Draftable Comparison Export

This document is an exported comparison with limited functionality, generated by Draftable Desktop. To access full functionality, use Draftable's powerful comparison viewer in any of our products.

Left document: Life_cycle_var_10.11.2023.pdf
Right document: Life_cycle_var_11.05.2024.pdf

What is this document?

This is a comparison of two documents. The two documents are interleaved such that the left document is displayed on even pages and the right document is displayed on odd pages.

Is there a specific way I should view this file?

This document is intended to be viewed in Two Page Continuous mode (or sometimes called 'Two Page Scrolling'). It should open in this mode by default when using Adobe Acrobat and most popular PDF readers.

If the document opens in a different view, you can often change this in the settings. In Adobe Acrobat, go to View > Page Display > Two Page Scrolling.

Why are there blank pages?

Blank pages are inserted to keep both documents as aligned as much as possible.

How do I read the changes?

Text deleted from the left document and, hence, not in right document is highlighted red. Text added to the right document and, hence, not in left document is highlighted green.

Tip for printing

When printing this document, we recommend printing double-sided and include this first page. This will result in the matching text being displayed on different pages and easily readable, much like a book.

For more information

Draftable offers powerful document comparison solutions for all use-cases. To view our products, please visit our website: draftable.com.
The role of resource dynamics in the distribution of life cycles within a female human population.

Registered Report

Pablo J. Varas Enriquez $^{1,2}$, Daniel Redhead$^1$, Monique Borgerhoff Mulder$^{1,4}$, Heidi Colleran$^2$, Dieter Lukas$^1$

November 10, 2023

$^1$ Department of Human Behavior, Ecology, and Culture, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.
$^2$ BirthRites Lise Meitner Max Planck Research Group, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.
$^3$ Department of Sociology, University of Groningen, Groningen, The Netherlands.
$^4$ Department of Anthropology, University of California at Davis, Davis, USA.

Contents

1 Introduction 3

2 Model description 9

2.1 Purpose and patterns . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 9
2.2 Entities, variables, and scale . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14
  2.2.1 Entities . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14
  2.2.2 Scale . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14
  2.2.3 Variables . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 14
2.3 Process overview and scheduling . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 24
2.4 Design concepts . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 25
  2.4.1 Basic principles . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 25
  2.4.2 Emergence . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 25
  2.4.3 Adaptation . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 25
  2.4.4 Learning . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 26
  2.4.5 Expectations . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 26
  2.4.6 Sensing . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 26
  2.4.7 Interaction . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 26
  2.4.8 Stochasticity . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 26
  2.4.9 Collectives . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 27
  2.4.10 Observation . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 27
The role of resource dynamics in the distribution of life cycles within a female human population.

Registered Report

Pablo J. Varas Enriquez 1,2, Daniel Redhead1, Monique Borgerhoff Mulder1,4, Heidi Colleran2, Dieter Lukas1

May 11, 2024

1 Department of Human Behavior, Ecology, and Culture, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.
2 BirthRites Lise Meitner Max Planck Research Group, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.
3 Department of Sociology, University of Groningen, Groningen, The Netherlands.
4 Department of Anthropology, University of California at Davis, Davis, USA.

Contents

1 Introduction 3

2 Model description 9

2.1 Purpose and patterns ................................................................. 9

2.2 Entities, variables, and scale ..................................................... 14

2.2.1 Entities .............................................................................. 14
2.2.2 Scale ................................................................................ 14
2.2.3 Variables ............................................................................ 14

2.3 Process overview and scheduling .............................................. 24

2.4 Design concepts ...................................................................... 25

2.4.1 Basic principles ................................................................... 25
2.4.2 Emergence .......................................................................... 25
2.4.3 Adaptation .......................................................................... 25
2.4.4 Learning .............................................................................. 26
2.4.5 Expectations ......................................................................... 26
2.4.6 Sensing ................................................................................ 26
2.4.7 Interaction ............................................................................ 26
2.4.8 Stochasticity ........................................................................ 27
2.4.9 Collectives .......................................................................... 27
2.4.10 Observation ........................................................................ 27
2.5 Initialisation ................................................................. 27
2.6 Input Data ................................................................. 27
2.7 Sub models ............................................................... 27

3 Model Analysis .......................................................... 27

4 Level of bias control .................................................... 30

5 Model insights ........................................................... 30

6 Funding ......................................................................... 32
Abstract

The evolution of the female human life cycle, which is characterised by having a reproductive career nested within juvenile and post-reproductive periods, has been linked to the surplus of adult resource production and downwards inter-generational transfers. These components of the female human life cycle vary highly within populations, but the extent to which resource production and transfers (i.e. resource dynamics) may also explain such differences remains unclear. In this registered report, we develop a framework to understand how variation in resource dynamics influences the variability of life cycles within a female human population. For this, we build an agent-based model with a stage-structured sub-model to define resource production, and a stage-structured network model to define how resources are transferred. The allocation of resources towards life history traits is deterministic, and based on surpassing the thresholds for survival, reproduction, and life cycle stage transition costs. We will use the agent-based model to show how resource production, transfers, and habitat quality—separately, and their interplay—shape the distribution of life cycles within a population. Our results will reveal possible mechanisms behind the demographic diversity observed in human populations, and the extent to which the female life cycle varies in reaction to social and environmental changes.

Keywords: human life history; resource production; resource transfer; evolutionary demography; agent-based modelling; variability.

1 Introduction

The female human life cycle can be described as having a reproductive career nested between juvenile and post reproductive periods. The life cycle has also being described with specific life history traits, such as a long lifespan, high reproductive output, and short interbirth intervals, in comparison to other primates (Kaplan et al. 2000) Kramer 2010 Hawkes et al. 1998). This representation of the female human life cycle is a common assumption in human life history theory, and is commonly observed in hunter-gatherer populations (Kaplan et al. 2000). Evidence from other human populations suggests that life history traits can exhibit large individual-level variation within human populations. The average life expectancy of women is estimated to differ by a factor of 2 and average reproductive output by a factor of 5 (eg. Migliano et al. 2007 versus de Beer et al. 2017). Furthermore, individuals within a population can also differ in their age at first reproduction—as can be seen in Germany, where ages range from ~15 to ~43 years old (Statistisches Bundesamt 2023). Evidence also suggests that reproductive inequality within a population can be high, with estimates of up to 40% of women in several sub-Saharan Africa populations being childless (Bailey and Aunger 1995 Belsey 1976). This variation in life cycles among women is crucial for demographic change (Borgerhoff Mulder 1998) and creating inequalities between individuals (Colleran et al. 2015), but the source of this variation is not fully understood (Sear et al. 2016). Most potential explanations are based on adaptive models that focus on variation in particular life history traits, ignoring the potential role of stochasticity Snyder and Ellner 2018) and the allocation of resources not only between different life history traits within individuals but also the redistribution of resources between individuals (e.g., through sharing behaviours, Jones 2015). Here, we develop a computational model to (1) determine how much variation among human female life cycles might arise from stochasticity in resource production, (2) assess which life history traits are more affected by habitat quality, and (3) investigate whether resource transfers between individuals might buffer the variations due to resource production and habitat quality.

The conditions under which a life cycle emerges can be understood by considering the environmental constraints experienced by individuals, and how individuals resolve these constraints through the allocation
Abstract

The evolution of the female human life cycle, which is characterised by having a reproductive career nested within juvenile and post-reproductive periods, has been linked to the surplus of adult resource production and downwards inter-generational transfers. These components of the female human life cycle vary highly within populations, but the extent to which resource production and transfers (i.e. resource dynamics) may also explain such differences remains unclear. In this registered report, we develop a framework to understand how variation in resource dynamics influences the variability of life cycles within a female human population. For this, we build an agent-based model with a stage-structured sub-model to define resource production, and a stage-structured network model to define how resources are transferred. The allocation of resources towards life history traits is deterministic, and based on surpassing the thresholds for survival, reproduction, and life cycle stage transition costs. We will use the agent-based model to show how resource production, transfers, and habitat quality—separately, and their interplay—shape the distribution of life cycles within a population. Our results will reveal possible mechanisms behind the demographic diversity observed in human populations, and the extent to which the female life cycle varies in reaction to social and environmental changes.

Keywords: human life history; resource production; resource transfer; evolutionary demography; agent-based modelling; variability.

1 Introduction

The female human life cycle can be described as having a reproductive career nested between juvenile and post-reproductive periods. When compared to other primates, the female human life cycle shows specific patterns for life history traits, such as a long lifespan, high reproductive output, and short interbirth intervals (Kaplan et al. 2000; Kramer 2010; Hawkes et al. 1998). This representation of the female human life cycle is a common assumption in human life history theory, mainly based in populations of hunter-gatherers (Kaplan et al. 2000). However, within this general pattern, the various traits that constitute the female human life cycle can exhibit a large individual-level variation. The average life expectancy of women is estimated to differ by a factor of 2 and average reproductive output by a factor of 5 (eg. Migliano et al. 2007 versus de Beer et al. 2017). Furthermore, women within a population can also differ in their age at first reproduction—as can be seen in Germany, where ages range from ∼15 to ∼43 years old (Statistisches Bundesamt 2023). Evidence also suggests that reproductive inequality within a female population can be high, with estimates of up to 40% of women in several sub-Saharan Africa populations being childless (Bailey and Aunger 1995; Belsey 1976). This variation in life cycles among women is crucial for demographic change (Borgerhoff Mulder 1998) and creating inequalities between individuals (Colleran et al. 2013), but the sources of variability of life cycles between women are not fully understood (Sear et al. 2016). Most potential explanations for the variability of life cycles between women are based on adaptive models that focus on the variation of particular life history traits, the allocation of resources between different life history traits within individuals, and the production and the redistribution of resources between individuals (Kaplan 1996; Lee 2003; Jones 2015). These adaptive models assume that the source of variability of life history traits are heterogeneous differences among individuals (van Daalen and Caswell 2020), and they ignore the role of stochasticity as a source of individual differences among women (Snyder and Ellner 2018). Here, we develop a computational model to (1) determine how much variation among human female life cycles might arise from stochasticity in resource production, (2) assess which life history traits of the female human life cycle are more affected by variation in habitat quality, and (3) investigate...
of resources towards growth, survival, or reproduction (Stearns, 2000; White et al., 2022). The surplus of adult resource production, and inter-generational resource transfers towards juveniles, are the two main resource dynamics that have been proposed to explain the evolution of the female human life cycle. The formal model “embodied capital” (Kaplan, 1996; Kaplan et al., 2000) poses that a larger difference between resource production and consumption (i.e. surplus of resource production) in adulthood allows high parental investment (i.e. resource transfers towards juveniles), and short interbirth intervals. Furthermore, long juvenile periods relate to the amount of time needed to acquire the skills necessary to produce surplus, and long post-reproductive periods would emerge from the need of parents to sustain their descendants (see Koster et al. (2020) for cross-cultural evidence). The principled model on “inter-generational resource transfers” Lee (2003) advances that—under the assumption of adult surplus of resource production, and transfer of this surplus towards juveniles—the potential for resource transfers at later ages can explain selection on reduced mortality at later ages. This would result in an extended lifespan, while the cumulative receipt of resources would explain the high mortality risk that juveniles experience early in life. This formulation of this model has been further developed to suggest that transfers co-evolve with low mortality, with adults being more efficient at producing resources and transferring them to juveniles, who are in turn more efficient at using these resources for somatic growth, reducing their mortality (Chu and Lee, 2006). The “pooled energy model” verbally extends this framework by suggesting that resources are not only transferred from parents to offspring, but that alloparenting from individuals of different generations reduces the load of parental investment, and therefore allows the allocation of more resources towards reproduction and growth (Kramer and Ellison, 2010). These models highlight that the key dynamics that constrain female human life cycles appear to be related to how both the physical and the social environment influence how individuals gain and invest resources. However, these models cannot be used to predict variability of life cycles between individuals within populations because, as adaptive models, they predict that there should be one optimal life cycle. Furthermore, because they focus on optimal strategies given an environment, they do not account for possible masking effects of life history trade offs within a population that are likely to occur from the differences among individuals within a population in their ability to acquire resources in a given environment, as demonstrated by the theoretical model from Van Noordwijk and de Jong (1986).

