternities. This is defined by $\alpha(h_i)$, which is dependent on the given strategy, h_i . I define competition to be an increasing function in h_i , such that the competitive standing for paternities increases with mating effort h_i . For example, if $\alpha(a) = 2$, then strategy M_a is twice as likely to obtain a paternity than a strategy M_b where $\alpha(b) = 1$. I consider a competition curve given by

$$\alpha(h_i) = (\alpha_{\max} - \alpha_{\min}) h_i^\gamma + \alpha_{\min}, \quad (4.12)$$

where h_i defines the given strategy, γ defines the shape of the competition curve, and parameters α_{\min} and α_{\max} are the minimum and maximum reproductive benefit given to males respectively. I set $\alpha_{\min} = 1$, without loss of generality. When $\gamma = 1$ the curve corresponds to a linear competition curve, when $\gamma > 1$ it is concave up, and when $\gamma < 1$ the curve is concave down. Examples of these curves are compared in Figure 4.4.

Regions of strategy stability are dependent on the shape of this competition curve. For the sensitivity analysis performed as follows, I ignore the implementation detail of the number of strategies, n , and rename h_i as the mating effort $h \in [0, 1]$. By choosing n sufficiently large, I approximate a continuous form of h .

4.4.1 Linear competition curve

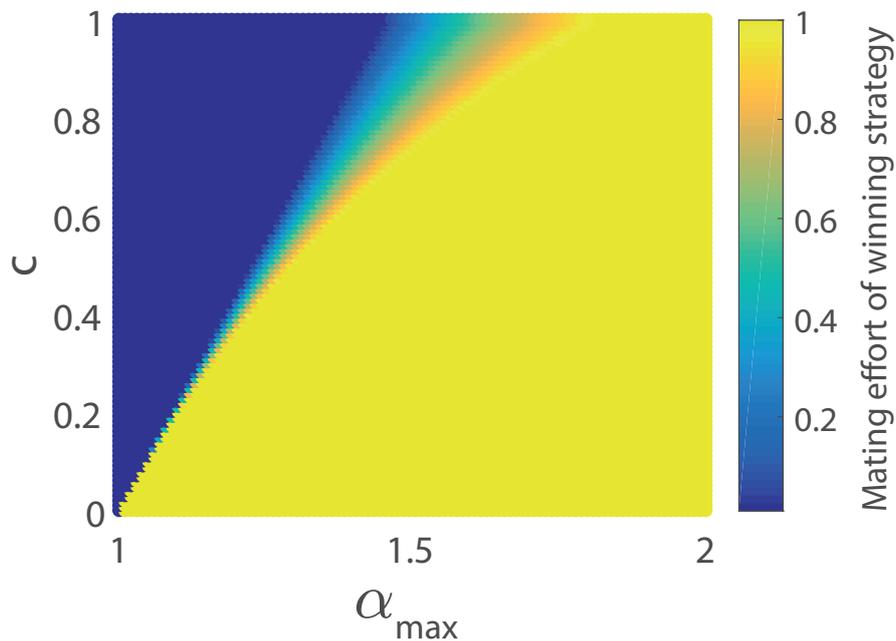


Figure 4.5: Scatter plot showing the mating effort, h , of the winning equilibrium strategy given various combinations of α_{\max} and c , and a linear competition curve as given by Equation (4.12) and $\gamma = 1$. Yellow here corresponds to maximum mating effort, $h = 1$, and dark blue corresponds to full paternal care investment, $h = 0$.

Using Equation (4.12), and setting $\gamma = 1$, the competition curve becomes linear. In this case, mixed strategies can overcome others. I investigate the equilibrium winning strategy given changes to parameters α_{\max} and c . With the linear competition curve the mating effort of the equilibrium winning strategies are given in Figure 4.5 with the colour bar representing the mating effort, h , of the winning strategy. Thus, yellow corresponds to the strategy of pure mating effort overcoming all others at equilibrium, and dark blue to the strategy of pure paternal care overcoming all others. For higher

values of care benefit, c , a region where mixed strategies overcome all others emerges, shown by the spectrum of colours in Figure 4.5. However, for much higher competition advantage, i.e., α_{\max} closer to 2, pure mating competition still overcomes care. For low α_{\max} and higher c , pure care can outcompete other strategies. This behaves in a similar way to that of the pure strategy case, but with an additional region where mixed strategies can persist.

4.4.2 Concave up competition curve (increasing paternity benefits)

I then consider the effect of a concave up competition curve, such that higher investment in competitive mating effort corresponds to a quadratically increasing paternity benefit. This follows from Equation (4.12) with $\gamma = 2$, which is visualised in Figure 4.4.

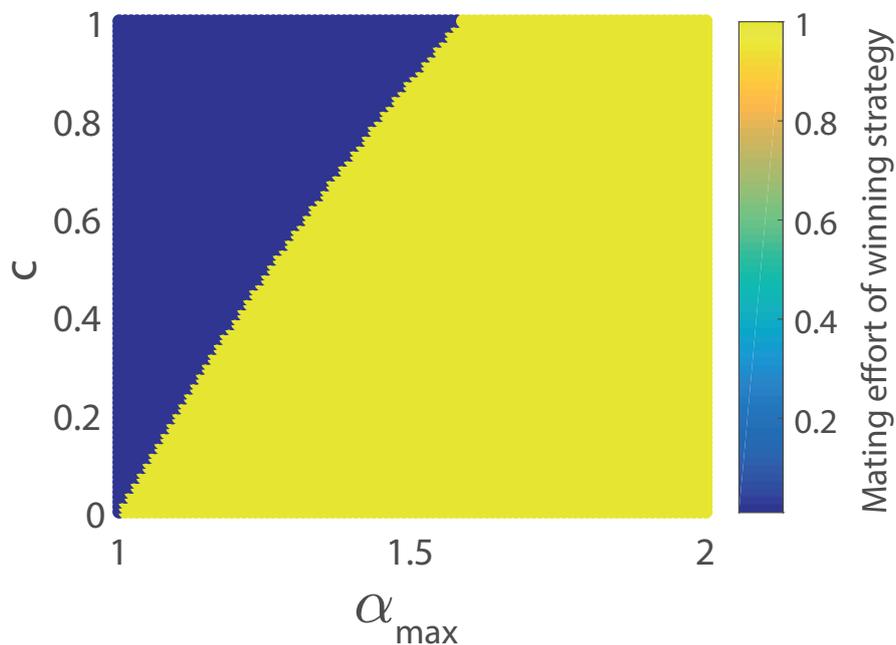


Figure 4.6: Scatter plot showing the mating effort, h , of the winning equilibrium strategy given various combinations of α_{\max} and c , and a quadratic, concave up competition curve as given by Equation (4.12) and $\gamma = 2$. Yellow here corresponds to maximum mating effort, $h = 1$, and dark blue corresponds to full paternal care investment, $h = 0$.

For the case where strategies with higher mating effort have a quadratically higher chance of obtaining paternities, using the concave up competition curve, the equilibrium winning strategies are given as in Figure 4.6. Equilibrium behaviour here is qualitatively similar to those of the simple pure strategy case in Section 4.2. Only pure strategies outcompete others, with a bifurcation showing that as parameters change, winning strategies will jump from a strategy of care (blue regions) to that of mating competition (yellow regions).

4.4.3 Concave down competition curve (diminishing returns)

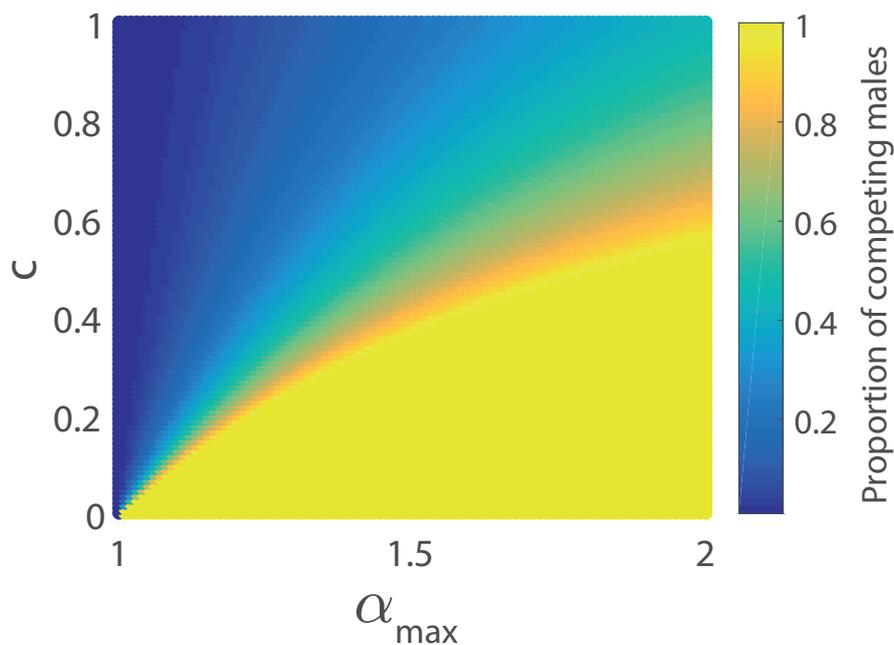


Figure 4.7: Scatter plot showing the mating effort, h , of the winning equilibrium strategy given various combinations of α_{\max} and c , and a concave down, diminishing returns competition curve as given by Equation (4.12) and $\gamma = 1/2$. Yellow here corresponds to maximum mating effort, $h = 1$, and dark blue corresponds to full paternal care investment, $h = 0$.

A concave down competition curve corresponds to diminishing returns on mating competition investment. I assume a curve following Equation (4.12), with $\gamma = 1/2$. There is a steep increase in paternity opportunities when more effort is invested in

competition at low proportions of mating effort, but as investment approaches a pure competitive strategy, i.e., $h = 1$, there is less incentive for further mating competition investment as the relative paternity benefits decrease. This is shown in Figure 4.4, with $\alpha_{\max} = 2$.

There is a greater chance of a mixed strategy outcompeting others when there are diminishing returns on mating competition investment, as can be seen in Figure 4.7. Here, for low care benefit and high α_{\max} , the pure competitive strategy still prevails as shown in yellow in Figure 4.7. Similarly, for low α_{\max} and high care, the pure strategy of care outperforms all other strategies. However, between these regions is a gradient of mixed strategy persistence.

4.5 LARGE-GAME HUNTING AS A SHARED PUBLIC GOOD

The generality of the ODE system allows for its use in a number of applications. One such application is the question of hunter-gatherer hunting behaviours, as outlined in the introduction.

The simple ODE model given by Equations (4.4) in Section 4.2 assumed that benefits to offspring survival came directly and solely from a caring male and offspring mortality was adjusted by a constant proportion, c . However, as was noted in the introduction of this chapter, the question of why men hunt large game instead of providing a more consistent resource via small game is emblematic of the larger question of competition versus care. This follows from observations of hunter-gatherer groups that show a lack of correlation between an individual's large-game hunting success and the shares of meat the successful hunter is able to retain and thus provide to his offspring. Large-game hunting does not appear to be a provisioning or paternal care strategy, though some continue to argue otherwise. Instead, bonanzas of acquired meat return to communities as a public good, with no bias to successful hunters or their families (Hawkes, 1993). The show-off hypothesis instead proposes that the payoff to large-game hunters

is in increased paternities or competitive advantages. Further, a hunter's investment and hunting success provides a benefit of meat to all members of the community regardless of the receivers' strategy, success, or individual acquisition and sharing history.

Ignoring potential differences in nutritional value between large- and small-game, I investigate the effect of adjusting offspring mortality by the population of hunters multiplied by a constant c_h . This assumes that hunters will be successful at catching large game and that this acquired game will provide a certain survival benefit to all, quantified by c_h . I assume this is also inversely proportional to the total number of males in the population, representing the share of acquired game provided to each male and his family.

Thus, I define the mortality of the offspring of carers by

$$\mu_c = \left(1 - c_h \frac{M}{M+C}\right) (1 - c_c) \mu, \quad (4.13)$$

where c_h is the benefit of large-game, c_c is the survival benefit provided by carers, and μ is baseline mortality, with male populations of large-game hunters M and carers C . Here, c_c is equivalent to the parameter c in the model from Section 4.2 and defines the direct offspring survival benefit from care.

The mortality of the offspring of competing males is

$$\mu_h = \left(1 - c_h \frac{M}{M+C}\right) \mu, \quad (4.14)$$

with parameters as above. Using the two-compartment ODE model, large-game hunting versus paternal care can be represented by the following ODE model:

$$\begin{aligned}
 \frac{dC}{dt} &= \underbrace{\frac{b}{2} \exp\left(-\tau \left(1 - c_h \frac{M}{M+C}\right) (1 - c_c) \mu\right)}_{\text{Birth rate}} (C+M) \underbrace{\frac{C}{C+\alpha M}}_{\text{Paternities won by carers}} - \underbrace{(\mu + \epsilon T) C}_{\text{Density-dependent death rate}}, \\
 \frac{dM}{dt} &= \underbrace{\frac{b}{2} \exp\left(-\tau \left(1 - c_h \frac{M}{M+C}\right) \mu\right)}_{\text{Birth rate}} (C+M) \underbrace{\frac{\alpha M}{C+\alpha M}}_{\text{Paternities won by competitors}} - \underbrace{(\mu + \epsilon T) M}_{\text{Density-dependent death rate}}.
 \end{aligned} \tag{4.15}$$

Sensitivity analysis can then be performed to investigate the effect of parameters relating to survival benefits, c_h and c_c , as well as the competitive advantage, α .

Investigation of the winning strategy as c_h and c_c vary, given two different competitive benefits α , is given in Figure 4.8. As the survival benefit from large-game hunting increases, i.e., c_h increases, the direct care benefit c_c required for paternal care to overcome large-game hunting increases. In Figure 4.8(a), where $\alpha = 1.05$, large-game hunting persists for low values of survival benefit to carers. This is shown in the yellow region. As α increases, comparing Figure 4.8(b) to (a), this region of large-game hunting persistence pushes further into the region of paternal care. As the competitive benefit of large-game hunting increases, the region within which large-game hunting outcompetes paternal care grows. Hunting can outcompete care when care yields a greater survival benefit, even when hunting provides a survival benefit to all.

I then consider the behaviour of the bifurcation in α and c_c given a low and high value of hunting survival benefit, c_h . This is given in Figure 4.9, where panel (a) shows the numerical bifurcation with low survival benefit from large-game hunting, $c_h = 0.1$, and panel (b) shows the bifurcation with high benefit, $c_h = 0.9$. These simulations are qualitatively similar to that of the analytic bifurcation for the constant offspring mortality case (Figure 4.1). As c_h increases, the region where paternal care persists reduces in size (the blue region). The slope of the boundary increases, thus shrinking

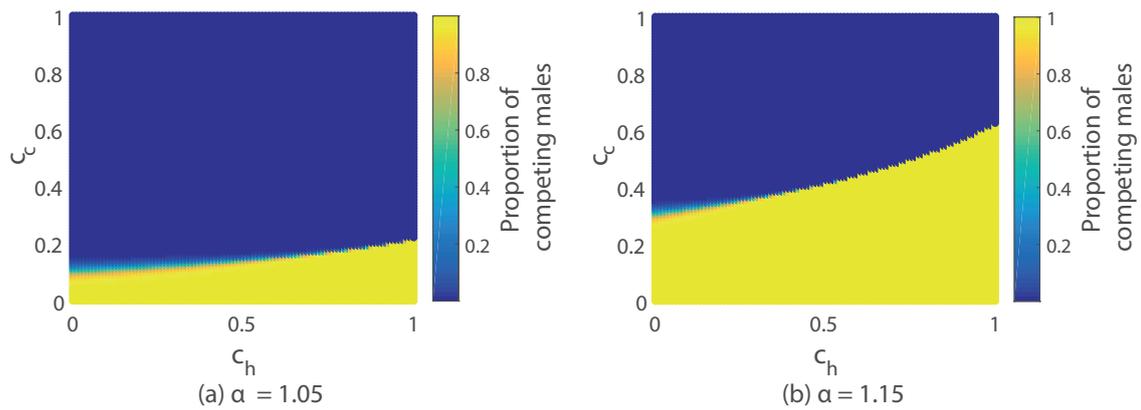


Figure 4.8: Equilibrium strategies at varying c_c and c_h for different values of competitive benefit, α . Blue corresponds to care overcoming large-game hunting, and yellow to large-game hunting outcompeting care. For very low competitive benefit, $\alpha = 1.05$, the region where large-game hunting is successful is where the survival benefit of paternal care is low, but as the survival benefit of large-game hunting, c_h , increases, large-game hunting pushes into this region of care.

the region within which paternal care overcomes the strategy of competition through large-game hunting. The greater the benefit provided to all, the larger the region within which hunting can outcompete care.

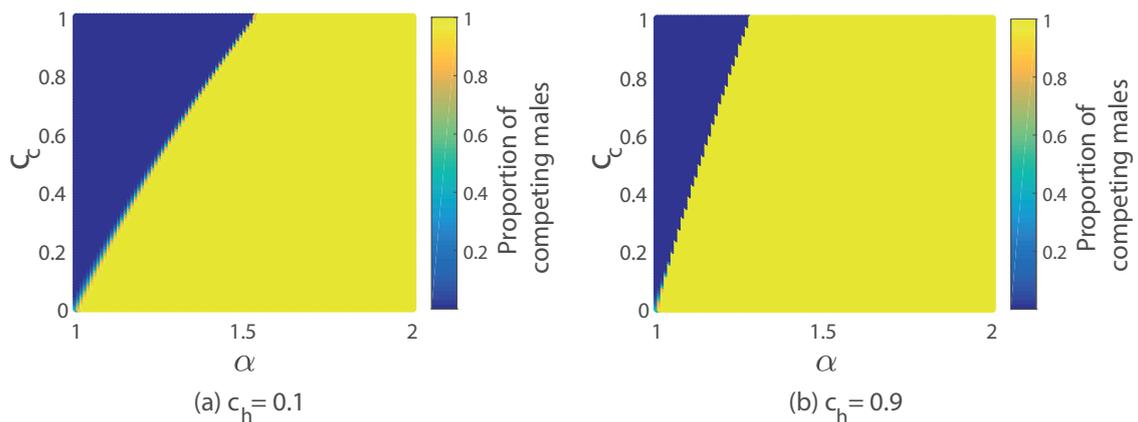


Figure 4.9: Bifurcation in c_c and α for different values of benefit from large-game acquisition; (a) low $c_h = 0.1$, and (b) high $c_h = 0.9$. Yellow corresponds to large-game hunting persistence, and blue to paternal care persistence.

4.6 DISCUSSION

The question of sex-role divergence and reproductive effort has sparked much investigation. As noted in the introduction to this chapter, this differentiation of post-mating roles has its foundations in anisogamy. In this attempt to better understand the selection pressures on strategies of care and competition, a simple model was developed to capture the fundamental question of the payoffs to competition and care as two alternative reproductive pathways. I provide a formal model that accommodates the evolutionary dynamics of both parental care and mating competition without assuming that they necessarily trade off. Using this model, regions dependent on life history parameters where care and competition outperformed each other were found. Where care provides improved offspring survivorship, only a relatively small competitive benefit is necessary for the strategy of mating competition to perform better than the strategy of care. By adding increasingly realistic parameters and interpretations, it became evident that the region of care persistence is highly sensitive to uncertainty, where increased uncertainty leads to a decrease in the prevalence of care. The fact that the stability results for the different variants of the pure strategy model in Section 4.2 conform to what one would intuitively expect if mating and parenting trade off is a result of the model rather than an assumption.

The dependence of the equilibrium stability on life history parameters is important in comparing species both within our lineage and elsewhere. From the analytic solution and stability analysis in Section 4.2, it can be seen that the system is sensitive to the birth rate b , age of independence τ and death rate μ . Making comparisons to other species, I highlight the example of callitrichids. Callitrichids are a small, short-life monkey and are a rare example of primate care (Bales *et al.*, 2000; Dunbar, 1995; Ziegler, 2000). The results given here demonstrate possible links between this differentiation in primate strategies and life span. It is possible that the short life span of these callitrichids creates a selection pressure for care, while the much longer life span of chimpanzees and humans results in a greater selection pressure for competition.

The interbirth interval is another important life history determinant between species. I note that the birth rate b modelled here is not strictly a female rate of conception as it absorbs weaning time. This convolutes potential mechanisms and may result in a decrease in the benefit of competition as, due to the way in which this birth rate is defined, unpaired males are also subject to this weaning time. Males are unable to produce new offspring during this time when females are otherwise occupied as well. This may be better interpreted as the interbirth interval for females. However, this also curtails the rate at which potential multiple maters can have offspring. Males who would otherwise be able to mate with multiple females are required to wait for another conception. This is an important distinction as b has a strong effect on the system. The lower the value of b , the larger the region of care. However, if males were able to invest in additional competitive mating effort where they might otherwise be occupied by care for unweaned offspring, the payoff to mating competition would likely outweigh that of care.

Further, the effect of sex ratios and subsequent availability of females is highly influential when considering the evolution of male reproductive strategies (Loo *et al.*, 2017b,a), but these effects are not considered here. The model presented here assumes that males are competing against each other when females are readily available. However, when females are scarce the selective pressure of competition will only increase. Consideration of female availability would be instrumental in further exploring the persistence of competition, particularly in male-biased hunter-gatherer populations where large-game hunting (as described in Section 4.5) and the provision of public goods is observed.

Investigation of the strength of natural selection on maintaining traits that improve reproductive success through mating competition over those that are driven by care shows that increasing one's number of paternity opportunities outweighs the potential survival benefits of care for increasingly realistic situations. This points to a selection pressure for traits that increase one's status or standing as an attractive mate or intimidating rival. Pathways that lead to differential treatment and increased reproductive suc-

cess have selective benefits even if, as in the case of large-game hunting, they provide an additional benefit to all in the population. In the specific case of large-game hunting explored in this chapter, it can be seen that when the competitive strategy provides a public good to all, there is an even stronger selective pressure for that trait or behaviour.