The evolutionary models that predict variability in life cycles within populations focus on how individual differences in resource acquisition and allocation at different life cycle stages might result in differences in fitness. One set of models predicts that differences in how many resources individuals receive during their early life might have far reaching consequences for the whole life cycle. The “silver spoon model” predicts that individuals who receive more resources early in life will have the highest fitness irrespective of the adult environmental conditions (Pigeon et al., 2019; Lummaa and Clutton-Brock, 2002). In contrast, the “adaptive developmental plasticity model” proposes that individuals whose experience in early life matches what they experience later in life would develop a phenotype that allows a higher fitness than those that have a mismatch between early and late life (Bateson et al., 2004; Nettle and Bateson, 2015). The “environmental saturation model” expands these early life models to point out that differences between individuals should be most visible in environments with intermediate conditions, because harsh environments would constrain all individuals while abundant ones would permit individuals with a disadvantage to catch up (Engqvist and Reinhold, 2016). Another set of models focuses on the resources that adults have available for the trade-offs between different life history traits (Van Noordwijk and de Jong, 1986). These models suggest that high variability in resource acquisition between individuals reduces the variability of resource allocation within individual. This is because individuals who have few resources cannot allocate resources equally towards
how resource transfers between female individuals might influence the variability of the female human life cycle due to stochasticity in resource production and habitat quality.

The conditions under which a life cycle emerges can be understood by considering the environmental constraints experienced by individuals, and how individuals resolve these constraints through the allocation of resources towards growth, survival, or reproduction (Stearns, 2000; White et al., 2022). The surplus of adult resource production, and inter-generational resource transfers towards juveniles, are the two main resource dynamics that have been proposed to explain the evolution of the female human life cycle. The formal model “embodied capital” (Kaplan, 1996; Kaplan et al., 2000) poses that a larger difference between resource production and consumption (i.e. surplus of resource production) in adulthood allows high parental investment (i.e. resource transfers towards juveniles), and short interbirth intervals. Furthermore, long juvenile periods relate to the amount of time needed to acquire the skills necessary to produce surplus, and long post-reproductive periods would emerge from the need of parents to sustain their descendants (see Koster et al. (2020) for cross-cultural evidence). The principled model on “inter-generational resource transfers” (Lee, 2003) advances that—under the assumption of adult surplus of resource production, and transfer of this surplus towards juveniles—the potential for resource transfers at later ages can explain selection on reduced mortality at later ages. This would result in an extended lifespan, while the cumulative receipt of resources would explain the high mortality risk that juveniles experience early in life. This formulation of this model has been further developed to suggest that transfers co-evolve with low mortality, with adults being more efficient at producing resources and transferring them to juveniles, who are in turn more efficient at using these resources for somatic growth, reducing their mortality (Chu and Lee, 2006). The “pooled energy model” verbally extends this framework by suggesting that resources are not only transferred from parents to offspring, but that alloparenting from individuals of different generations reduces the load of parental investment, and therefore allows the allocation of more resources towards reproduction and growth (Kramer and Ellison, 2010). These models highlight that the key dynamics that constrain female human life cycles appear to be related to how both the physical and the social environment influence how individuals gain and invest resources. However, these models cannot be used to predict variability of life cycles between individuals within populations because, as adaptive models, they predict that there should be one optimal life cycle. Furthermore, because they focus on optimal strategies given an environment, they do not account for possible masking effects of life history trade offs within a population that are likely to occur from the differences among individuals within a population in their ability to acquire resources in a given environment, as demonstrated by the theoretical model from Van Noordwijk and de Jong (1986).

The evolutionary models that predict variability in life cycles within populations focus on how individual differences in resource acquisition and allocation at different life cycle stages might result in differences in fitness. One set of models predicts that differences in how many resources individuals receive during their early life might have far reaching consequences for the whole life cycle. The “silver spoon model” predicts that individuals who receive more resources early in life will have the highest fitness irrespective of the adult environmental conditions (Pigeon et al., 2019; Lummaa and Clutton-Brock, 2002). In contrast, the “adaptive developmental plasticity model” proposes that individuals whose experience in early life matches what they experience later in life would develop a phenotype that allows a higher fitness than those that have a mismatch between early and late life (Bateson et al., 2004; Nettle and Bateson, 2015). The “environmental saturation model” expands these early life models to point out that differences between individuals should be most visible in environments with intermediate conditions, because harsh environments would constrain all individuals while abundant ones would permit individuals with a disadvantage to catch up (Engqvist and
different life history traits (i.e. life history trade-offs). Through this logic, individuals with many resources may have enough resources to allocate resources to survival and reproduction equally. The differences created by resource availability can explain why individuals who live longer can also have the highest reproductive output within a population, masking the trade-offs expected to exist among life history traits. Recent reviews from the pace-of-life syndrome framework on these trade-off models show that resource acquisition appears to indeed play an equal, or larger, role than resource allocation in explaining life cycle differences between individuals [Laskowski et al., 2021] [Haave-Audet et al., 2022]. However, in all of these evolutionary models, resource acquisition is the variable that is manipulated, which precludes that ability of these models to predict the expected amount of variation in a population. Alongside this, existing models have not examined the possibility of resource transfers between individuals (beyond that which is observed between parents and offspring), which diversifies the ways in which resources are acquired and distributed within a population.

Resource transfers, which have been proposed as a key component for understanding female human life cycles, complicate patterns of resource acquisition because sharing limited resources typically benefits some individuals at the cost of others. The benefits of sharing resources have been linked to two strategies that matter in terms of variability in fitness: bet-hedging and cooperative breeding. In environments where resource production might be unpredictable, flexible resource transfers that are based on surpluses and need can be a way for individuals to hedge their bets [Carter et al., 2017]. This redistribution of resources is expected to lead to a decrease in the variance of life cycles between individuals. Therefore, sharing behaviour might reduce the risk that the fitness of an individual will drop to zero in unpredictable environmental conditions, increasing the long-term fitness of individuals exhibiting such a strategy within a population [Cohen, 1966] [Gillespie, 1974] [Caswell, 1983] [Starrfelt and Kokko, 2012]. In primates, including humans, life history strategies are characterised by delayed reproduction, reduced fertility, and extended generation times. These strategies can be viewed as adaptive responses to highly unstable environments, which leads to also high fluctuations in population size (i.e. non-equilibrium ecological conditions) [Jones, 2011]. These strategies enable individuals to explore diverse environments over longer periods, thereby enhancing the likelihood that their descendants will survive, and decreasing the influence of variability over the mean fitness [Jones, 2011]. Cooperative breeding has also been proposed as a bet-hedging strategy [Rubenstein, 2011]. However, in this case the idea is that dominant individuals maximise their fitness because the contribution of the helpers reduces any environmentally-induced fecundity variance. This leads to higher variability in life cycles between individuals in the group. Evidence in humans supports models of bet-hedging, and speaks more closely to cooperative breeding (i.e. communal breeding), due to the common practice of resources transfers between individuals of a population (e.g. alloparenting [Ivey, 2000] [Sear and Mace, 2008] [Sear and Coall, 2011] [Kramer and Veile, 2018] or food sharing [Gurven et al., 2000] [Gurven, 2004] [Jaeggi and Gurven, 2013] [Bird et al., 2002] [Gettler et al., 2023] [Ready and Power, 2018]). However, there is also evidence showing that resource dynamics in humans is influenced by competitive dynamics that occurs over limited social and material resources [Nitsch et al., 2013] [Mace and Alvergne, 2012] [Lahdenperä et al., 2012] [Redhead and von Rueden, 2021] [Redhead and Power, 2022]. The mixed evidence regarding the nature of resource transfers in human populations can be explained because such dynamics can change depending on the genetic relatedness between individuals [Strassmann, 2011] or by the amount of resource available [Borgerhoff Mulder, 2007]. One common, but not exclusive, pattern regarding sharing dynamics in human populations are inter-generational resource transfers that go from older individuals in the population towards younger ones (i.e. downward resource transfers), in order to
Another set of models focuses on the resources that adults have available for the trade-offs between different life history traits (Van Noordwijk and de Jong, 1986). These models suggest that high variability in resource acquisition between individuals reduces the variability of resource allocation within individual. This is because individuals who have few resources cannot allocate resources equally towards different life history traits (i.e. life history trade-offs). Through this logic, individuals with many resources may have enough resources to allocate resources to survival and reproduction equally. The differences created by resource availability can explain why individuals who live longer can also have the highest reproductive output within a population, masking the trade-offs expected to exist among life history traits. Recent reviews from the pace-of-life syndrome framework on these trade-off models show that resource acquisition appears to indeed play an equal, or larger, role than resource allocation in explaining life cycle differences between individuals (Laskowski et al., 2021; Haave-Audet et al., 2022). However, in all of these evolutionary models, resource acquisition is the variable that is manipulated, which precludes that ability of these models to predict the expected amount of variation in a population. Alongside this, existing models have not examined the possibility of resource transfers between individuals (beyond that which is observed between parents and offspring), which diversifies the ways in which resources are acquired and distributed within a population.

Resource transfers, which have been proposed as a key component for understanding female human life cycles, complicate patterns of resource acquisition because sharing limited resources typically benefits some individuals at the cost of others. The benefits of sharing resources have been linked to two strategies that matter in terms of variability in fitness: bet-hedging and cooperative breeding. In environments where resource production might be unpredictable, flexible resource transfers that are based on surpluses and need can be a way for individuals to hedge their bets (Carter et al., 2017). This redistribution of resources is expected to lead to a decrease in the variance of life cycles between individuals. Therefore, sharing behaviour might reduce the risk that the fitness of an individual will drop to zero in unpredictable environmental conditions, increasing the long-term fitness of individuals exhibiting such a strategy within a population (Cohen, 1966; Gillespie, 1974; Caswell, 1983; Starrfelt and Kokko, 2012). In primates, including humans, life history strategies are characterised by delayed reproduction, reduced fertility, and extended generation times. These strategies can be viewed as adaptive responses to highly unstable environments, which leads to also high fluctuations in population size (i.e. non-equilibrium ecological conditions) (Jones, 2011). These strategies enable individuals to explore diverse environments over longer periods, thereby enhancing the likelihood that their descendants will survive, and decreasing the influence of variability over the mean fitness (Jones, 2011). Cooperative breeding has also been proposed as a bet-hedging strategy (Rubenstein, 2011). However, in this case the idea is that dominant individuals maximise their fitness because the contribution of the helpers reduces any environmentally-induced fecundity variance. This leads to higher variability in life cycles between individuals in the group. Evidence in humans supports models of bet-hedging, and speaks more closely to cooperative breeding (i.e. communal breeding), due to the common practice of resource transfers between individuals of a population (e.g. alloparenting (Ivey, 2000; Sear and Mace, 2008; Sear and Coal, 2011; Kramer and Veille, 2018) or food sharing (Gurven, 2004; Jaeggi and Gurven, 2013; Bird et al., 2002; Gettler et al., 2023; Ready and Power, 2018)). However, there is also evidence showing that resource dynamics in humans is influenced by competitive dynamics that occurs over limited social and material resources (Nitsch et al., 2013; Mace and Alvergne, 2012; Lahdenperä et al., 2012; Redhead and von Rueden, 2021; Redhead and Power, 2022). The mixed evidence regarding the nature of resource transfers in human populations can be explained because such
ensure that juveniles survive and develop until adulthood (Chu and Lee 2006; Lee 2003; Kramer and Ellison 2010; Hooper et al. 2015).