The simple model developed and built upon in this chapter sheds light on the importance of competition as a male reproductive strategy by characterising the marginal advantages of both paternal care and mating competition and investigating their interaction. When males are faced with the choice of investment in these alternative pathways, the model has shown that mating competition more often wins out in increasingly realistic situations.

THE CULTURAL EVOLUTION OF LOW FERTILITY AT HIGH
SOCIO-ECONOMIC STATUS

5.1 INTRODUCTION

As socio-cultural and economic structures have changed, defined by the shift from pre- to post-industrial society, so too has fertility. This global transition of fertility from high to low has been widely investigated by cultural evolutionists and human behavioural evolutionists (e.g. Borgerhoff Mulder, 1998; Boyd and Richerson, 1985; Bryant, 2007; Kaplan, 1996; Livi-Bacci, 1986; Mace, 1996). This shift has resulted in over half of the global population now living in countries with below-replacement fertility (Wilson, 2004). Life history theory would predict that individuals would invest in strategies to maximise lifetime reproductive success, which implies that greater wealth would result in more surviving offspring. However, improvements in socio-economic status are instead observed to be negatively correlated with fertility (Borgerhoff Mulder, 1998; Bryant, 2007; Livi-Bacci, 1986).

This fertility shift can be understood on two levels. Longitudinally, demographic transition is the shift in average population fertility from high to low as populations move from pre-industrial to industrialised economic systems. The other transversal dimension distinguishes individuals within populations, where individuals of higher socio-economic status in a given population have lower fertility than those of lower socio-economic status. The mechanisms of the shift in fertility in both of these directions are distinct and require separate investigation.

Demographic transition researchers argue that cultural, sociological, and economic factors are too intrinsically defined to be analysed separately (review in Colleran, 2016, and references therein) and that these factors are keenly dependent on different social interactions and networks. Models based in evolutionary anthropology have explored these different aspects of fertility decline from a number of perspectives, including investigations of socio-economic and socio-cultural factors, resource-allocation strategies, fitness optimisation and human behavioural ecology (e.g. Alvergne *et al.*, 2011; Barkow and Burley, 1980; Borgerhoff Mulder, 1998; Brown *et al.*, 2011; Kaplan, 1996; Mace, 1996; Nettle *et al.*, 2013; Shenk *et al.*, 2013; Shenk, 2009). The underlying assumption of many

of these models is that with fewer children, a parent can invest more time and effort into the survival, well-being, or performance of each individual child. This may be interpreted as a question of quality versus quantity. Individual fitness is increased by producing so-called 'higher quality' offspring. There is a strong focus in the literature on the tradeoff between quantity and quality of surviving offspring (Kaplan, 1996; Lack, 1968; Turke, 1989), with 'higher quality' offspring often taking varying definitions — be it economic quality, survival quality, or an alternative definition. This assumes that individuals with high relative fitness will produce offspring with a similarly high relative fitness. However, this does not strictly follow the pattern displayed in modern societies.

Cultural evolutionists have pointed to fertility decline as a key example of cultural transmission resulting in behaviours that do not maximise fitness, where fitness is calculated as surviving offspring (Boyd and Richerson, 1985; Cavalli-Sforza and Feldman, 1981). Investigations into the mechanisms underlying this cultural evolution need to not only consider tradeoffs between the quantity and quality of offspring, but also the effects of status seeking and social learning on the fertility decisions of parents. Separating trait transmission into genetic and cultural components can be difficult (Laland and Brown, 2011) but studies in the literature highlight the utility of exploring cultural evolution through the lens of natural selection (e.g. Boyd and Richerson, 1985; Cavalli-Sforza and Feldman, 1981; Dawkins and Carlisle, 1976; Mesoudi *et al.*, 2007; Richerson and Boyd, 1984). These studies consider non-genetic Darwinian mechanisms of inheritance to demonstrate the selection of traits of high-status individuals.

Maladaptive effects of competition can result from this selective imitation. This is the notion that strategies or traits that increase an individual's chance of outcompeting its competitors are selected despite the decrease in overall population fitness. Boyd and Richerson (1985) hypothesise that decreases in fertility are due to these such inheritance mechanisms that dictate the preferential imitation of traits associated with high socio-economic status individuals. This echoes the investigation in Chapter 4, where competition is shown to outcompete care in a wide range of cases.

This chapter focuses on the mechanisms that drive high socio-economic status individuals to low fertilities by considering this relationship from a transversal perspective rather than directly addressing demographic transition. An integro-difference equation model is developed to compare individuals of varying socio-economic status within a given population and investigate the coevolution of fertility with changes in socio-economic status. This is constructed within the framework of cultural evolution, wherein an individual's target offspring endowment or provision is a transmitted cultural trait. Thus, transmission is not restricted to biological inheritance of behaviour through parents. As culture is passed from one individual to another by nurture — through observation, imitation, teaching, etc. (Cavalli-Sforza and Feldman, 1981) — behaviours can be transmitted through any member of a population, including those other than one's biological parents. Using this model, I seek to explore the mechanisms that drive the sacrifice of fertility for socio-economic status.

5.2 MODEL

An integro-difference equation model is developed and analysed to investigate the effect of (i) the disposable wealth of parents as dependent on their own socio-economic status, (ii) parents basing their fertility decisions on the decisions of other parents with similar socio-economic status, and (iii) role models being chosen probabilistically across the whole range of socio-economic status with a gradual preference for imitating high-socio economic status individuals from the parent generation.

The coevolution of two traits are explored: socio-economic status, $s \in [0, 1]$, and endowment target, $e \in [e_{\min}, 1]$. Socio-economic status is a dynamic trait describing an individual's position in a given generation relative to one's peers. This relative status can be thought of in terms of possession of income, education or occupation. Endowment target is an inherited, evolving trait. Endowment target e is bounded below by

e_{\min} , following the assumption that there is a minimum endowment requirement necessary for the survival of children or that there exists a baseline level of provision given to children by way of welfare assistance.

Endowment target represents the investment strategy of a parent, which defines the proportion of an individual's disposable wealth that is endowed, or provided, to each of their children. This can be interpreted as provision of monetary or material inheritance, or investment in the development of certain skills, education or values. The mechanisms by which either high or low endowment targets are selected for is dependent on the coevolution of, and competition embedded within, socio-economic status. With a foundation in cultural evolution, I assume that endowment target transmission can occur through learning from one's parent or through an alternative role model chosen from the parent generation via mechanisms of social learning.

The population distribution is defined as a bivariate probability density $f(s, e)$, which is updated with each subsequent generation of parents. The sex of populations is undefined. Thus, I assume that individuals in parent generations represent reproducing pairs. The coevolution of average endowment target, and subsequently average fertility, with socio-economic status is investigated. I establish three sub-steps within the model defining events that occur in each generation, as shown below:

1. Children born via fertility decision,
2. Socio-economic status acquisition,
3. Endowment target transmission.

This is summarised by

$$f_t(s_p, e_p) \rightarrow f_c(s_p, e_p) \rightarrow f_s(s, e_p) \rightarrow f_e(s, e) = f_{t+1}(s, e),$$

where $f_i, i \in \{t, c, s, e\}$ are probability densities in the trait space, with f_t giving the population distribution at a given time t .

5.2.1 Fertility decision

The first sub-step is the production of children. The number of children born to each parent of socio-economic status s_P and endowment target e_P is given by

$$n(s_P, e_P) = \frac{W(s_P, \hat{e}_P)}{e_P}, \quad (5.1)$$

where \hat{e}_P is the average endowment target of the population; and $W(s_P, \hat{e}_P)$ is the total disposable wealth of a parent who has socio-economic status s_P . This is defined such that the number of children born to a parent with socio-economic status s_P and endowment target e_P is a choice dependent on how to divide one's wealth. This is driven by the investment strategy, or endowment target, e_P . If endowment target is large a parent chooses to invest a larger proportion of its wealth into fewer children, whereas if endowment target is small a parent divides its wealth between more numerous offspring, thus providing smaller proportions to each child.

Disposable wealth is dependent on the parent's socio-economic status and may also depend on the average endowment target of the population, \hat{e}_P . I assume that wealth increases as socio-economic status increases, such that $\partial W/\partial s_P > 0$, and $W \in [0, 1]$. The maximum disposable wealth is scaled to 1, without loss of generality. The magnitude of $\partial W/\partial s_P$ quantifies the extent of competition and inequality within a society. For example, if $\partial W/\partial s_P$ is much larger than 0, high socio-economic status individuals hold much larger proportions of wealth relative to those with lower socio-economic status; there are high levels of inequality.

The dependence of disposable wealth on the population average endowment target, \hat{e}_P , is important for investigating the longitudinal change in fertility, also known as demographic transition. However, for simplicity, I consider a wealth distribution that is solely dependent on socio-economic status, $W(s)$. This assumes only latitudinal, within-population variation without taking into account the transition that occurs longitudinally over decades. Thus, I focus on the competitive mechanisms that drive

the coevolution of endowment target and socio-economic status between individuals within a given population.

This wealth function is given by

$$W(s_P) = ((1 - r_W)s_P + r_W) W_{\max}, \quad (5.2)$$

where r_W is a measure describing the disposable wealth available to an individual with minimum socio-economic status relative to that of an individual with maximum socio-economic status, i.e., $r_W = W_{\min}/W_{\max}$. Thus, the parameter r_W can be interpreted as a measure of inequality; if r_W is high, inequality is low and if r_W is low, inequality is high. The wealth function given by Equation (5.2) is a linear interpolating function that defines the extent of competition.

The result of this sub-step is the frequency distribution of children, $f_c(s_P, e_P)$, prior to the determination of socio-economic status within that peer group and the adoption of their own endowment target investment strategy. Thus, the distribution of offspring $f_c(s_P, e_P)$ gives the proportion of offspring born to parents with traits (s_P, e_P) and the state distribution is given by

$$f_c(s_P, e_P) = \frac{1}{Z_c} n(s_P, e_P) f_t(s_P, e_P), \quad (5.3)$$

where $Z_c = \int_0^1 \int_{e_{\min}}^1 n(s, e) f_t(s, e) de ds$ normalises the distribution of children.

5.2.2 Acquisition of socio-economic status

In the next sub-step, the distribution of socio-economic status in the child generation is determined. This involves ranking children based on the endowment received from their parents and using this rank to determine the child's socio-economic status, assuming a certain degree of accuracy in parental endowment of wealth. I assume that

parents who invest more in their children, i.e., the larger the endowment provided to their children, have a higher chance of producing children of higher socio-economic status. The dynamics of this socio-economic status determination is given by

$$S(s|s_P, e_P, f_C) = \frac{1}{Z_s(s_P, e_P, f_C)} N(s|r(e_P, f_C), D(s_P)), \quad (5.4)$$

which gives the distribution of socio-economic status s . The term $Z_s(s_P, e_P, f_C)$ normalises socio-economic status such that $\int_0^1 S(s|s_P, e_P, f_C) ds = 1$, to maintain a stable population. The term $N(s|r(e_P, f_C), D(s_P))$ is the probability density of offspring socio-economic status s , taken from a truncated normal distribution with mean $r(e_P, f_C)$ and standard deviation $D(s_P)$. This is truncated so as to obtain an offspring socio-economic status distribution that is also bounded by 0 and 1. Note that f_C here is the distribution of children found in the previous sub-step.

The standard deviation $D(s_P)$ is a decreasing function of parental socio-economic status, i.e., $D'(s_P) < 0$. I assume variance decreases exponentially. This implies that the higher the parent socio-economic status, the smaller the variance from the child's rank and therefore, the greater the influence the parent has on their child's socio-economic status. This is defined as

$$D(s_P) = \exp(-ds_P), \quad (5.5)$$

where d is a constant. Section 5.3.3 considers the effect of a constant form of $D(s_P)$ and also the effect of d in this exponentially decreasing form of standard deviation for socio-economic status transmission.

The ranking term, $r(e_P, f_C)$, orders offspring from the distribution of children f_C by the endowment provided by the parent generation, e_P . Thus, if a child receives a

large relative endowment from their parent, they will have a higher rank in their own generation. The endowment rank is defined as

$$\begin{aligned} r(e_p, f_c) &= \frac{1}{Z_r(f_c)} \int_{e_{\min}}^{e_p} \int_0^1 f_c(s_2, e_2) ds_2 de_2 \\ &= \frac{1}{Z_r(f_c)} \int_{e_{\min}}^{e_p} \int_0^1 n(s_2, e_2) f_t(s_2, e_2) ds_2 de_2 \end{aligned}$$

where $Z_r(f_c)$ normalizes the rank such that $r(1, f_c) = 1$, that is, the highest ranking individual holds the highest rank of 1. Implementation details of this ranking function are given in Appendix D.

The state distribution following socio-economic status transmission, describing the transition from $f_c(s_p, e_p)$ to $f_s(s, e_p)$ is given by

$$f_s(s, e_p) = \int_0^1 S(s|s_p, e_p, f_c) f_c(s_p, e_p) ds_p. \quad (5.6)$$

5.2.3 Social learning of fertility strategy

Within the framework of cultural evolution, the endowment target investment strategy of an individual can be learned from one's parent or from a role model chosen from the parent population. This process of cultural evolution describes the extent of social learning. The probability that a child learns its strategy from a role model is defined by a constant ν , and the probability it learns from its own parents by $(1 - \nu)$. The distribution of role models imitated is given by the imitation kernel, $K(s, s_M, f_t)$, where s_M is the status distribution of role models from the parent population, $f_t(s_p, e_p)$, and s is the status of the offspring generation.

Overall endowment target transmission occurs with the transmission kernel

$$E(e|s, e_p, s_M, e_M, f_t) = \nu K(s, s_M, f_t) \delta(e - e_M) + (1 - \nu) \delta(e - e_p), \quad (5.7)$$

where δ is the Dirac delta function. The first term represents imitation from role models and the second term represents imitation from parents. This transmission function, $E(e|s, e_P, s_M, e_M, f_t)$, describes the transmission of endowment target e using the probability density that a child adopts endowment target e when it has socio-economic status s , its parents have endowment target e_P , and it imitates a role model characterised by traits (s_M, e_M) . This probability is given by an imitation kernel described below.

Role models are chosen from the parent population and characterised by socio-economic status s_M and endowment target e_M . The parent population $f_t(s_P, e_P)$ corresponds to the equivalent role model population $f_t(s_M, e_M)$.

I define an imitation kernel that gives the probability that a child of socio-economic status s successfully imitates a role model of socio-economic status s_M from the parent population f_t . This is given by

$$K(s, s_M, f_t) = \frac{1}{Z_i(s, f_t)} \frac{N(s_M|s, 1/a)}{1 + \exp(-w(s_M - s))}, \quad (5.8)$$

where $Z_i(s, f_t)$ normalizes the kernel such that the whole parent population, $f_t(s_P, e_P)$, is available for imitation and, given that imitation occurs, $Z_i(s, f_t)$ ensures that a role model is indeed chosen, i.e., the probability that a role model of any socio-economic status is chosen from the parent population is 1. This corresponds to the mathematical condition that $\int_0^1 \int_{e_{\min}}^1 K(s, s_M, f_t) f_t(s_M, e_M) de_M ds_M = 1$. When the normal distribution in the numerator of Equation (5.8) is divided by the Fermi update rule in the denominator, the kernel gives preference for role models with socio-economic status greater than that of the imitator.

The imitation kernel assumes that a role model is assortatively chosen from the parent population. The numerator of Equation (5.8) gives the probability that a role model of socio-economic status s_M is chosen by a child of socio-economic status s based on assortative imitation. This assumes that preference is given to role models whose

socio-economic status is close to that of the imitating offspring. This choice is normally distributed around the socio-economic status of the offspring, with standard deviation $1/\alpha$, where $\alpha \geq 0$ is a constant. If α is small, a child will be able to imitate any role model and if α is large, a child can only imitate those whose socio-economic status is close to their own. This follows from the interpretation that a child will be less likely to imitate the investment strategy of a role model whose socio-economic status is vastly different from their own. This takes into account the probable lack of mixing between individuals of very different socio-economic status and can also be interpreted as a child's assessment that imitating a role model of much higher socio-economic status is unachievable.

The denominator of Equation (5.8) represents a sigmoidal Fermi function which accounts for perception — or implementation — error and sets preference for role models with higher socio-economic status. If a role model has socio-economic status much larger than the offspring there is likely to be error in imitating this strategy, and therefore, the accuracy of imitation diminishes. The degree of imitation error is modelled by a constant $w \geq 0$.

Special cases of this imitation kernel can be obtained by taking different values of α and w . For example, small values of α correspond to a large variance and therefore all role models with larger socio-economic status than that of the child are available for imitation. A further example can be seen where $w \rightarrow \infty$, corresponding to a step function that mimics wholly accurate imitation of role models of higher socio-economic status.

Thus, the distribution of the child population following endowment target transmission is given by

$$f_e(s, e) = \int_{e_{\min}}^1 \int_0^1 \int_{e_{\min}}^1 E(e|s, e_P, s_M, e_M, f_t) f_s(s, e_P) de_P ds_M de_M. \quad (5.9)$$

Parameter	Interpretation	Value
e_{\min}	Minimum endowment target	0.2
e_n	Maximum endowment target	1
s_1	Minimum socio-economic status	0
s_n	Maximum socio-economic status	1
ν	Probability of imitation	0.4
d	Uncertainty in socio-economic status transmission	2
α	Extent of assortative role model choice	10
w	Effect of perception or imitation error	10
r_W	Ratio of minimum disposable wealth over maximum disposable wealth	0.8
W_{\max}	Maximum disposable wealth available	1

Table 5.1: Summary of baseline parameters used for population simulations of stability and equilibrium. Baseline parameters are chosen such that the baseline demonstrates a negative correlation between socio-economic status and fertility. Parameters are as given, unless otherwise stated.

The total intergenerational dynamics are obtained by combining the transmission functions given in Equations (5.4) and (5.7), and the population densities given by Equations (5.3), (5.6) and (5.9):

$$f_{t+1}(s, e) = \int_{e_{\min}}^1 \int_0^1 \int_{e_{\min}}^1 E(e|s, e_P, s_M, e_M, f_t) \int_0^1 S(s|s_P, e_P, f_c) \frac{1}{Z_c} n(s_P, e_P) f_t(s_P, e_P) ds_P de_P ds_M de_M. \quad (5.10)$$

Details of the implementation of the model are given in Appendix D at the end of this chapter.

5.3 RESULTS

I consider the effect of parameters in the model and investigate the mechanisms that drive those of higher socio-economic status to invest in better endowed children. I first

explore the effect of the distribution of wealth, parametrised by varying the ratio of wealth. Then, I consider the effects of other parameters including the extent of social learning, v ; the influence a parent has on their child's socio-economic status, $D(s_p)$ with particular focus on the parameter d ; and parameters that define the assortative nature and success of imitation, a and w . Baseline parameters are defined as in Table 5.1 and sensitivity analysis is performed by perturbing parameters from the baseline.

For baseline parameters given in Table 5.1, the distribution of the population in trait space is given as in Figure 5.1. High socio-economic status individuals move towards high endowment targets and low socio-economic status to low endowment targets, corresponding to low and high fertilities respectively.

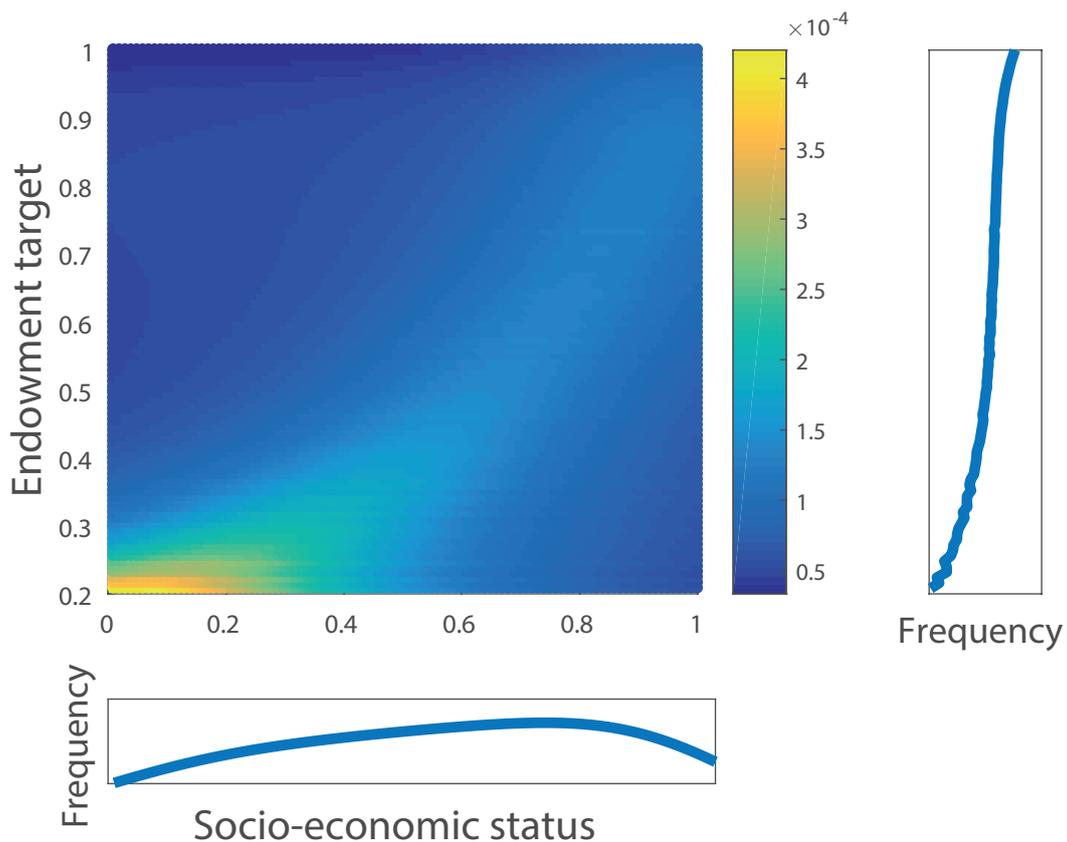


Figure 5.1: Population distribution over the trait space of endowment targets and socio-economic status at an early time, showing initial imitation behaviours. Parameters are baseline parameters given in Table 5.1.