Our model aims to understand how the variability of life cycles within a population change based on the influence of different resource dynamics and habitat quality. Extant models have focused on the resource dynamics under which the female human life cycle evolved (e.g. embodied capital model (Kaplan, 1996) or resource transfer model (Chu and Lee, 2006)), while the model here advances the literature by focusing on the mechanisms that drive the variability of life cycles within a population, rather than on the emergence of a specific life cycle. Additionally, the model is more explicit in modelling resource dynamics than previous models (Price and Jones, 2020; Kaplan, 1996; Chu and Lee, 2006; Lee, 2003; Kramer and Ellison 2010; Van Noordwijk and de Jong, 1986), as it assumes that networks of resource transfers follow stage-structure. The model will focus on answering four research questions, which increase in complexity.

(1) How is the variability of life cycles within a female human population influenced by stochasticity in individual resource production? Building upon Van Noordwijk and de Jong (1986), we expect that there will be a higher variability of life cycles in a population under higher stochastic differences of resource production between individuals due to larger individual differences in the amount of resources available that can be allocated towards survival and reproduction. (2) How does the relationship between resource production and life cycle variability change under different environmental conditions (i.e. habitat quality)? We expect that the variability of life cycles within a female human population decreases as habitat quality increases. With higher habitat quality, individuals can have a larger amount of resources available to allocate towards survival and/or reproduction—buffering the individual differences in resource production and, therefore, homogenising the life cycles in the population such that variability is reduced (Bolund, 2020). (3) How does stochastic variation in resource transfers influence the variability of life cycles within a female human population? Considering the literature related to bet-hedging (Jones, 2011), we expect that the redistribution of resources within the population will act as a buffer against environmental uncertainty, and therefore decrease the variability of life cycles as the probabilities of individual resource transfers increase. (4) How does the variability of life cycles within a population change due to the interplay between individual resource dynamics and environmental conditions? We will look at the full interplay between habitat quality, resource production and transfers to determine how their interaction may change the ways in which resource availability influences the variability of life history traits within a human population (see Fig. 1 for a graphical representation).
dynamics can change depending on the genetic relatedness between individuals (Strassmann, 2011) or by
the amount of resource available (Borgerhoff Mulder, 2007). One common, but not exclusive, pattern
regarding sharing dynamics in human populations are inter-generational resource transfers that go from
older individuals in the population towards younger ones (i.e. downward resource transfers), in order to
ensure that juveniles survive and develop until adulthood (Chu and Lee, 2006; Lee, 2003; Kramer and
Ellison, 2010; Hooper et al., 2015).

Our model aims to understand how the variability of life cycles within a female population change
based on the influence of different resource dynamics and habitat quality. Extant models have focused
on the resource dynamics under which the female human life cycle evolved (e.g. embodied capital model
(Kaplan, 1996) or resource transfer model (Chu and Lee, 2006)), while the model here advances the literature
by focusing on the mechanisms that drive the variability of life cycles within a population, rather than
on the emergence of a specific life cycle. Additionally, the model is more explicit in modelling resource
dynamics than previous models (Price and Jones, 2020; Kaplan, 1996; Chu and Lee, 2006; Lee, 2003;
Kramer and Ellison, 2010; Van Noordwijk and de Jong, 1986), as it assumes that networks of resource
transfers follow stage-structure. The model will focus on answering four research questions, which increase
in complexity, following a generative inference approach (Kandler and Powell, 2018). Hence, the patterns
stated here are meant as possible scenarios that would emerge based on the assumptions and parameter
settings of the model. (1) How is the variability of life cycles within a female human population influenced
by stochasticity in individual resource production? Building upon Van Noordwijk and de Jong (1986),
it would be expected a higher variability of life cycles in a population under higher stochastic differences
of resource production between individuals due to larger individual differences in the amount of resources
available that can be allocated towards survival and reproduction. (2) How does the relationship between
resource production and life cycle variability change under different environmental conditions (i.e. habitat
quality)? The variability of life cycles within a female human population should decrease as habitat quality
increases. With higher habitat quality, individuals can have a larger amount of resources available to
allocate towards survival and/or reproduction—buffering the individual differences in resource production
and, therefore, homogenising the life cycles in the population such that variability is reduced (Bolund, 2020).
(3) How does stochastic variation in resource transfers influence the variability of life cycles within a female
human population? Considering the literature related to bet-hedging (Jones, 2011), the redistribution of
resources within the population should act as a buffer against environmental uncertainty, and therefore
decrease the variability of life cycles as the probabilities of individual resource transfers increase. (4)
How does the variability of life cycles within a population change due to the interplay between individual
resource dynamics and environmental conditions? We will look at the full interplay between habitat quality,
resource production and transfers to determine how their interaction may change the ways in which resource
availability influences the variability of life history traits within a human population (see Fig. 1 for a
graphical representation).
Figure 1: Graphical summary of the model, which explains that the differences in the amount of resources available between individuals, and the redistribution of them via resource transfers, can lead to variations in the distribution of life cycles within a population (e.g., longevity and lifetime reproductive output). Because individuals can have dissimilar amount of resources, and share different amounts as well, they have variations in the number of resources they can allocate towards survival and reproduction. These individual differences can be seen at the population level, by having distributions where either individuals have very homogeneous longevity and lifetime reproductive output (dotted line) or very diverse life cycles (solid line), while also existing the possibility that the variability of life cycles shows some medium values (dashed line).

In this registered report, we developed a computational framework to address these questions. This framework includes the complexity of environmental conditions, resource dynamics, as well as life history dynamics that might arise in different environmental and social conditions. By focusing on resource dynamics, our framework can show the potential biological limits to life cycle variation. The framework will be explored using an agent-based model. This is because agent-based models have the capacity to address complex phenomena from individual and population levels and because of its implicit way to incorporate stochasticity by allowing agents to behave differently, despite being all under the same rules (Judson 1994; Wilensky and Rand 2015). The key parameters in the model are: habitat quality, defined as the maximum amount of resources available in the environment at any given time; production probability, which is the probability that individuals successfully acquire resources from the environment at any given time; and transfer probability, the probability that individuals will share resources with each other. In the following section, we describe the model following an ODD (Overview, Design concepts, Details) protocol, as a standardised approach for clarifying the scope, assumptions, and parameters used to answer our research questions (Grimm et al. 2006, 2020). For question 1, we will run the agent-based model without sharing, setting the habitat quality to baseline, and change the production probabilities to range between 0.1 and 0.9, producing a total of 41 values in our parameter sweep. For question 2, we will set sharing to zero, habitat quality to high, and change the production probabilities to range between 0.1 and 0.9 (an additional 41 values). For question 3, we set habitat quality to baseline, production probabilities to average, and change
In this registered report, we developed a computational framework to address these questions. This framework includes the complexity of environmental conditions, resource dynamics, as well as life history dynamics that might arise in different environmental and social conditions. By focusing on resource dynamics, our framework can show the potential biological limits to life cycle variation. The framework will be explored using an agent-based model. This is because agent based models have the capacity to address complex phenomena from individual and population levels and because of its implicit way to incorporate stochasticity by allowing agents to behave differently, despite being all under the same rules (Judson 1994; Wilensky and Rand 2015). The key parameters in the model are: habitat quality, defined as the maximum amount of resources available in the environment at any given time; production probability, which is the probability that individuals successfully acquire resources from the environment at any given time; and transfer probability, the probability that individuals will share resources with each other. The output of the model will be the population distribution of key life history traits that characterise female human life cycle: longevity, lifetime reproductive output, age at sexual maturity, age at first reproduction, and age at menopause. In the following section, we describe the model following an ODD (Overview, Design concepts, Details) protocol, as a standardised approach for clarifying the scope, assumptions, and parameters used to answer our research questions (Grimm et al. 2006, 2020). For question 1, we will run the agent-based
the stage-specific sharing values to range between 0.05 and 0.95 (656 values), while maintaining the structure of the network. For question 4, we set habitat quality to baseline and high, production probabilities to range between 0.1 and 0.9 (41 values), and change the stage-specific values of sharing to range between 0.05 and 0.95 (656 values), leading to a maximum of 53792 combinations in our final simulation regime (see Table 1 for a summary). The total number of resulting combinations could be smaller than this maximum because populations die out if certain combinations lead to too few resources being generated (e.g., in preliminary explorations we noticed that populations with a habitat quality of 12 and a production probability of 0.3 will grow exponentially, whereas populations with the same habitat quality and a production probability of 0.2 quickly go extinct). We will repeat each unique combination 10 times. The model will allow us to understand the conditions and mechanisms that allow higher variability of life history traits within a population. Furthermore, the results will help to understand the demographic diversity observed among human populations, as well as offer a tool to further test the complexity of the environmental and social components that link resource availability with the development of life cycles.
model without sharing, setting the habitat quality to baseline, and change the production probabilities to range between 0.1 and 0.9, producing a total of 17 values in our parameter sweep. For question 2, we will set sharing to zero, habitat quality to high, and change the production probabilities to range between 0.1 and 0.9 (an additional 17 values). For question 3, we set habitat quality to baseline, production probabilities to average, and change the stage-specific sharing values to range between 0.05 and 0.95 (19 values, and 323 combinations), while maintaining the structure of the network. For question 4, we set habitat quality to baseline and high, production probabilities to range between 0.1 and 0.9 (17 values), and change the stage-specific values of sharing to range between 0.05 and 0.95 (19 values, and 323 combinations), leading to a maximum of 10982 combinations in our final simulation regime (see Table 1 for a summary). The total number of resulting combinations could be smaller than this maximum because populations die out if certain combinations lead to too few resources being generated (e.g. in preliminary explorations we noticed that populations with a habitat quality of 12 and a production probability of 0.3 will grow exponentially, whereas populations with the same habitat quality and a production probability of 0.2 quickly go extinct). We will repeat each unique combination 10 times. Afterwards, we will describe and compare the population distributions of the different life history traits (e.g. longevity, lifetime reproductive output, age at sexual maturity, first reproduction, and menopause) that result from each parameter sweep designed to answer each research question. The model will allow us to understand the conditions and mechanisms that allow higher variability of life history traits within a population. Furthermore, the results will help to understand the demographic diversity observed among human populations, as well as offer a tool to further test the complexity of the environmental and social components that link resource availability with the development of life cycles.
Table 1: Summary of the different combinations of resource production, transfers, and habitat quality that will be used to answer the different research questions. For each question, we will perform simulations across the range of parameter values shown in ‘production probability’. The values of 0.5 in “Production probability”, and 4 in “Habitat quality”, refer to the initial values used to design the model, which works as a baseline model. A value of 0 for resource transfers, refers to simulation regimes where there are no sharing dynamics. Finally, a value of 8 in “Habitat quality” refers to double the value set as baseline in habitat quality (4) to see how the dynamics change under abundant environments.