5.3.1 Wealth distribution

The effect of population wealth distributions on the correlation between socio-economic status and fertility is explored. Using the wealth distribution defined in Equation (5.2), I assume $W_{\max} = 1$, and consider the effect of varying the ratio parameter r_W . Results for this sensitivity analysis are given in Figure 5.2 for a baseline moderate level of social learning, $\nu = 0.4$. Figure 5.2(a) presents the equilibrium average fertility at each socio-economic status for a range of ratio values r_W , where the blue curve corresponds to the lowest ratio and green to the highest ratio where wealth is distributed equally across socio-economic status.

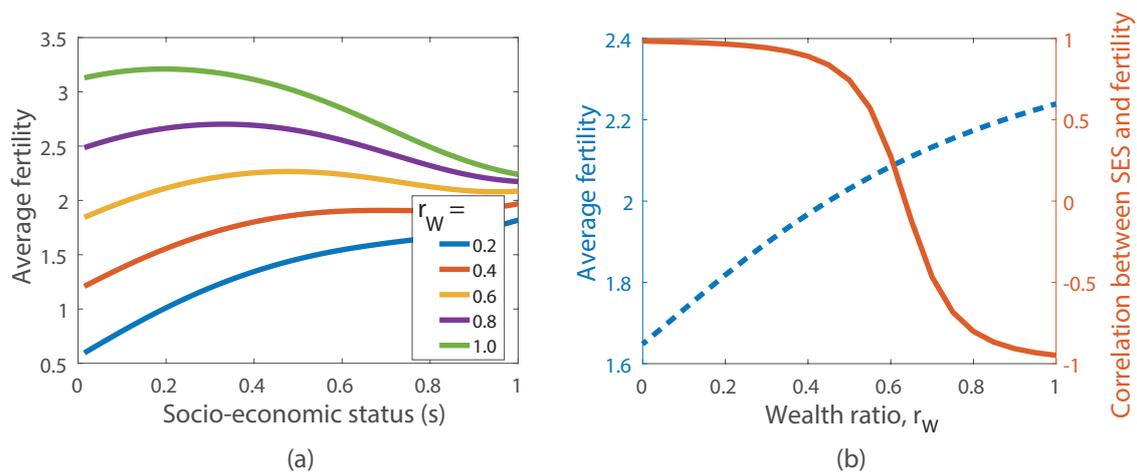


Figure 5.2: The effect of wealth distribution or inequality, r_W , on (a) the relationship between average fertility at a given socio-economic status; and (b) the Pearson's correlation coefficient of this relationship between fertility and socio-economic status (red, solid line), and the average population fertility (blue, dashed line). The wealth function is defined as in Equation (5.2), and other parameters used are given in Table 5.1.

When r_W is high, the difference in wealth between the highest and lowest socio-economic status individual is small, i.e., the population is more equal. For these relatively equal situations, the benefit of higher endowment targets is greater. Individuals start from a more level playing field and therefore the relative benefit of higher endowment targets and better placed children is greater in comparison to having more

children. Therefore, endowment targets increase and fertility decreases with socio-economic status when the ratio r_W is high. Maladaptive effects of competition can be seen in these cases where competition is strong.

When r_W is lower, that is, when there is a large difference in wealth between individuals in a population, the relationship between socio-economic status and fertility is monotonically positive, as represented by the blue and red curves in Figure 5.2(a). Low socio-economic status individuals have much lower relative wealth and they are unable to produce offspring who are relatively well placed in their subsequent generations, even if these offspring receive large proportions of parental wealth.

The correlation between fertility and socio-economic status is summarised in Figure 5.2(b), where the Pearson's correlation coefficient is calculated and plotted along the red axis (the solid line). There is a distinct transition from positive to negative correlation as wealth ratio decreases. Further, since W_{\max} is set as constant, as the ratio r_W increases the total wealth of the population increases. This leads to an increase in population average fertility, represented by the blue, dashed line in Figure 5.2(b).

The transition from positive to negative correlation as r_W increases occurs as the benefit of having more children is outweighed by the benefit of producing offspring who are more likely to be of higher socio-economic status in their own generation. This demonstrates the maladaptive effect of competition, but this effect can be overshadowed. At very high socio-economic status, the relative benefit of high endowment targets decreases as these children are already likely to receive greater relative wealth from their much wealthier parents. When higher socio-economic status corresponds to high relative wealth in this way, those of high socio-economic status are still able to bear the costs of having more children. They have sufficient means to have more children who are still relatively well endowed in the succeeding generation.

5.3.2 Effect of social learning

The greater the extent of social learning, or the stronger the effect of cultural evolution through imitation of role models, the lower the population average fertility at equilibrium, corresponding to a higher average endowment target. This can be seen in the blue, dashed line in Figure 5.3(b). Maladaptive competition drives the imitation of the traits of higher socio-economic status individuals despite the overall fitness deficit, leading to the evolution of higher endowment targets and lower fertilities.

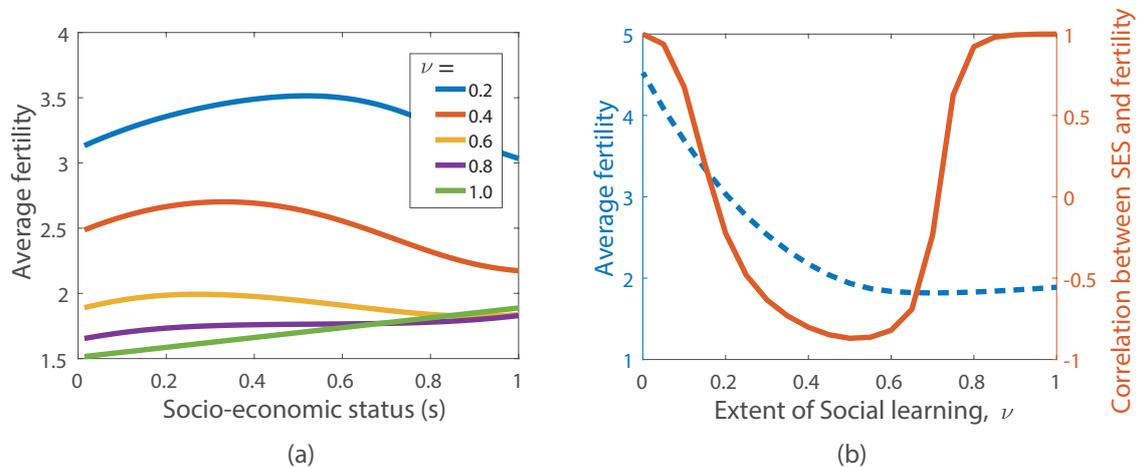


Figure 5.3: The effect of the extent of social learning, ν , on (a) the relationship between average fertility at a given socio-economic status; and (b) the Pearson's correlation coefficient of this relationship between fertility and socio-economic status (red, solid line), and the average population fertility (blue, dashed line). Other parameters used are given in Table 5.1.

Again, the correlation between fertility and socio-economic status is shown in Figure 5.3(a), and on the red axis in (b) showing the correlation coefficient. When social learning is low and limited imitation occurs, the correlation between socio-economic status and fertility is positive. As the extent of social learning increases, the correlation becomes negative before becoming positive again.

However, as ν continues to increase, despite the decrease in average fertility, the within-population heterogeneity between socio-economic status and fertility maintains

a positive correlation at high levels of social learning. When there is a high level of social learning individuals will, almost with certainty, imitate an individual with higher socio-economic status. There is less incentive to outperform competitors by ensuring a high endowment and relative socio-economic status for offspring, as others of low socio-economic status will follow suit by similarly imitating this high endowment. Thus, offspring end up equally well endowed.

5.3.3 *Likelihood of influencing child's socio-economic status*

I explore the effect of a constant standard deviation, which relates to the normal distribution of child acquisition of socio-economic status, independent of parental socio-economic status and then consider different values of the parameter of influence, d within $D(s_P)$ in Equation (5.5). The larger the standard deviation, the less likely a parent is able to influence their child's socio-economic status. If $D(s_P) = 0$, the parent ensures the child's socio-economic status is directly proportional to their endowment received.

5.3.3.1 *Constant standard deviation*

In Figure 5.4, constant $D(s_P) = d$ is investigated, with varying values of $d \in [0, 1]$. Thus the likelihood of influencing the socio-economic status of offspring is independent of parental socio-economic status. In Figure 5.4(a) the relationship between fertility and socio-economic status is presented. Low standard deviation means that parents are more able to ensure their offspring are similarly well positioned in their subsequent generation. For these low values of standard deviation maladaptive competition is strong and high socio-economic status individuals have a much lower fertility in comparison to low socio-economic status. This is seen in blue in Figure 5.4(a).

As standard deviation increases, this relationship transitions to being positively correlated. Large standard deviation corresponds to a large transmission error in trans-

ferring endowment of wealth to ensure offspring socio-economic status. This is summarised in Figure 5.4(b) on the red axis, where the Pearson's correlation coefficient transitions from negative to positive as constant standard deviation D increases.

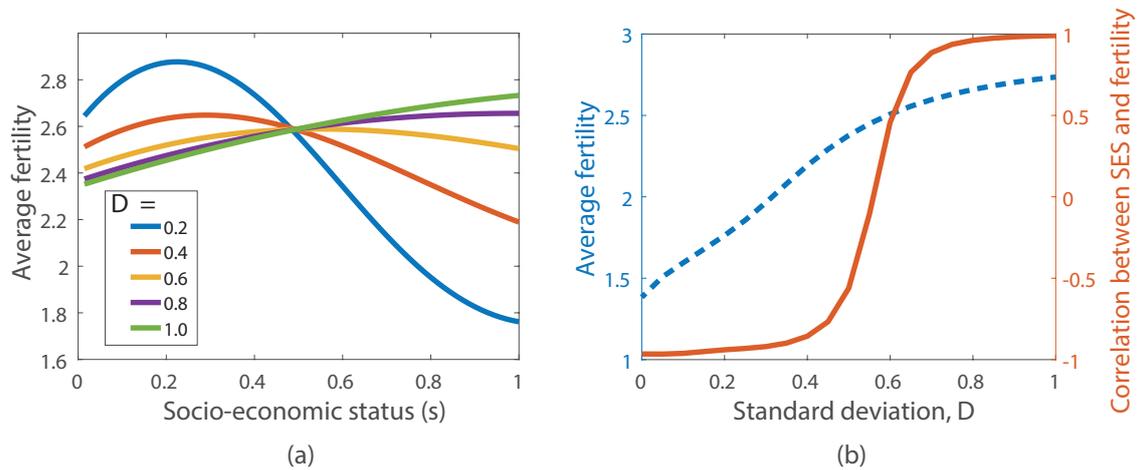


Figure 5.4: The effect of constant standard deviation, D , on the equilibrium (a) relationship between average fertility at a given socio-economic status; and (b) the Pearson's correlation coefficient of this relationship between fertility and socio-economic status (red, solid line), and the average population fertility (blue, dashed line). Other parameters used are given in Table 5.1.

5.3.3.2 Standard deviation dependent on parental socio-economic status

The effect of a more realistic exponential form of this standard deviation that is dependent on parental socio-economic status as given by Equation (5.5) is presented in Figure 5.5. I investigate the effect of changing the parameter d in this equation, where $d > 0$. For low values of the constant d , seen in blue in Figure 5.5(a), the relationship between fertility and socio-economic status is slightly positive. As d increases, high socio-economic status individuals are increasingly able to ensure a similarly high socio-economic status for their children. With this increase the correlation becomes negative, as is evident when $d = 5$, the red curve in Figure 5.5(a). Continually increasing d leads to a stronger negative correlation. However, the effect of this is limiting, as in the cases where $d = 10, 15, 20$ are seen to overlap. This is further emphasised by the correlation coefficient plotted in Figure 5.5(b) in red where the curve approaches a

limiting correlation. As d increases, the standard deviation is very close to 0 and the offspring's socio-economic status is directly determined by their parent. Thus, the apparent stochasticity in the average fertilities at high d seen in Figure 5.5(a) correspond to very small proportions of the adult population being at that given socio-economic status.

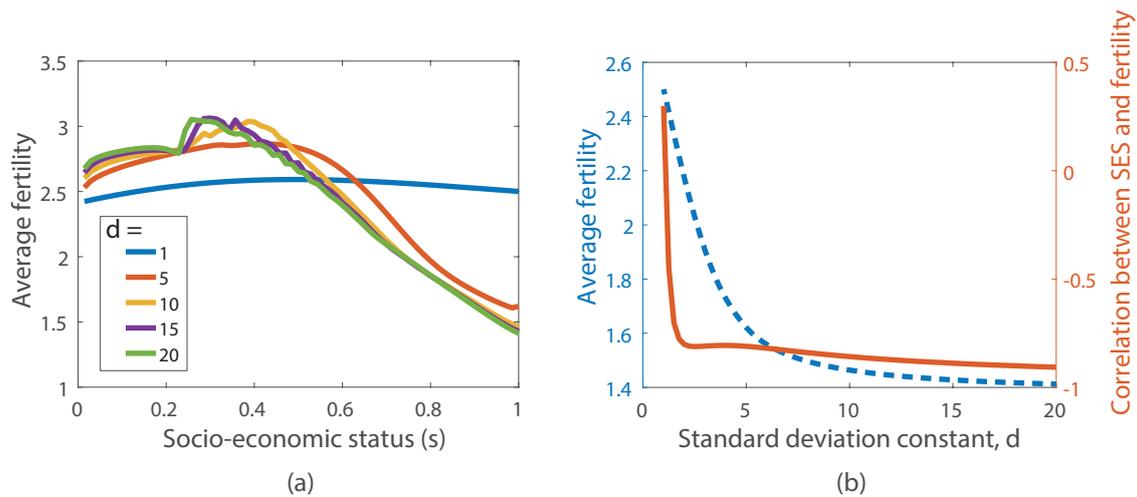


Figure 5.5: The effect of varying values of parameter d in the exponential form of the standard deviation given by Equation (5.5) on (a) the relationship between average fertility at a given socio-economic status; and (b) the Pearson's correlation coefficient of this relationship between fertility and socio-economic status (red, solid line), and the average population fertility (blue, dashed line). Other parameters are as defined in Table 5.1.

The average fertility of the population also declines, as can be seen in Figure 5.5(b). As a parent's influence on the subsequent socio-economic status of offspring becomes more precise, high socio-economic status individuals will coevolve with high endowment targets, and subsequently fertility will decrease.

5.3.4 Imitation parameters

Embedded within the imitation kernel, given by Equation (5.8), are the effects of assortment of imitation and imitation error. These are modelled by the parameters α and w respectively. To investigate the effect of these parameters, I increase the baseline im-

itation parameter ν to 0.7. With this value, the effect of parameters relating to imitation can be more easily visualised and investigated.

5.3.4.1 Assortative choice

Small values of assortative choice, a , correspond to being able to imitate those of much higher socio-economic status than oneself. Conversely, larger values of a correspond to a narrow window of imitation such that only those of nearby socio-economic status can be imitated. The effect of this assortment in imitation is investigated and presented in Figure 5.6.

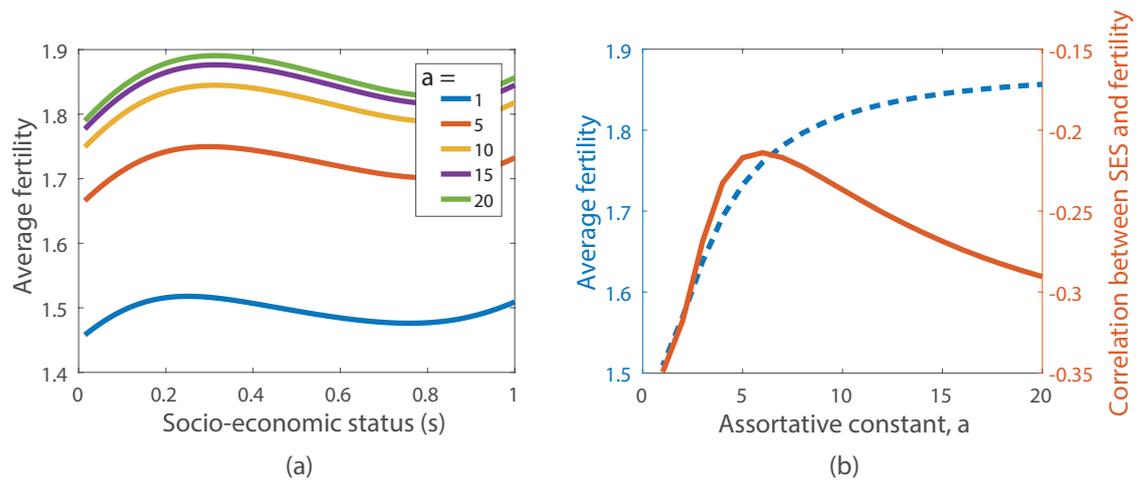


Figure 5.6: The effect of varying strengths of assortative choice, a , on (a) the relationship between average fertility at a given socio-economic status; and (b) the Pearson's correlation coefficient of this relationship between fertility and socio-economic status (red, solid line), and the average population fertility (blue, dashed line). Other parameters used are given in Table 5.1.

As assortative choice increases, average fertility of the total population increases. This corresponds to a decrease in the average endowment target strategy and can be seen in Figure 5.6(a) and (b). In panel (a) the relationship between fertility and socio-economic status shifts up while retaining a similar curvature for increased values of a . This increase in a decreases the ability of individuals to imitate those of much higher status than themselves. Thus, the high endowment target strategy of high socio-

economic status individuals cannot be easily imitated, and therefore the average population fertility increases. The effect of maladaptive competition is weakened.

Figure 5.6(b) shows the effect of α on the correlation coefficient relating socio-economic status and fertility. This correlation increases as α approaches 5 before again decreasing. The correlation plateaus as the assortative constant continues to increase past 20 as the corresponding variance in the normal distribution of Equation (5.8) approaches zero and the parameter has a diminishing effect. The correlation coefficient is positive for all values of α presented as the curvature of the relationship seen in Figure 5.6(a) remains the same.

5.3.4.2 Imperfect imitation

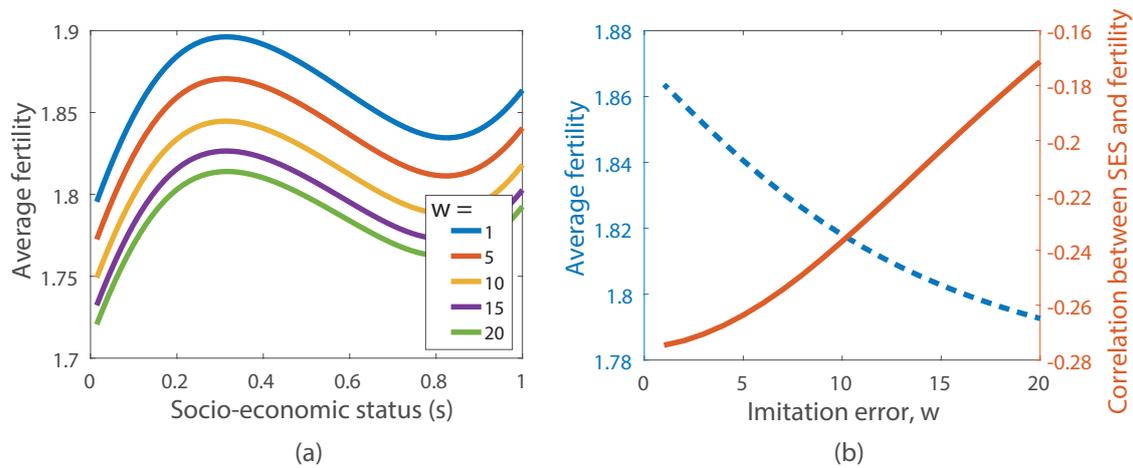


Figure 5.7: The effect of changes to imitation error, w , on (a) the relationship between average fertility at a given socio-economic status; and (b) the Pearson’s correlation coefficient of this relationship between fertility and socio-economic status (red), and the average population fertility (blue). Higher values of w correspond to higher accuracy in imitation. As described in Section 5.2.3, as $w \rightarrow \infty$, imitation approaches a Dirac delta step function corresponding to wholly accurate imitation of the role model. Other parameters used are given in Table 5.1.

Conversely, as imitation error w increases, the average fertility decreases. When imitation error is modelled and is large, there is a small likelihood that a larger endowment strategy is imitated than was intended. Thus, the average population endowment tar-

get at equilibrium increases, corresponding to lower average fertility. This can be seen in Figure 5.7(a) where the distribution shifts downwards as w increases, and in the blue curve in (b). However, the Pearson's correlation coefficient increases as imitation error increases, seen in Figure 5.7(b) in red. This demonstrates the decreased effect of maladaptive competition within a population.

5.4 DISCUSSION

Taking the concepts explored in previous qualitative and quantitative studies, I developed a quantitative, dynamic model and explored the use of cultural evolution in explaining the fertility choices observed in modern societies. Using this framework, it is evident that increased sociality or social learning through cultural imitation of either parents or role models and the wealth distribution of the population may help to explain the paradox of the negative correlation between fertility and socio-economic status.