<table>
<thead>
<tr>
<th>Research question</th>
<th>Production probability</th>
<th>Habitat quality</th>
<th>Transfers probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>How is the variability of life cycles within a female human population influenced by individual resource production?</td>
<td>0.1 to 0.9 (41 values)</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>How does the relationship between resource production and life cycle variability change under different environmental conditions (i.e. habitat quality)?</td>
<td>0.1 to 0.9 (41 values)</td>
<td>4 and 8</td>
<td>0</td>
</tr>
<tr>
<td>How does variation in resource transfers at the individual level influence the variability of life cycles within a female human population?</td>
<td>0.5</td>
<td>4</td>
<td>0.05 to 0.95 (656 values)</td>
</tr>
<tr>
<td>How does the variability of life cycles within a population change due to the interplay of individual resource dynamics and environmental conditions?</td>
<td>0.1 to 0.9 (41 values)</td>
<td>4 and 8</td>
<td>0.05 to 0.95 (656 values)</td>
</tr>
</tbody>
</table>

2 Model description

2.1 Purpose and patterns

The purpose of our model is to understand how different resource dynamics influence the distribution of female life cycles within a population. The distribution of female human life cycles at the population level—the focus of our analyses—arises from differences in life history traits at the individual level. The life cycle of an individual is set to be influenced by the interplay of resource production, which partly depends
Table 1: Summary of the different combinations of resource production, transfers, and habitat quality that will be used to answer the different research questions. For each question, we will perform simulations across the range of parameter values shown in ‘production probability’. The values of 0.5 in “Production probability”, and 4 in “Habitat quality”, refer to the initial values used to design the model, which works as a baseline model. A value of 0 for resource transfers, refers to simulation regimes where there are no sharing dynamics. A value of 8 in “Habitat quality” refers to double the value set as baseline in habitat quality (4) to see how the dynamics change under abundant environments.

<table>
<thead>
<tr>
<th>Research question</th>
<th>Production probability</th>
<th>Habitat quality</th>
<th>Transfers probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>How is the variability of life cycles within a female human population influenced by individual resource production?</td>
<td>0.1 to 0.9 (17 values)</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>How does the relationship between resource production and life cycle variability change under different environmental conditions (i.e. habitat quality)?</td>
<td>0.1 to 0.9 (17 values)</td>
<td>4 and 8</td>
<td>0</td>
</tr>
<tr>
<td>How does variation in resource transfers at the individual level influence the variability of life cycles within a female human population?</td>
<td>0.5</td>
<td>4</td>
<td>0.05 to 0.95 (19 values, and 323 combinations)</td>
</tr>
<tr>
<td>How does the variability of life cycles within a population change due to the interplay of individual resource dynamics and environmental conditions?</td>
<td>0.1 to 0.9 (17 values)</td>
<td>4 and 8</td>
<td>0.05 to 0.95 (19 values, and 323 combinations)</td>
</tr>
</tbody>
</table>

2 Model description

2.1 Purpose and patterns

The purpose of our model is to understand how different resource dynamics influence the distribution of female life cycles within a population. The distribution of female human life cycles at the population level—the focus of our analyses—arises from differences in life history traits at the individual level. The life cycle of an individual is set to be influenced by the interplay of resource production, which partly depends...
on habitat quality, and resource transfers. Together, these parameters determine the amount of resources available for an individual to allocate towards survival, life stage transitions, and reproductive timing and output.

The life cycle of an individual, understood as the different life history traits describing the pace of events through life related to survival, reproduction, and growth and development, is described by her longevity, lifetime reproductive output, and the timing of life cycle stage transition. Longevity is the total number of years that an individual is alive. Lifetime reproductive output refers to the total number of descendants produced by the end of the life cycle of an individual. The timing of life cycle stage transition refers to the age at which an individual transitions through four discrete stages (i.e. juvenile, adult, reproductive-career, post-reproductive). Each transition represents a specific event in the life cycle of an individual: age at sexual maturity, age at first reproduction, and age at menopause.

Resource dynamics are characterised by the amount of resources available, produced, transferred, and stored throughout the life cycle. Resources available is the total amount of resources that are available to an individual before they are allocated towards survival, reproduction, and life cycle transition. Production is the amount of resources that an individual can acquire from her habitat, depending on habitat quality and the probability of producing resources. Storage of resources is defined as the amount of resources that an individual owns, of which pass from one iteration to the next one.

Resource transfers are operationalised as sharing dynamics, where an individual is provided the opportunity to send resources to other individuals in the population. The maximum number of transfers that an individual can send is determined by their surplus of available resources (i.e. amount of resources that an individual has once they account for the costs of reproduction and survival). The number of transfers an individual sends is stochastically determined, where the maximum number of transfers provide an upper limit. Who individuals choose to transfer resources to is probabilistically determined by the life cycle-stage structure of the population. We use a variation of a stochastic block model to construct these stage-structured resource transfers (Redhead et al., 2023; Ross et al., 2023; Lee and Wilkinson, 2019; Hollander et al., 1983). Furthermore, we use a block matrix, as part of the social network model, to specify the values for resource transfers within and between life cycle stages. This means that individuals of a given life cycle stage are more, or less, likely to transfer resources to other individuals, based on the life cycle stage that both individuals occupy. We use a block matrix, as part of the social network model, to specify the values for resource transfers within and between life cycle stages. For instance, in certain regimes, adults are more likely to share food with juveniles and post-reproductive individuals than other adults or those in their reproductive career within the population. An example of such sharing pattern can be seen among the Tsimane in Bolivian Amazonia, where parents, grandparents, and siblings provide significant net downward transfers of food across generations (Hooper et al., 2015).

We expect that the patterns of life cycle variation will depend on the resource dynamics that individuals experience. Therefore, changes in the probabilities of resource production and transfers, together with habitat quality, are predicted to produce individual differences of life history traits within the population (i.e. longevity, lifetime reproductive output, age at menarche, age at first reproduction, and age at menopause). First, an increase in the individual probabilities for resource production is expected to increase the average timing of transitions and the average reproductive output, and should lead to an inverted U-shaped pattern in the expected variation between individuals. These patterns would be expected because more resources mean that, on average, individuals are more likely to survive and reproduce. Regarding variability, individuals would experience more homogeneous resource dynamics on the extreme individual probabilities (e.g.
on habitat quality, and resource transfers. Together, these parameters determine the amount of resources available for an individual to allocate towards survival, life stage transitions, and reproductive timing and output.

The life cycle of an individual, understood as the different life history traits describing the pace of events through life related to survival, reproduction, and growth and development, is described by her longevity, lifetime reproductive output, and the timing of life cycle stage transition. Longevity is the total number of years that an individual is alive. Lifetime reproductive output refers to the total number of descendants produced by the end of the life cycle of an individual. The timing of life cycle stage transition refers to the age at which an individual transitions through four discrete stages (i.e. juvenile, adult, reproductive-career, post-reproductive). Each transition represents a specific event in the life cycle of an individual: age at sexual maturity, age at first reproduction, and age at menopause (see Fig. 2 for a graphical representation of the female human life cycle).

Resource dynamics are characterised by the amount of resources available, produced, transferred, and stored throughout the life cycle. Resources available is the total amount of resources that are available to an individual before they are allocated towards survival, reproduction, and life cycle transition. Production is the amount of resources that an individual can acquire from her habitat, depending on habitat quality and the probability of producing resources. Storage of resources is defined as the amount of resources that an individual owns, of which pass from one iteration to the next one (Fig. 2).

Resource transfers are operationalised as sharing dynamics, where an individual is provided the opportunity to send resources to other individuals in the population. The maximum number of transfers that an individual can send is determined by their surplus of available resources (i.e. amount of resources that an individual has once they account for the costs of reproduction and survival). The number of transfers an individual sends is stochastically determined, where the maximum number of transfers provide an upper limit. Who individuals choose to transfer resources to is probabilistically determined by the life-cycle-stage structure of the population. We assume a stochastic approach to remain agnostic regarding who transfers resources to whom because the focus of our research is on the relationship between resource dynamics and the variability of life history traits, and not the mechanisms behind the sharing dynamics. This assumption is based on the evidence showing that the different mechanisms behind the sharing dynamics in human populations are quite diverse (e.g. genetic relatedness, need-based, reciprocity, costly signaling (Gurven 2004; Allen-Arave et al. 2008; Sear and Mace 2008; Smith et al. 2019)), and therefore it would require a wider number of parameters, and an increase of the parameter space, in order to test the different mechanisms. Our aim here is to more generally understand if the presence of sharing dynamics in a population in general has the potential to shift life history dynamics, rather than to account for the specific sharing dynamics that might occur in different social and environmental contexts.

We use a variation of a stochastic block model to construct the stage-structured resource transfers (Redhead et al. 2023; Ross et al. 2023; Lee and Wilkinson 2019; Holland et al. 1983). We use a block matrix, as part of the social network model, to specify the values for resource transfers within and between life cycle stages. This means that individuals are more, or less, likely to transfer resources to other individuals, based on the life cycle stage that both individuals occupy. We assume an downward inter-generational resource transfer structure within the block matrix, meaning that individuals in younger stages of the life cycle (e.g. juveniles) are more likely to receive resources from those in older stages (e.g. adult). This assumption is based on previous theoretical work (Chu and Lee 2006; Kramer and Ellison 2010) and empirical work (Hooper et al. 2015; Lee 2020), which shows that it is a common pattern observed
with low resource production everyone is poor whereas with high resource production everyone is rich), reducing diversity in resource allocation towards survival and reproduction throughout their lives. Second, the patterns described above should be more extreme if the amount of resources that an individual acquires from her environment increases. Hence, the average life cycle would increase and the variability would show a shape with higher kurtosis. Finally, the inclusion of resource transfers is predicted to have a buffering effect, where the increase of the average life cycle and the inverted U-shaped pattern in variability would be more smooth compared to the patterns described before. This buffering is caused by the redistribution of resources within a population, which would reduce the probability that many individuals will show extreme life cycles (e.g. having no descendants or shorter lifespans) (see Table 2 and 1 for a summary). A graphical representation of how the distribution of life history traits can vary can be seen in Fig. 1, and the ways that resource dynamics are expected to influence the life cycle is shown in Fig. 2.
across human populations. Hence, resource transfers within the population are randomly directed, with the probability of a particular transfer occurring under the constraints of the resource surplus of an individual, her life cycle stage, and a downward inter-generational resource transfer regime.

Maternal investment is defined separately from resource transfers. The amount of resource an individual gives to her dependent descendants follows a need-base dynamic, providing sufficient resources to cover the survival costs of the descendant if the mother has sufficient resources (Aktipis 2016). Maternal dynamics are defined separately from general resource transfers because they are governed by separate evolutionary mechanisms (e.g. kin selection, parent-offspring conflict, reproductive conflict) from those that shape resource transfers among other individuals (Hamilton 1964; Godfray 1995; Cant and Johnstone 2008; Mace and Alvérne 2012). Hence, we assume it is a dynamic required for the development of the female human life cycle that works separately from the sharing dynamics within a population.

We expect that the patterns of life cycle variation will depend on the resource dynamics that individuals experience. Therefore, changes in the probabilities of resource production and transfers, together with habitat quality, are predicted to produce individual differences of life history traits within the population (i.e. longevity, lifetime reproductive output, age at menarche, age at first reproduction, and age at menopause). First, an increase in the individual probabilities for resource production is expected to increase the average timing of transitions and the average reproductive output, and should lead to an inverted U-shaped pattern in the expected variation between individuals. These patterns would be expected because more resources mean that, on average, individuals are more likely to survive and reproduce. Regarding variability, individuals would experience more homogeneous resource dynamics on the extreme individual probabilities (e.g. with low resource production everyone is poor whereas with high resource production everyone is rich), reducing diversity in resource allocation towards survival and reproduction throughout their lives. Second, the patterns described above should be more extreme if the amount of resources that an individual acquires from her environment increases. Hence, the average life cycle would increase and the variability would show a shape with higher kurtosis. Finally, the inclusion of resource transfers is predicted to have a buffering effect, where the increase of the average life cycle and the inverted U-shaped pattern in variability would be more smooth compared to the patterns described before. This buffering is caused by the redistribution of resources within a population, which would reduce the probability that many individuals will show extreme life cycles (e.g. having no descendants or shorter lifespans) (see Table 1 and 2 for a summary). A graphical representation of how the distribution of life history traits can vary can be seen in Fig. 1, and the ways that resource dynamics are expected to influence the life cycle is shown in Fig. 2.
Table 2: Summary of the study design. *Question* shows the research questions that motivated the development of the model. *Hypothesis* is an outline of our the predictions for each research question. *Analysis plan* describes the approach that we take to answer each research question. *Interpretation* is a description of a range of possible outcomes of our study, and their interpretation in relation to our hypotheses. *Contested theory* is a description on how the possible outcomes could prove wrong or show how incomplete are current theories.