The greater the degree of cultural evolution, i.e., increased sociality and interaction between individuals of different socio-economic status, the higher the average endowment target strategy and correspondingly, the lower the population average fertility. This increase in the extent of cultural evolution could be a result of globalisation or, on a smaller scale, increased networking due to changes in technology. Increased networking and mixing of individuals from different socio-economic status allows for higher likelihood of imitation from a role model whose strategy seems attractive. From the sensitivity analysis of the parameter of social learning in Section 5.3.2 it is evident that the increase in cultural evolution is sufficient to drive a decrease in total average fertility. This supports the hypothesis in Boyd and Richerson (1985), which states that decreases in fertility are due to inheritance mechanisms that dictate the preferential imitation of traits associated with high socio-economic status individuals.

However, the question remains as to why these high socio-economic status individuals are those associated with low fertility in the first place. Investigating this question requires further exploration of the mechanisms driving the relationship between high socio-economic status and low fertility.

Additional answers to this question may be found in alternative investigations. As outlined in the introduction of this chapter, diverting resources away from offspring production towards other pathways may result in an overall decrease in fertility. For example, the change in women's labour choices informs the investment of individual effort into areas outside of the production of offspring, which may divert resources into pathways that improve mating success or individual maintenance. The introduction of individual consumption of disposable wealth and differences of this consumption based on sex could be an interesting further avenue of exploration.

By instead focusing on the mechanisms above that drive high socio-economic status individuals to low fertilities, I have shown that the evolution of low fertilities at high socio-economic status is particularly sensitive to population wealth distributions. Within the model, wealth is a direct determinant of the number of children produced; thus it follows that the distribution of wealth between individuals of varying socio-economic status is important in considering the average total fertility of the population. Wealth distribution outlines societal inequalities, and this distribution has a strong influence on the relationship between socio-economic status and fertility. It is perhaps the differences in inequality of different societies that drives the differences in fertility rates both between populations and within populations.

The sensitivity of the relationship between socio-economic status and fertility to the relative distribution of wealth in a population informs future work in the direction of corroboration of the model with measures of inequality in contemporary societies. This may be achieved by using metrics of inequality such as the Gini coefficient of

education or income distribution. This has potential to illuminate differences between countries where fertility has remained stable, such as Sweden, and comparing these to countries where fertility has dropped drastically, such as South Korea.

A quantitative analysis of the link between low fertility and high socio-economic status was achieved, and results emphasised the overwhelming effect of the maladaptive competition that drives parental attempts to maximise their offspring's socio-economic status. While this demonstrates the link between high socio-economic status and low fertilities, I have shown that the overall negative correlation between socio-economic status and fertility is strongly dependent on disposable wealth and levels of social learning. In populations with high levels of inequality, the exorbitant wealth of those of high socio-economic status may allow for the correspondingly high fertility of those on top of the socio-economic ladder. Where wealth is more equally distributed, the coevolution of socio-economic status with endowment investment targets results in low fertilities at higher socio-economic status.

APPENDIX C: NUMERICAL SCHEME FOR MODEL

To implement this model, I discretise the bivariate trait space in socio-economic status, s , and endowment target, e . Thus, I define n possible states, equally spaced within each set, such that

$$s \in \{s_1, s_2, \dots, s_{n-1}, s_n\} = S, \quad (5.11)$$

$$e \in \{e_1, e_2, \dots, e_{n-1}, e_n\} = E, \quad (5.12)$$

where $s_1 = 0$ and $s_n = 1$ are the minimum and maximum possible values of socio-economic status, and $e_1 = e_{\min}$ and $e_n = 1$ are the minimum and maximum possible values of endowment target. Taking large values of n possible states approximates the continuous formulation.

Sub-step population distributions are defined by

$$f_t \rightarrow f_c \rightarrow f_s \rightarrow f_e = f_{t+1}, \quad (5.13)$$

where population distributions $f_y(i, j) \in [0, 1]^{n \times n}$ represent the proportion of individuals in the population with socio-economic status s_i and endowment target e_j , and where the subscript $y \in \{c, s, e, t\}$ describes the distribution at a given sub-step or generation t . The mechanisms within the sub-steps in this discrete trait system, and details of their implementation are described below.

Child population

The number of children born to each state is dependent on parental disposable wealth, itself a function of parental endowment target, socio-economic status, and the average endowment target of the population. This is given by

$$f_c(i, j) = \frac{1}{Z_c} \frac{W(s_i, \hat{e})}{e_j} f_t(i, j), \quad (5.14)$$

where the wealth function $W(s_i, \hat{e})$ is given by Equation (5.2), \hat{e} is the average population endowment target, and Z_c normalizes f_c such that

$$Z_c = \sum_{i=1}^n \sum_{j=1}^n f_c(i, j). \quad (5.15)$$

Status transmission

Socio-economic status is then transmitted by ranking children based on the endowment target of their parents. Ranks are equally spaced and of equal size. The set of possible ranks is given by

$$r \in \{r_1, r_2, \dots, r_{m-1}, r_m\} = R. \quad (5.16)$$

A ranking mechanism is established that maps parental endowment target to a child's rank relative to its peers, i.e., from $e_P \in [e_{\min}, 1]$ to $r \in [0, 1]$. Thus, we require the ranking function $r(e)$ that divides the set of endowment targets, $[e_{\min}, 1]$, into m equally spaced intervals, $[g_\alpha, g_{\alpha+1}]$, to be defined by

$$r(e) = \begin{cases} r_1, & e \in [e_{\min}, g_1] \\ r_2, & e \in [g_2, g_3] \\ \vdots \\ r_m, & e \in [g_{m-1}, g_m] \end{cases} \quad (5.17)$$

where intervals are such that there are an equal proportion of individuals in each rank, independent of socio-economic status, i.e., $\int_{g_\alpha}^{g_{\alpha+1}} \int_0^1 f_c(e, s) ds de = 1/m$, for all α .

To apply this ranking function to the distribution of children, f_c , in a discrete trait space I first consider the proportion of individuals at each rank, given their parental endowment target. I define a matrix $a^{k \times j}$ where $a(k, j)$ is the proportion of individuals with rank k who receive parental endowment j . To calculate these proportions, I use the cumulative distribution of the endowment target distribution.

Let p_j be the proportion of children with parental endowment target e_j ,

$$p_j = \sum_{i=1}^n f_c(i, j). \quad (5.18)$$

Thus, the cumulative sum of children with endowment target up to e_k is given by

$$S_k = \begin{cases} 0, & i = 0, \\ \sum_{j=1}^k p_j, & 1 \leq k < n. \end{cases} \quad (5.19)$$

I then use this cumulative sum to determine the proportion of individuals in each rank, given the endowment target of their parent. Straightforwardly, $p_k = S_k - S_{k-1}$.

Given S_k , I define $x_k \in \mathbb{Z}$ as the smallest integer greater than or equal to the cumulative sum S_k . Here, each x_k is so defined such that each $x_k/m \in R$, where R is the set of all possible ranks, given in Equation (5.16). This determines the rank within which a given proportion of endowment targets lies. This definition implies $x_{k-1} \leq x_k$, and

$$\frac{x_{k+1} - 1}{m} \leq S_k \leq \frac{x_{k+1}}{m}. \quad (5.20)$$

To determine $a_{k,j}$ the proportion in rank r_k given endowment target e_j , I determine the proportion of that rank present in the given endowment target, and then calculate this as a proportion of the given proportion of that endowment target, e_j . An example of this matrix is represented by

$$a^{k \times j} = \begin{bmatrix} 1 & \dots & \dots & \dots & 0 \\ 0 & 0.8 & 0.2 & \dots & 0 \\ 0 & 0 & 1 & \ddots & \vdots \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & \dots & \dots & 0.1 & 0.9 \end{bmatrix}^{m \times n}$$

Therefore, the following properties hold. If $x_{k-1} = x_k$, then all of that endowment

target has rank $r = x_k$, and the proportion of endowment target k with rank x_k is $a_{x_k,k} = 1$. Otherwise, where $x_{k-1} < x_k$

$$a_{x_k,k} = \frac{S_k - R(x_{k-1})/m}{p_k} \quad \text{and} \quad (5.21)$$

$$a_{x_{k-1},k} = \frac{R(x_{k-1})/m - S_{k-1}}{p_k}, \quad (5.22)$$

and if there exists an integer α such that $x_{k-1} < x_{k-1} + \alpha < x_k - 1$, then it follows that

$$a_{x_{k-1}+\alpha} = \frac{1}{mp_k}. \quad (5.23)$$

Given the distribution of the proportion matrix a , I then assume that transmission is imperfectly accurate. Error in transmission from a child's rank to its eventual socio-economic status is modelled by a moving average. This moving average is the convolution of the proportions present in each rank r_k given an endowment target e_j with a truncated normal distribution $N(s_i|r_k, D(s_l))$ of the child's resulting socio-economic status after transmission, s_i . This truncated normal distribution has mean r_k and standard deviation dependent on parental socio-economic status, itself given by $D(s_l)$, and is truncated at 0 and 1, so as to ensure the resulting socio-economic status s_i remains bounded. This is achieved using a discrete convolution method, described in Appendix D.

Thus, the transmission of socio-economic status can be expressed as the change in proportion of the population with endowment target e_j and socio-economic status s_i , and mathematically given by

$$f_s(i, j) = \sum_{l=1}^n \sum_{k=1}^m a_{k,j} N(s_i|r_k, D(s_l)) f_c(l, j). \quad (5.24)$$

Endowment target transmission

After socio-economic status transmission, individuals in the child population make a choice regarding their own endowment target. To establish the cultural evolution mech-

anism acting on the endowment target trait, I assume that a child adopts the strategy of a role model with probability $\nu \in [0, 1]$ and from its parent with the converse probability $(1 - \nu)$. I assume that role models are chosen from the given population of parents according to an imitation kernel $K(s, s_M, f_s)$, given in Equation (5.8) and described in Section 5.2.3.

The transmission of endowment target from the parent generation to the next generation can be summarised by,

$$f_s(i, j) = \nu K(i, j) \sum_{k=1}^n f_s(M, k) + (1 - \nu) f_s(i, j), \quad (5.25)$$

where the imitation kernel is discretised by

$$K(i, M) = \frac{1}{\sum_i \sum_j f_t(i, j)} \frac{N(s_M | s_i, 1/a)}{1 + \exp(-w(s_M - s_i))}, \quad (5.26)$$

where i here is the socio-economic status of the child, and M is the socio-economic status of the role model.

APPENDIX D: MOVING AVERAGE

A moving average is a convolution that acts to reduce noise in an output response. In a continuous form, convolutions take the form

$$(f * g) = \int_{-\infty}^{\infty} f(t - \tau)g(\tau)d\tau, \quad (5.27)$$

using the dummy variable τ . If thought of in terms of a function of time, this can be interpreted as a weighted average of the function $f(\tau)$ at a given moment t , with the weighting determined by the function $g(-\tau)$ shifted by t .

For implementation, discrete convolution of two functions, or vectors, f and g , is defined as

$$(f * g)[i] = \sum_{m=-\infty}^{\infty} f[i]g(i - m). \quad (5.28)$$

CONCLUSION

In this thesis, I investigated the mechanisms that drive the evolution of uniquely human behaviours such as pair bonding in Chapters 2 and 3, and large-game hunting in Chapter 4, Section 4.5. I also explored the payoffs to competing strategies of mating competition and paternal care by comparing the strength of natural selection on each pathway in Chapter 4. These dynamic models of competing male strategies enabled me to compare the evolutionary stable strategies at great ape-like life history parameters with those at human-like parameters to investigate the mechanisms that drive these divergent evolutionary trajectories.

In Chapter 2, I developed an ordinary differential equation of male reproductive strategies. This model provided a framework within which I performed sensitivity analysis on parameters of interest. In this case, I investigated the effect of the sex ratio as it shifted from female-biased to male-biased. As the sex ratio becomes increasingly male-biased, the effects of mate scarcity increase, seen in Figures 2.7–2.8. This leads to a change in the payoffs to competing strategies, as it becomes harder to obtain available mates. In hunter-gatherer-like male-biased sex ratios where there are fewer females readily available for mating opportunities, male-male competition between peers is strong. Thus, guarding outperforms other strategies as the likelihood of obtaining the paternity of guarded partners is greater than that of finding a new partner. This provides insight into the selection pressures that drive the evolution of pair bonding in humans.

In my model, the guarding strategy trades off with paternal care and multiple mating strategies. Despite the greater differential offspring survivorship that can be obtained through investment in care, I have shown that the strategy of paternal care is an insufficient explanation for the evolution of pair bonding, though some continue to stress its significance (Kaplan, 1996; Wood and Marlowe, 2013). Paternal care fails to outcompete other strategies at most realistic male-biased sex ratios. Instead, my model agrees with the work of Hawkes *et al.* (1995), who demonstrated the promise of mate guarding as a pathway to human pair bonding over caring and multiple mating strategies but ignored the effects of sex ratio. These results align with the work

of Schacht and Bell (2016), who outlined the effect of the sex ratio on strategies that increase individual fitness. By developing an ODE model of these three competing strategies I used analytic and numerical analysis to show the stability of strategies at varying sex ratios, and showed that multiple mating outcompetes other strategies at a chimpanzee-like sex ratio while guarding outperforms others at hunter-gatherer-like parameters. This shows mate guarding to be a probable non-caring pathway to pair bonding in humans.

The results from the difference equation model in Chapter 3, Sections 3.3–3.5 further support this notion. In this model I included an explicitly modelled female population, introduced female mortality, dependence of offspring survival on maternal survival, and further emphasised the effect of guarding inefficiencies. With these additional assumptions, I showed that guarding still outperforms multiple mating and care in human-like male-biased populations where the male's dilemma is fully realised. Where the likelihood of theft of paternities by multiple maters is greater for caring males than for guarders, the guarding strategy outperforms other competing strategies.

By including theft of paternities from guarded pairs, I demonstrated the sensitivity of the guarding strategy to these imperfections in guarding (Chapter 3, Section 3.4). I highlighted the importance of modelling these inefficiencies, as male paternities are necessarily uncertain. Accurately modelling the male's dilemma requires the inclusion of the possibility of theft from all males regardless of strategy. Though it is more likely that the paternities of the offspring of guarded females is that of the guarding male rather than a multiple mater, there must be at least the possibility of theft. Thus, I showed that a small proportion of multiple mating can survive in the population.

Additionally, the mates of carers must be more available for theft than guarded females. This is the fundamental definition of mate guarding — that guarding increases one's chance of paternities. Assuming otherwise can implicitly include guarding effects into the caring strategy by assuming paternity certainty or protection from theft. Thus, since caring only outperforms guarding where the availability of paternities of

the mates of guarders is greater than or equal to that of carers ($\epsilon_G \geq \epsilon_P$) or the females of both guarding and caring males are relatively unavailable (both ϵ_G and ϵ_P very small), the persistence of caring in these situations further supports the proposal that it is through pathways of guarding that pair bonding evolved. Differential offspring survival benefits obtained through care do not lead to the evolution of human pair bonding.

The models I developed in Chapters 2 and 3 show examples where the benefits of competition and the increased relative likelihood of obtaining paternities through mate guarding outweigh that of multiple mating and differential offspring survival obtained through care. In Chapter 4 I investigated the reproductive payoffs of competition and care using an ODE model, to show the tendency of males to invest in competition. This follows from the clear distinction between male and female reproductive behaviour; males tend towards competition while females tend towards care. This was influenced by the work of Lehtonen *et al.* (2016) who framed these pathways using anisogamy and the effect of gametic differences on reproductive investment. The ODE model presented in Chapter 4 elegantly describes the payoffs to each strategy; increased relative likelihood of paternities through investment in competition, and differential offspring survivorship through investment in care. By parametrising these benefits, I explored these separate pathways of reproductive success and performed sensitivity analysis on these parameters. In this way, the model showed regions where the payoffs of competition outweighed that of care and vice versa, thus showing regions where natural selection acts more strongly on traits that increase the payoffs to either strategy.

The general construction of the ODE in Chapter 4 allows for modification and application to more specific pathways. I presented several extensions to the model, including paternity uncertainty. The importance of paternity uncertainty was emphasised in Chapters 2 and 3 and follows from anisogamy. Again, introducing paternity uncertainty that allows competitive males the opportunity to steal paternities reduces the payoff to caring. Selection for competitive traits increases.

I then applied the model to the problem of large-game hunting in Section 4.5, and showed that selection favours the wide sharing of large-game through payoffs in increased paternity opportunities, despite the simultaneous provision of a public good that is provided by one and consumed by all. This agrees with observations of many hunter-gatherer populations (Hawkes, 1993; Hawkes and Bliege Bird, 2002; O'Connell *et al.*, 1988) where bonanzas are shared widely with no resource bias to the hunter's family. Rather than large-game acquisition providing resources to nuclear families as suggested by some (Lancaster and Lancaster, 1983; Washburn and Lancaster, 1968), I showed that the benefits of large-game hunting through increased paternity opportunities, despite the benefit provided to all, are large enough to drive its evolutionary stability. When acquired meat is provided to all without bias to the hunter himself, and when this meat is highly valued, the caring strategy is unable to outcompete mating competition through large-game hunting.

This outstanding problem of competition versus care can be easily confused with the tradeoff of quantity versus quality. However, as noted in Chapter 4, the misconception that males invest in quantity while females invest in quality is a misunderstanding of these reproductive pathways. The model in Chapter 4 is able to avoid these issues by modelling the payoffs to each strategy without necessarily assuming that they trade off. The quality-quantity tradeoff in females would necessarily take a different form and, as such, making the generalisation that males invest in quantity and females in quality is an incorrect corollary. The model presented in Chapter 4 outlines a simple version of this payoff structure in males that does not automatically assume this tradeoff.

These findings from Chapters 2, 3 and 4 show the importance of correctly interpreting anthropological literature. For example, I noted the importance of defining guarding and paternity certainty in modelling male reproductive strategies (Chapters 2 and 3), and in defining the payoffs to competition and care (Chapter 4). In these three chapters, male reproductive strategies were modelled to show regions within which unique human behaviours emerge and to investigate the possible evolutionary trajectories of behavioural strategies. What life history parameters result in a human-like

behaviour, compared to a chimpanzee-like behaviour? What does this tell us about ancestral human behaviour? Ensuring increased relative likelihood of obtaining paternities is shown to outcompete other strategies of care for a wide range of hunter-gatherer-like life history parameters in all of these models.

In Chapter 5 mechanisms of competition were analysed in a contemporary example by considering the coevolution of low fertility at high socio-economic status, modelled within the framework of cultural evolution. Using concepts of trait inheritance from Darwinian evolution, studies in cultural evolution have explored selection gradients and strategic choice of behaviour by including non-parental 'inheritance', or imitation. The integro-difference equation model developed in this chapter addressed the tradeoff between parental provision of greater wealth to offspring and investment in producing more numerous offspring who receive smaller proportions of parental wealth. This can be interpreted as a quality versus quantity tradeoff, which is similar to that discussed in Chapter 4.

However, since individuals in the model reproduce asexually, I note that anisogamy driven differences in payoffs to parental and mating effort in males and females are ignored. Payoffs to parental care, or greater provisioning investments, take the form of improved offspring quality by assuming offspring are subsequently similarly well placed in their generation. Alternative payoffs to producing more offspring are received immediately in number of direct offspring. Interestingly, although mechanisms of maladaptive competition drive the coevolution of low fertilities at high socio-economic status, individuals in the model invest in the provisioning or quality of their offspring, which may be interpreted as care, rather than quantity or increased likelihood of obtaining paternities, which may be interpreted as mating competition. While the metric of socio-economic status quantifies competition for wealth within a generation, competition for mates is not modelled in this one-sex model. As such, I propose that introducing two-sex dynamics would be an interesting further step of exploration.

Including sex-specific dynamics would further demonstrate the effect of competition for mates and mate scarcity, which was shown to have a strong effect on male reproductive strategies in Chapters 2 and 3. Additionally, developing a two-sex model would allow for the inclusion of additional mechanisms such as female labour choice, which have changed drastically as societies have moved from the pre- to post-industrial era (Brewster and Rindfuss, 2000; Schultz, 1990).

This model of the cultural evolution of low fertility at high socio-economic status provides a basis for understanding the mechanisms that drive the decrease in fertility in many countries. As wealth distribution has a strong effect on the relationship between socio-economic status and fertility, exploring this effect further by including empirical demographic research and comparing the fertility levels and inequality of contemporary societies would be an interesting avenue of further research. This corroboration with data could be used by demographers to highlight mechanisms that cause fertility shifts. Understanding these drivers could influence policy makers to implement policies that attempt to curtail drastically declining fertilities or ageing populations.

Overall, my thesis sheds light on some of the mechanisms that drive selection for counter-intuitive behaviours. Dynamic mathematical modelling of human interactions has demonstrated the utility of these techniques in investigating human behavioural evolution. As evident in the studies presented in this thesis, the competitive benefits of increased relative paternities can select for uniquely human traits such as pair bonding in humans and mating competition in general. Though paternal care is often cited as the main driver of these behaviours, I have shown that it is an insufficient evolutionary pathway for the behaviours analysed here given hunter-gatherer-like life history parameters.

Addressing the male side of the story through creative modelling, I attempted to uncover some of the mechanisms of human behavioural evolution. I investigated the evolution of male reproductive strategies, and captured some of the mechanisms of

certain tradeoffs in reproductive effort in males. This contribution emphasised the significant effect of the sex ratio on male behaviour, and noted the possibility of caring and multiple mating strategic persistence at some hunter-gatherer-like life history parameters, given that guarding is significantly imperfect. This may point to the differences in behaviour that can be observed between societies. The ODE model of the payoffs to competition and care further demonstrates the significance of male-male competition, even at hunter-gatherer-like life history parameters where paternal care is often touted as the main evolutionary driver.

Addressing some of these tradeoffs with two-sex models would be an important avenue for further investigation. This would require careful quantification of reproductive tradeoffs where payoffs to each sex come in drastically different forms, as is informed by anisogamy. Pre-mating investments and post-mating investments for each sex are important distinctions to make, and attempts to combine these will continue to provide significant contributions to the field of mathematical modelling in evolutionary anthropology.

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