<table>
<thead>
<tr>
<th>Question</th>
<th>Hypothesis</th>
<th>Analysis plan</th>
<th>Interpretation</th>
<th>Contested Theory</th>
</tr>
</thead>
<tbody>
<tr>
<td>How is the variability of life cycles within a female human population influenced by individual resource production?</td>
<td>There will be a higher variability of life cycles in a population under intermediate (but stochastic) differences of resource production between individuals. This is due to larger individual differences in the amount of resources available to allocate towards survival and reproduction.</td>
<td>We will run a simulation regime using our agent-based model and fix the probability of resource transfers to 0 for all individuals (i.e., there will be no sharing dynamics). We will set our habitat quality parameter to baseline (4), and vary the parameter that controls production probabilities to range between 0.1 and 0.9 (across 41 values).</td>
<td>Higher production probabilities allow, on average, for more individuals to obtain resources, which support extended lifespan and increased reproduction. Lower life cycle variability would happen under more extreme production probabilities as individuals would experience similar conditions of scarcity or abundance.</td>
<td>A lack of variability of life cycles after changes in production probabilities could be explained if selection processes have optimised the female human life cycle, allowing individuals to withstand fluctuations in resource production.</td>
</tr>
<tr>
<td>How does the relationship between resource production and life cycle variability change under different environmental conditions (i.e. habitat quality)?</td>
<td>The variability of life cycles within a female human population decreases as habitat quality increases. Under conditions of higher habitat quality, individuals can have a larger amount of resources available to allocate towards life history traits, buffering the individual differences in resource production and homogenising the life cycles in the population.</td>
<td>We will perform a simulation regime where the probability of resource transfers is set to 0 for all individuals (i.e., there will be no sharing dynamics). We will fix habitat quality to high (8), and perform a parameter sweep over the production probabilities, ranging between 0.1 and 0.9 (41 values).</td>
<td>Habitat quality acts as a buffering effect as resources will be so abundant that individuals will be able to sustain themselves, even though individuals they may be more often unsuccessful in production. This will reduce the variability in life cycles within the population.</td>
<td>If the increase in habitat quality leads to no changes in life cycle variability, it could be that either phenotypic masking is happening or that variability only shows in intermediate levels of habitat quality (Van Noordwijk and de Jong 1986; Engqvist and Reinhold 2010).</td>
</tr>
<tr>
<td>How does variation in the probabilities of resource transfers at the individual level influence the variability of life cycles within a female human population?</td>
<td>The redistribution of resources within the population will act as a buffer against environmental stochasticity, and therefore decrease the variability of life cycles as the probabilities of receiving resource transfers increase.</td>
<td>We will perform a simulation regime where we set our habitat quality and production probabilities to baseline (4 and 0.5, respectively), and equally vary the values of the block matrix for the resource transfers, while maintaining the network structure, to range between 0.05 and 0.95 (656 values).</td>
<td>Resource transfers buffers the effects of fluctuations in resource production on the life cycles within a population. The redistribution of resources allows individuals who fail to produce their own resources to sustain themselves and potentially reproduce, and therefore avoid extreme life cycles. On the other extreme, individuals who are successful in producing resources would avoid extreme life cycles by decreasing their resource surplus via resource transfers.</td>
<td>An increase in life cycle variability with higher resource transfers could be explained because the redistribution of limited resources could lead to other social behaviours that enhance inequality between individuals.</td>
</tr>
<tr>
<td>How does the variability of life cycles within a population change due to the interplay of individual resource dynamics and environmental conditions?</td>
<td>Scenarios where resource production is higher will display more extreme amounts of life cycle variability. This is because higher probabilities of resource transfers, and richer habitat quality, would act as buffers against larger amounts of life cycle variation between individuals.</td>
<td>We will perform a simulation regime where habitat quality is set to baseline (4) and high (8). We will vary production probabilities to range between 0.1 and 0.9 (41 values), and change the values of the block matrix, while maintaining the structure of the sharing network, to range between 0.05 and 0.95 (656 values). Overall, this will produce a maximum of 3362 combinations of parameter values.</td>
<td>Production is the main driver of individual differences in life cycles, while resource transfer always acts as a buffer. Habitat quality can act as a buffer only when there is enough resource abundance for individuals to compensate for years, or iterations, where they are unsuccessful.</td>
<td>If resource transfers have a higher impact on life cycle variability than production, then social dynamics would play a more fundamental role than individual performance in determining life cycles. If habitat quality is the main driver of life cycle variability, this would mean that the female human life cycle is more responsive to environmental changes than to individual resource dynamics.</td>
</tr>
</tbody>
</table>
Table 2: Summary of the study design. Question shows the research questions that motivated the development of the model. Hypothesis is an outline of the expected patterns that should be observed in the output of our model, based on the literature. Analysis plan describes the approach that we take to answer each research question. Interpretation is a description of a range of possible outcomes of our study, and their interpretation in relation to our hypotheses. Contested theory is a description on how the possible outcomes could prove wrong or show how incomplete are current theories. Finally, “life cycle variability” refers to the population distribution of the life history traits that characterise the female human life cycle (i.e., longevity, lifetime reproductive output, age at sexual maturity, age at first reproduction, and age of menopause), which are the outcomes of the model.

<table>
<thead>
<tr>
<th>Question</th>
<th>Hypothesis</th>
<th>Analysis plan</th>
<th>Interpretation</th>
<th>Contested Theory</th>
</tr>
</thead>
<tbody>
<tr>
<td>How is the variability of life cycles within a female human population influenced by individual resource production?</td>
<td>There will be a higher variability of life cycles in a population under intermediate (but stochastic) differences of resource production between individuals. This is due to larger individual differences in the amount of resources available to allocate towards survival and reproduction.</td>
<td>We will run a simulation regime using our agent-based model and fix the probability of resource transfers to 0 for all individuals (i.e., there will be no sharing dynamics). We will set our habitat quality parameter to baseline (4), and vary the parameter that controls production probabilities to range between 0.1 and 0.9 (across 41 values).</td>
<td>Higher production probabilities allow, on average, for more individuals to obtain resources, which support extended lifespan and increased reproduction. Lower life cycle variability would happen under more extreme production probabilities as individuals would experience similar conditions of scarcity or abundance.</td>
<td>A lack of variability of life cycles after changes in production probabilities could be explained if selection processes have optimised the female human life cycle, allowing individuals to withstand fluctuations in resource production.</td>
</tr>
<tr>
<td>How does the relationship between resource production and life cycle variability change under different environmental conditions (i.e. habitat quality)?</td>
<td>The variability of life cycles within a female human population decreases as habitat quality increases. Under conditions of higher habitat quality, individuals can have a larger amount of resources available to allocate towards life history traits, buffering the individual differences in resource production and homogenising the life cycles in the population.</td>
<td>We will perform a simulation regime where the probability of resource transfers is set to 0 for all individuals (i.e., there will be no sharing dynamics). We will fix habitat quality to high (8), and perform a parameter sweep over the production probabilities, ranging between 0.1 and 0.9 (41 values).</td>
<td>Habitat quality acts as a buffering effect as resources will be so abundant that individuals will be able to sustain themselves, even though individuals may be more often unsuccessful in production. This will reduce the variability in life cycles within the population.</td>
<td>If the increase in habitat quality leads to no changes in life cycle variability, it could be that either phenotypic masking is happening or that variability only shows in intermediate levels of habitat quality. [Van Noordwijk and de Jong, 1986; Kingvist and Reinhold, 2016]</td>
</tr>
<tr>
<td>How does variation in the probabilities of resource transfers at the individual level influence the variability of life cycles within a female human population?</td>
<td>The redistribution of resources within the population will act as a buffer against environmental stochasticity, and therefore decrease the variability of life cycles as the probabilities of receiving resource transfers increase.</td>
<td>We will perform a simulation regime where we set our habitat quality and production probabilities to set to baseline (4 and 0.5, respectively), and equally vary the values of the block matrix for the resource transfers, while maintaining the network structure, to range between 0.05 and 0.95 (656 values).</td>
<td>Resource transfers buffer the effects of fluctuations in resource production on the life cycles within a population. The redistribution of resources allows individuals who fail to produce their own resources to sustain themselves and potentially reproduce, and therefore avoid extreme life cycles. On the other extreme, individuals who are successful in producing resources would avoid extreme life cycles by decreasing their resource surplus via resource transfers.</td>
<td>An increase in life cycle variability with higher resource transfers could be explained because the redistribution of limited resources could lead to other social behaviours that enhance inequality between individuals.</td>
</tr>
<tr>
<td>How does the variability of life cycles within a population change due to the interplay of individual resource dynamics and environmental conditions?</td>
<td>Scenarios where resource production is higher will display more extreme amounts of life cycle variability. This is because higher probabilities of resource transfers, and richer habitat quality, would act as buffers against larger amounts of life cycle variation between individuals.</td>
<td>We will perform a simulation regime where habitat quality is set to baseline (4) and high (8). We will vary production probabilities to range between 0.1 and 0.9 (41 values), and change the values of the block matrix, while maintaining the structure of the sharing network, to range between 0.05 and 0.95 (656 values). Overall, this will produce a maximum of 3362 combinations of parameter values.</td>
<td>Resource transfers buffer the effects of fluctuations in resource production on the life cycles within a population. The redistribution of resources allows individuals who fail to produce their own resources to sustain themselves and potentially reproduce, and therefore avoid extreme life cycles. On the other extreme, individuals who are successful in producing resources would avoid extreme life cycles by decreasing their resource surplus via resource transfers.</td>
<td>If resource transfers have a higher impact on life cycle variability than production, then social dynamics would play a more fundamental role in determining life cycles. If habitat quality is the main driver of life cycle variability, this would mean that the female human life cycle is more responsive to environmental changes than to individual resource dynamics.</td>
</tr>
</tbody>
</table>
Figure 2: A graphical representation of the female human life cycle as specified by our model. The female human life cycle (a) is represented with a life cycle graph, dividing the life cycle in four stages: J is the sexually immature stage (i.e. juvenile), A is the sexually mature but without descendants stage (i.e. adult), RC is the stage where individuals reproduce (i.e. reproductive career), and PR is the stage where individuals no longer can reproduce (i.e. post-reproductive). The influence of resource dynamics on survival (b), reproduction (c) and life cycle stage transition (d), is based on the amount of resources stored from the previous iteration ($SR_{t-1}$), the amount of resources produced during the current iteration ($RP_t$), the resources involved in maternal investment ($MI_t$), the amount of resources that an individual has transferred ($RR_t/RT_t$), and the resources available after all of the above have occurred ($RA_t$) in the current iteration. The resources stored from one iteration to the next one ($RA_{t+1}$) are the amount of resources available updated after the resource dynamics and the life history dynamics of survival, reproduction, and transition occur (i.e. end of each iteration). Loop arrows below life cycle stages refer to the probability of remaining in that stage (i.e. survival). A newborn is produced either when an individual transitions from adult to reproductive career or when an individual reproduces during their reproductive career stage. The dashed arrows refer to the production of a descendant in a given life cycle (i.e. reproduction). The dashed arrow from A to J refers to the age at first reproduction, which is also the transition from A to RC, whereas the one from RC to J refers to reproduction within the reproductive career. The solid arrows between life cycle stages show the transition from one stage to the other. The solid arrows between resource dynamics display the directed relationship between variables, and how they relate to a life history trait of interest.
Figure 2: A graphical representation of the female human life cycle as specified by our model. The female human life cycle (a) is represented with a life cycle graph, dividing the life cycle in four stages: J is the sexually immature stage (i.e. juvenile), A is the sexually mature but without descendants stage (i.e. adult), RC is the stage where individuals reproduce (i.e. reproductive career), and PR is the stage where individuals no longer can reproduce (i.e. post-reproductive). The influence of resource dynamics on survival (b), reproduction (c) and life cycle stage transition (d), is based on the amount of resources stored from the previous iteration (SR\(_{t-1}\)), the amount of resources produced during the current iteration (RP\(_t\)), the resources involved in maternal investment (MI\(_t\)), the amount of resources that an individual has transferred (RR\(_t\)/RT\(_t\)), and the resources available after all of the above have occurred (RA\(_t\)) in the current iteration. The resources stored from one iteration to the next one (RA\(_{t+1}\)) are the amount of resources available updated after the resource dynamics and the life history dynamics of survival, reproduction, and transition occur (i.e. end of each iteration). Loop arrows below life cycle stages refer to the probability of remaining in that stage (i.e. survival). A newborn is produced either when an individual transitions from adult to reproductive career or when an individual reproduces during their reproductive career stage. The dashed arrows refer to the production of a descendant in a given life cycle (i.e. reproduction). The dashed arrow from A to J refers to the age at first reproduction, which is also the transition from A to RC, whereas the one from RC to J refers to reproduction within the reproductive career. The solid arrows between life cycle stages show the transition from one stage to the other. The solid arrows between resource dynamics display the directed relationship between variables, and how they relate to a life history trait of interest.
2.2 Entities, variables, and scale

2.2.1 Entities

An individual represents a female in a single-sex population. A single-sex population is a simplifying assumption that is commonly used in the field that operates under the assumption that the female population evolves independent of a male counterpart (Wood, 2017). Individuals are considered juveniles from birth until they reach menarche. Adults are individuals that are sexually mature but have not yet produced their first descendant, or reached menopause. Adults transition to a reproductive-career stage once they have their first reproduction, and remain in this stage until they reach menopause. From menopause onward, individuals are considered post-reproductive. An individual only dies if she has not enough resources to cover the survival costs. The population is run for about 10 generations (300 years) to assess the overall population dynamics produced by these assumptions, without inheritance from individuals towards their descendants, nor changes between generations in the strategies that individuals can follow, because we only record the reactions of individuals to the given conditions.

2.2.2 Scale

Each iteration in the model represents one year. One resource unit is non-divisible, and therefore values are rounded so resources are always natural numbers. Resource production is generated by sampling from a binomial distribution, which is informed by parameters controlling a stage-specific maximum amount of resource that can be produced ($n_{i,s}$) and a parameter controlling production probability ($p_{i,s}$). That is, the amount of resources and probability that an individual produces are stage-specific. During the resource transfer stage of our model, the number of resources transferred can range from zero (i.e. no receiving/giving) to a maximum based on the surplus of resources available for all individuals ($RTS_{i,t}$). At the individual-level, individuals can therefore decide to transfer 0 resources to others—and keep the resources for themselves—or transfer resources up to the amount of resources that they have available at that stage of the iteration. We simulate resources transfers from a multinomial distribution. Intuitively, the probability of an individual transferring one unit of their available resources to others within population is structured by life cycle stage; there are different probabilities assigned to resource transfers based on the stage that the deciding individual occupies and the stage in which the other individuals in the population occupy. The total amount of resources that an individual transfers is typically referred to as their out-degree, whereas the total amount that an individual receives denotes their in-degree. Life history dynamics are evaluated after the resource dynamics, starting with reproduction, followed by stage transition, and finishing with survival. Finally, the amount of resources available by the end of the iteration is stored and passed from one year to the next.

2.2.3 Variables

Every individual in the simulation is characterised by the resource and life history dynamics that they go through in each iteration. These dynamics are defined by different state and auxiliary variables. The state variables are those that are either recalculated in each iteration or modified from one iteration to the next. Auxiliary variables are those that define the boundaries for the state variables, so they are set at initialisation and apply to all individuals equally. Here, we first describe the variables related to the resources dynamics, followed by variables related to life history dynamics. Furthermore, we describe the
2.2 Entities, variables, and scale

2.2.1 Entities

An individual represents a female in a single-sex population. A single-sex population is a simplifying assumption that is commonly used in the field that operates under the assumption that the female population evolves independent of a male counterpart [Wood 2017]. Individuals are considered juveniles from birth until they reach menarche. Adults are individuals that are sexually mature but have not yet produced their first descendant, or reached menopause. Adults transition to a reproductive-career stage once they have their first reproduction, and remain in this stage until they reach menopause. From menopause onward, individuals are considered post-reproductive. An individual only dies if she has not enough resources to cover the survival costs. The population is run for about 10 generations (300 years) to assess the overall population dynamics produced by these assumptions, without inheritance from individuals towards their descendants, nor changes between generations in the strategies that individuals can follow, because we only record the reactions of individuals to the given conditions.

2.2.2 Scale

Each iteration in the model represents one year. One resource unit is non-divisible, and therefore values are rounded so resources are always natural numbers. Resource production is generated by sampling from a binomial distribution, which is informed by parameters controlling a stage-specific maximum amount of resource that can be produced \( (n_{i,s}) \) and a parameter controlling production probability \( (p_{i,s}) \). That is, the amount of resources and probability that an individual produces are stage-specific. During the resource transfer stage of our model, the number of resources transferred can range from zero (i.e. no receiving/giving) to a maximum based on the surplus of resources available for all individuals \( (RTS_{i,t}) \). At the individual-level, individuals can therefore decide to transfer 0 resources to others—and keep the resources for themselves—or transfer resources up to the amount of resources that they have available at that stage of the iteration. We simulate resources transfers from a multinomial distribution. Intuitively, the probability of an individual transferring one unit of their available resources to others within population is structured by life cycle stage; there are different probabilities assigned to resource transfers based on the stage that the deciding individual occupies and the stage in which the other individuals in the population occupy. The total amount of resources that an individual transfers is typically referred to as their out-degree, whereas the total amount that an individual receives denotes their in-degree. Life history dynamics are evaluated after the resource dynamics, starting with reproduction, followed by stage transition, and finishing with survival. Finally, the amount of resources available by the end of the iteration is stored and passed from one year to the next.

2.2.3 Variables

Every individual in the simulation is characterised by the resource and life history dynamics that they go through in each iteration. These dynamics are defined by different state and auxiliary variables. The state variables are those that are either recalculated in each iteration or modified from one iteration to the next. Auxiliary variables are those that define the boundaries for the state variables, so they are set at initialisation and apply to all individuals equally. Here, we first describe the variables related to the resources dynamics, followed by variables related to life history dynamics. Furthermore, we describe the
variables within each category following the different modules that an individual goes through during an iteration (see Fig. 2 for a graphical representation, and Fig. 3 for a detailed description).

Resource dynamics

**Resources available (State variable):** Is the amount of resources that an individual has available through time, and different resource and life history dynamics. The amount of resources available by the end of the iteration, and are stored to the next one, is calculated as:

\[
RA_{i,t,m} = RA_{i,t-1} + RP_{i,t} - MI_{i,t} + DN_{i,t} - RT_{i,t} + RR_{i,t} - RC - TrC - SC
\]  

(1)

where \(RA_{i,t,m}\) is the amount of resources available for individual \(i\) at time \(t\) and module \(m\), \(RA_{i,t-1}\) the resources available for individual \(i\) from the previous iteration \((t-1)\), \(RP_{i,t}\) the amount of resources produced, \(MI_{i,t}\) the maternal investment, \(DN_{i,t}\) is the descendant need of individual \(i\) at time \(t\), \(RT_{i,t}\) is the amount of resources transferred, and \(RR_{i,t}\) is the amount of resources received by individual \(i\) at time \(t\). \(RC\), \(TrC\), and \(SC\) are the reproductive, transition, and survival costs, respectively. It is important to notice that maternal investment will have a value different to zero only while the individual is in her reproductive career stage, and descendant need only while the individual is in the juvenile stage.

The amount of resources available is constantly updated throughout the iteration, as the different resource (i.e. production, maternal investment, and resource transfers) and life history modules (i.e. reproduction, transition, and survival) occur.

**Resource production (State variable):** Is the amount of resources produced by an individual \(i\) at time \(t\). The amount is calculated by randomly sampling from a Binomial distribution, with stage-specific parameter values. Resource production is defined as:

\[
RP_{i,t} \sim \text{Binomial}(n_{i,s}, p_{i,s})
\]  

(2)

Where \(RP_{i,t}\) is the amount of resources produced by individual \(i\) at time \(t\), \(n_{i,s}\) is the maximum amount of resources individual \(i\) can produce at stage \(s\), and \(p_{i,s}\) is the probability of resource production of individual \(i\) at stage \(s\).

**Maximum resource production (Auxiliary variable):** Is the maximum amount of resources an individual can produce in the iteration \(n_{i,s}\) that is used in the state variable “Resource production”. The amount is stage-specific, so it can resemble the ontogeny of skill change in resource production [Kaplan et al., 2000; Lee and Kramer, 2002; Koster et al., 2020]. The stage-specific maximum resource production is defined as:

\[
n_{i,s} = HQ \times n_s
\]  

(3)

Where \(n_{i,s}\) is the maximum amount of resources an individual \(i\) can produce in stage \(s\), \(HQ\) is habitat quality, and \(n_s\) is the stage-specific resource production.

**Habitat quality (Auxiliary variable):** Is the maximum amount of resources available for any individual to acquire from the environment \((HQ)\).
variables within each category following the different modules that an individual goes through during an iteration (see Fig. 2 for a graphical representation, and Fig. 3 for a detailed description).

**Resource dynamics**

**Resources available (State variable):** Is the amount of resources that an individual has available through time, and different resource and life history dynamics. The amount of resources available by the end of the iteration, and are stored to the next one, is calculated as:

\[
RA_{i,t,m} = RA_{i,t-1} + RP_{i,t} - MI_{i,t} + DN_{i,t} - RT_{i,t} + RR_{i,t} - RC - TrC - SC
\]  

where \(RA_{i,t,m}\) is the amount of resources available for individual \(i\) at time \(t\) and module \(m\), \(RA_{i,t-1}\) the resources available for individual \(i\) from the previous iteration \((t-1)\), \(RP_{i,t}\) the amount of resources produced, \(MI_{i,t}\) the maternal investment, \(DN_{i,t}\) is the descendant need of individual \(i\) at time \(t\), \(RT_{i,t}\) is the amount of resources transferred, and \(RR_{i,t}\) is the amount of resources received by individual \(i\) at time \(t\). \(RC\), \(TrC\), and \(SC\) are the reproductive, transition, and survival costs, respectively. It is important to notice that maternal investment will have a value different to zero only while the individual is in her reproductive career stage, and descendant need only while the individual is in the juvenile stage.

The amount of resources available is constantly updated throughout the iteration, as the different resource (i.e. production, maternal investment, and resource transfers) and life history modules (i.e. reproduction, transition, and survival) occur.

**Resource production (State variable):** Is the amount of resources produced by an individual \(i\) at time \(t\). The amount is calculated by randomly sampling from a Binomial distribution, with stage-specific parameter values. Resource production is defined as:

\[
RP_{i,t} \sim \text{Binomial}(n_{i,s}, p_{i,s})
\]

Where \(RP_{i,t}\) is the amount of resources produced by individual \(i\) at time \(t\), \(n_{i,s}\) is the maximum amount of resources individual \(i\) can produce at stage \(s\), and \(p_{i,s}\) is the probability of resource production of individual \(i\) at stage \(s\).

**Maximum resource production (Auxiliary variable):** Is the maximum amount of resources an individual can produce in the iteration \((n_{i,s})\) that is used in the state variable “Resource production”. The amount is stage-specific, so it can resemble the ontogeny of skill change in resource production [Kaplan et al., 2000; Lee and Kramer, 2002; Koster et al., 2020]. The stage-specific maximum resource production is defined as:

\[
n_{i,s} = HQ * n_s
\]

Where \(n_{i,s}\) is the maximum amount of resources an individual \(i\) can produce in stage \(s\), \(HQ\) is habitat quality, and \(n_s\) is the stage-specific resource production.

**Habitat quality (Auxiliary variable):** Is the maximum amount of resources available for any individual to acquire from the environment \((HQ)\).
Algorithm 1 Pseudocode for an iteration in the agent-based model

Generate initial population with stage-specific uniform structure
Define habitat quality ($HQ$)
Define stage-specific maximum resource production ($n_{i,s}$)
Define stage-specific production probabilities ($p_{i,s}$)
Define block matrix ($B$)
Define survival cost ($SC$)
Define reproductive cost ($RC$)
Define reproductive threshold ($RT_h$)

for iteration=1,2, . . . , $t$ do
    Compute the amount of resources produced
    $RP_{i,t} = \text{Binomial}(n_{i,s}, p_{i,s})$
    Update resources available ($RA_{i,t}$)
    if $RA_{i,t} > SC$ and $RA_{j,i} < SC$ then
        Compute need-based maternal investment
        Update $RA_{i,t}$
    end if
    if $RA_{i,t} > SC$ and $s = J|PR$ or $RA_{i,t} > SC + RC$ and $s = A|RC$ then
        Compute maximum out-degree
        Generate social network
        Record out-degree and in-degree
        Update $RA_{i,t}$
    end if
    if $RA_{i,t} \geq RT_h$ then
        Reproduce and discount $RC$
        Update $RA_{i,t}$
    else
        Do not reproduce
    end if
    if $s = J$, older than 10 yo and $RA_{i,t} \geq RT_h$ OR $s = J$ and older than 18 yo then
        Transition to adult stage (A) and discount $RC$
    else if $stage = A$ and $RA_{i,t} \geq RT_h$ then
        Go through reproductive dynamics and transition to reproductive career stage (RC)
    else if $s = RC$, older than 40 yo, have not reproduced in the last 10 years and $RA_{i,t} \leq RT_h$ OR older than 60 yo then
        Transition to post-reproductive stage (PR)
    end if
    if $RA_{i,t} \geq SC$ then
        Survive and age
        Update resources available
        Update stored resources
    else
        Die
    end if
    Update population
end for

Figure 3: Algorithm representing the resource and life history dynamics that an individual goes through in one iteration (i.e. one year). First, are defined the different auxiliary variables, such as habitat quality ($HQ$), stage-specific maximum resource production ($n_{i,s}$), stage-specific production probabilities ($p_{i,s}$), block matrix ($B$), survival cost ($SC$), reproductive cost ($RC$), and reproductive threshold ($RT_h$). Furthermore, there are further definitions for the amount of resources available: for individual $i$ at time $t$ ($RA_{i,t}$) and for descendant $j$ of individual $i$ ($RA_{j,i}$). Finally, $i$ refers to the focus individual in the iteration, $j$ to the descendant of her, $t$ is the iteration, $s$ is the life cycle stage, and $J$, $A$, $RC$, $PR$ are the juvenile, adult, reproductive career, and post-reproductive stages, respectively.
Algorithm 1: Pseudocode for an iteration in the agent-based model

Generate initial population with stage-specific uniform structure
Define habitat quality \(HQ\)
Define stage-specific maximum resource production \(n_{i,s}\)
Define stage-specific production probabilities \(p_{i,s}\)
Define block matrix \(B\)
Define survival cost \(SC\)
Define reproductive cost \(RC\)
Define reproductive threshold \(RTh\)

for iteration=1,2, \ldots, t do

Compute the amount of resources produced
\(RP_{i,t} = \text{Binomial}(n_{i,s}, p_{i,s})\)
Update resources available \(RA_{i,t}\)
if \(RA_{i,t} > SC\) and \(RA_{j,i} < SC\) then
  Compute need-based maternal investment
  Update \(RA_{i,t}\)
end if

if \(RA_{i,t} > SC\) and \(s = J|PR\) or \(RA_{i,t} > SC + RC\) and \(s = A|RC\) then
  Compute maximum out-degree
  Generate social network
  Record out-degree and in-degree
  Update \(RA_{i,t}\)
end if

if \(RA_{i,t} \geq RTh\) then
  Reproduce and discount \(RC\)
  Update \(RA_{i,t}\)
else
  Do not reproduce
end if

if \(s = J\), older than 10 yo and \(RA_{i,t} \geq RTh\) OR \(s = J\) and older than 18 yo then
  Transition to adult stage (A) and discount \(RC\)
else if \(s = A\) and \(RA_{i,t} \geq RTh\) then
  Go through reproductive dynamics and transition to reproductive career stage (RC)
else if \(s = RC\), older than 40 yo, have not reproduced in the last 10 years and \(RA_{i,t} \leq RTh\) OR older than 60 yo then
  Transition to post-reproductive stage (PR)
end if

if \(RA_{i,t} \geq SC\) then
  Survive and age
  Update resources available
  Update stored resources
else
  Die
end if
Update population

end for

Figure 3: Algorithm representing the resource and life history dynamics that an individual goes through in one iteration (i.e. one year). First, are defined the different auxiliary variables, such as habitat quality \(HQ\), stage-specific maximum resource production \(n_{i,s}\), stage-specific production probabilities \(p_{i,s}\), block matrix \(B\), survival cost \(SC\), reproductive cost \(RC\), and reproductive threshold \(RTh\). Furthermore, there are further definitions for the amount of resources available: for individual \(i\) at time \(t\) \((RA_{i,t})\) and for descendant \(j\) of individual \(i\) \((RA_{j,i})\). Finally, \(i\) refers to the focus individual in the iteration, \(j\) to the descendant of her, \(t\) is the iteration, \(s\) is the life cycle stage, and \(J, A, RC, PR\) are the juvenile, adult, reproductive career, and post-reproductive stages, respectively.
Stage-specific resource production (Auxiliary variable): Is the offset, as proportion between 0 and 1, that is used in the auxiliary variable “Maximum resource production” to define the amount of resource production an individual can produce depending on her life cycle stage ($n_s$).

Production probability (Auxiliary variable): Is the stage-specific probability of producing resources ($p_{i,s}$) that is used in the state variable “Resource production”. The probabilities are stage-specific so they can follow the ontogeny of resource production that characterise humans, where juveniles and post-reproductive individuals are less likely to produce resources than individuals in the adult and reproductive career stages [Kaplan et al. 2000; Lee and Kramer 2002; Koster et al. 2020]. Hence, production probability of an individual $p_{i,s}$ is defined as:

$$ p_{i,s} = \max(p) \ast p_s $$

Where $p_{i,s}$ is the stage-specific production probability of individual $i$ in stage $s$, $\max(p)$ is the maximum production probability for any individual in the population, and $p_s$ is the stage-specific offset that defines the production probability for the individual.

Maximum production probability (Auxiliary variable): Is the maximum probability of resource production for all individuals in the population ($\max(p)$).

Stage-specific production probability (Auxiliary variable): Is the offset of the production probability that individuals have depending on their life cycle stage ($p_s$).

The dynamics regarding production would work then as follows: if the habitat quality ($HQ$) is set at 4 resource units, and the stage-specific resource production ($n_s$) is set at 0.7. Then, the maximum amount of resource production of an individual ($n_{i,s}$) would be 3 resource units, since resource units are non-divisible, and therefore they are rounded to be natural numbers. If the maximum production probability ($\max(p)$) is set at 0.8, and the stage-specific production probability ($p_s$) is set at 0.7, then the production probability of an individual ($p_{i,s}$) would be 0.56. Now that the maximum amount of resource production (3) and the production probability (0.56) are defined, then it is possible to say that the amount of resources an individual can produce in one iteration $RP_{i,t}$ would range from producing between 0 and 3 resources with a probability of 0.56, based on a binomial probability distribution.

The amount of resources available by the end of the production module is updated as follows:

$$ RA_{i,t,m1} = RA_{i,t-1} + RP_{i,t} $$

Where $RA_{i,t,m1}$ is the amount of resources available for individual $i$ at time $t$ in production module $(m1)$, $RA_{i,t-1}$ is the amount of resources that individual $i$ has from the previous iteration $(t-1)$, and $RP_{i,t}$ is the amount of resources produced.

Maternal investment (State variable): Is the amount of resources an individual transfers to her descendants. We assume that an individual transfers resources to her descendants that do not have enough resources to cover the costs of survival—with mothers transferring to descendants that has the greatest need first [Aktipis 2016]. If a mother does not have adequate resources to cover the need of her most needy descendant, she will transfer resources to the descendant next most in need (and so on until she has gone
Stage-specific resource production (Auxiliary variable): Is the offset, as proportion between 0 and 1, that is used in the auxiliary variable “Maximum resource production” to define the amount of resource production an individual can produce depending on her life cycle stage \(n_s\).

Production probability (Auxiliary variable): Is the stage-specific probability of producing resources \(p_{i,s}\) that is used in the state variable “Resource production”. The probabilities are stage-specific so they can follow the ontogeny of resource production that characterise humans, where juveniles and post-reproductive individuals are less likely to produce resources than individuals in the adult and reproductive career stages [Kaplan et al., 2000; Lee and Kramer, 2002; Koster et al., 2020]. Hence, production probability of an individual \(p_{i,s}\) is defined as:

\[
p_{i,s} = \max(p) \ast p_s
\]  

(4)

Where \(p_{i,s}\) is the stage-specific production probability of individual \(i\) in stage \(s\), \(\max(p)\) is the maximum production probability for any individual in the population, and \(p_s\) is the stage-specific offset that defines the production probability for the individual.

Maximum production probability (Auxiliary variable): Is the maximum probability of resource production for all individuals in the population (\(\max(p)\)).

Stage-specific production probability (Auxiliary variable): Is the off-set of the production probability that individuals have depending on their life cycle stage \(p_s\).

The dynamics regarding production would work then as follows: if the habitat quality \((HQ)\) is set at 4 resource units, and the stage-specific resource production \(n_s\) is set at 0.7. Then, the maximum amount of resource production of an individual \((n_{i,s})\) would be 3 resource units, since resource units are non-divisible, and therefore they are rounded to be natural numbers. If the maximum production probability \((\max(p))\) is set at 0.8, and the stage-specific production probability \((p_s)\) is set at 0.7, then the production probability of an individual \((p_{i,s})\) would be 0.56. Now that the maximum amount of resource production \((3)\) and the production probability \((0.56)\) are defined, then it is possible to say that the amount of resources an individual can produce in one iteration \(RP_{i,t}\) would range from producing between 0 and 3 resources with a probability of 0.56, based on a binomial probability distribution.

The amount of resources available by the end of the production module is updated as follows:

\[
RA_{i,t,m1} = RA_{i,t-1} + RP_{i,t}
\]

(5)

Where \(RA_{i,t,m1}\) is the amount of resources available for individual \(i\) at time \(t\) in production module \((m1)\), \(RA_{i,t-1}\) is the amount of resources that individual \(i\) has from the previous iteration \((t-1)\), and \(RP_{i,t}\) is the amount of resources produced.

Maternal investment (State variable): Is the amount of resources an individual transfers to her descendants. A mother will only invest in her descendants if she has enough resources to ensure her own survival, first. We assume that an individual transfers resources to her descendants that do not have enough resources to cover the costs of survival—with mothers transferring to descendants that has the greatest need first [Aktipis, 2016]. If a mother does not have enough resources to cover the need of her
through all of her descendants). A mother will only invest in her descendants if they have enough resources to ensure their own survival, first. Therefore, maternal investment is based on the surplus of resources that a mother has, and the need that her descendants, and is defined as:

$$MI_{i,t} = \begin{cases} RA_{i,t} - \sum DN_{j,i} , & RA_{i,t} \geq \sum DN_{j,i} \\ 0 , & RA_{i,t} < \sum DN_{j,i} \end{cases}$$

(6)

Where $MI_{i,t}$ is the amount of maternal investment of individual $i$ at time $t$, $RA_{i,t}$ is the amount of resources available an individual $i$ at time $t$ has for maternal investment, and $DN_{j,i}$ is the amount of resources that descendant $j$ needs from individual $i$.

The amount of resource surplus for maternal investment is defined as:

$$RA_{i,t} = RA_{i,t-1} + RP_{i,t} - SC$$

(7)

Where $RA_{i,t}$ is the amount of resources available for maternal investment of individual $i$ at time $t$, $RA_{i,t-1}$ are the stored resources that the individual $i$ carried from the previous time step ($t - 1$), $RP_{i,t}$ is the amount of resources produced by individual $i$ at time $t$, and $SC$ is the survival cost.

The amount of resources that a descendant need is defined as:

$$DN_{j,i} = \begin{cases} 0 , & SC - RA_{j,t} \leq 0 \\ SC - RA_{j,t} , & SC - RA_{j,t} > 0 \end{cases}$$

(8)

Where $DN_{j,i}$ is the amount of resources that descendant $j$ from individual $i$ needs, $SC$ is the survival cost, and $RA_{j,t}$ is the amount of resources available to descendant $j$ at time $t$.

The logic behind the maternal investment module would mean that, if an individual has 5 resources in total, her surplus would be 4 resource units. If she has three descendants, and they have 1, 0, and 0 resources available, respectively, then she would transfer 0 resources to the first descendant, and 1 resource to each of those descendants who have no resources. This way, every descendant would have enough resources to cover the survival cost ($SC = 1$), while the amount of resources that the focal individual has after investing in her descendants would be 3.

The dynamics regarding production would work then as follows: if the habitat quality ($HQ$) is set at 4 resource units, and the stage-specific resource production ($n_s$) is set at 0.7. Then, the maximum amount of resource production of an individual ($n_{i,s}$) would be 3 resource units, since resource units are non-divisible, and therefore they are rounded to be natural numbers. If the maximum production probability ($\max(p)$) is set at 0.8, and the stage-specific production probability ($p_s$) is set at 0.7, then the production probability of an individual ($p_{i,s}$) would be 0.56. Now that the maximum amount of resource production (3) and the production probability (0.56) are defined, then it is possible to say that the amount of resources an individual can produce in one iteration $RP_{i,t}$ would range from producing between 0 and 3 resources with a probability of 0.56, based on a binomial probability distribution.

By the end of maternal investment, the amount of resources available is updated as:

$$RA_{i,t,m2} = RA_{i,t,m1} - MI_{i,t} - SC$$

(9)

Where $RA_{i,t,m2}$ is the amount of resources available for maternal investment of individual $i$ at time $t$ in the maternal investment module ($m2$), $RA_{i,t,m1}$ are the resources available for individual $i$ from the
most needy descendant, she will not give any resources to this descendant and transfer resources to the next
descendant that is most in need (and so on until she has gone through all of her descendants). This decision
follows parent-offspring theory, which predicts that mothers will invest resources to maximise overall fitness.
Therefore, maternal investment is based on the surplus of resources that a mother has, and the need that
her descendants, and is defined as:

\[
MI_{i,t} = \begin{cases} 
RA_{i,t} - \sum DN_{j,i}, & RA_{i,t} \geq \sum DN_{j,i} \\
0, & RA_{i,t} < \sum DN_{j,i}
\end{cases}
\]  

(6)

Where \( MI_{i,t} \) is the amount of maternal investment of individual \( i \) at time \( t \), \( RA_{i,t} \) is the amount of
resources available an individual \( i \) at time \( t \) has for maternal investment, and \( DN_{j,i} \) is the amount of
resources that descendant \( j \) needs from individual \( i \).

The amount of resource surplus for maternal investment is defined as:

\[
RA_{i,t} = RA_{i,t-1} + RP_{i,t} - SC
\]  

(7)

Where \( RA_{i,t} \) is the amount of resources available for maternal investment of individual \( i \) at time \( t \),
\( RA_{i,t-1} \) are the stored resources that the individual \( i \) carried from the previous time step \((t-1)\), \( RP_{i,t} \) is
the amount of resources produced by individual \( i \) at time \( t \), and \( SC \) is the survival cost.

The amount of resources that a descendant need is defined as:

\[
DN_{j,i} = \begin{cases} 
0, & SC - RA_{j,t} \leq 0 \\
SC - RA_{j,t}, & SC - RA_{j,t} > 0
\end{cases}
\]  

(8)

Where \( DN_{j,i} \) is the amount of resources that descendant \( j \) from individual \( i \) needs, \( SC \) is the survival
cost, and \( RA_{j,t} \) is the amount of resources available to descendant \( j \) at time \( t \).

The logic behind the maternal investment module would mean that, if an individual has 5 resources in
total, her surplus would be 4 resource units. If she has three descendants, and they have 1, 0, and 0 resources
available, respectively, then she would transfer 0 resources to the first descendant, and 1 resource to each
of those descendants who have no resources. This way, every descendant would have enough resources to
cover the survival cost \((SC = 1)\), while the amount of resources that the focal individual has after investing
in her descendants would be 3.

The dynamics regarding production would work then as follows: if the habitat quality \((HQ)\) is set at 4
resource units, and the stage-specific resource production \( (n_s) \) is set at 0.7. Then, the maximum amount of
resource production of an individual \((n_{i,s})\) would be 3 resource units, since resource units are non-divisible,
and therefore they are rounded to be natural numbers. If the maximum production probability \((\text{max}(p))\) is
set at 0.8, and the stage-specific production probability \((p_s)\) is set at 0.7, then the production probability
of an individual \((p_{i,s})\) would be 0.56. Now that the maximum amount of resource production \((3)\) and
the production probability \((0.56)\) are defined, then it is possible to say that the amount of resources an
individual can produce in one iteration \(RP_{i,t} \) would range from producing between 0 and 3 resources with
a probability of 0.56, based on a binomial probability distribution.

By the end of maternal investment, the amount of resources available is updated as:

\[
RA_{i,t,m2} = RA_{i,t,m1} - MI_{i,t} - SC
\]  

(9)
previous module (m1), $MI_{i,t}$ is the amount of maternal investment of individual $i$ at time $t$, and $SC$ is the survival cost.

**Resource transfers (State variable):** Tracks the amount of resources that an individual transfers to others within the population at during each iteration. Every transfer that an individual makes within the population represents the sharing of one resource unit to another individual. Therefore, an individual will transfer can transfer unto the maximum number of resources that she has available. The probability of transfers is stage-structured through use of the principles of a stochastic block model. That is, resource transfers are assumed to be a network, and this network assumed to be partitioned by life cycle stage—with individuals in a given stage having the same probability of transferring resources to any individual occupying another specific stage (e.g. all individuals in reproductive career stage have the same probability of making resource transfers to all individuals in the juvenile stage). These probabilities vary based on the stages in which both the deciding individual and the target individual occupy (e.g., adult individuals are more likely to transfer resources to juveniles than they are to transfer resources to post-reproductive individuals). Resource transfers occur after maternal investment, and are therefore not guided by relatedness (e.g. genetic relatedness). The social network module is described as follows:

$$y_{i,j,t} \sim \text{Multinomial}(RA_{i,t}, \sigma(K_{(1:N),t} + \theta_{i,i,j,t}))$$

(10)

Where $y_{i,j}$ denotes the amount of resources that individual, $i$, transferred to individual, $j$, at time $t$, $RA_{i,t}$ is the amount of resources available that individual $i$ at time $t$ has for resource transfers, $\sigma$ is a softmax function that normalizes the values of $K$ and $\theta$ to be on the probability scale. $K_{(1:N),t}$ is a vector with the length of the total population ($N$), at time $t$, that contains a 1 in the entry that corresponds to individual $i$ and 0 in all other entries (i.e. it is an indicator variable containing 0 or 1, and not probabilities). $\theta_{i,i,j,t}$ is a vector containing the stage-specific probabilities that individual $i$ transfers resources to other individual $j$, at time $t$.

The surplus of resources than an individual has for resource transfers ($RA_{i,t}$) is the maximum number of ties an individual can form in the iteration. The surplus of resources considers the costs of survival, reproduction, and life cycle stage transition so individuals prioritise their own survival and reproduction, together with their descendants, before engaging in sharing dynamics. It is defined as follows:

$$RA_{i,t} = RA_{i,t-1} + RP_{i,t} - MI_{i,t} - SC - RC$$

(11)

Where $RA_{i,t}$ is the amount of resources available for individual $i$ at time $t$, which defines the maximum number of ties an individual can form in the iteration (i.e. their maximum out-degree), $RA_{i,t-1}$ is the stored resources from the previous iteration, $RP_{i,t}$ and $MI_{i,t}$ are the amount of resources produced and maternal investment of individual $i$ at time $t$, respectively, and $SC$ and $RC$ are the survival and reproductive costs.

The vector $K_{(1:N),t}$ is used to control for individual tendencies to keep resources for themselves, containing 0 or 1 as real numbers and not probabilities. The vector contains a 1 in the $ith$ entry and 0 in all other entries. The length of the vector is defined by the population size ($N$) at time $t$. $K$ can be defined as:

$$K_{(1:N),t} = \begin{cases} 1 & K_x = i \\ 0 & K_x \neq i \end{cases}$$

(12)

where $K_x$ is the element $x$ in the vector and $i$ is the $ith$ entry in the vector. Hence, the vector would
Where $RA_{i,t,m2}$ is the amount of resources available for maternal investment of individual $i$ at time $t$ in the maternal investment module ($m2$), $RA_{i,t,m1}$ are the resources available for individual $i$ from the previous module ($m1$), $MI_{i,t}$ is the amount of maternal investment of individual $i$ at time $t$, and $SC$ is the survival cost.

**Resource transfers (State variable):** Tracks the amount of resources that an individual transfers to others within the population at each iteration. Every transfer that an individual makes within the population represents the sharing of one resource unit to another individual. Therefore, an individual will transfer can transfer up to the maximum number of resources that she has available. The probability of transfers is stage-structured through use of the principles of a stochastic block model. That is, resource transfers are assumed to be a network, and this network assumed to be partitioned by life cycle stage—with individuals in a given stage having the same probability of transferring resources to any individual occupying another specific stage (e.g. all individuals in reproductive career stage have the same probability of making resource transfers to all individuals in the juvenile stage). These probabilities vary based on the stages in which both the deciding individual and the target individual occupy (e.g., adult individuals are more likely to transfer resources to juveniles than they are to transfer resources to post-reproductive individuals). Resource transfers occur after maternal investment, and are therefore not guided by relatedness (e.g. genetic relatedness). The social network module is described as follows:

$$y_{i,j,t} \sim \text{Multinomial}(RA_{i,t}, \sigma(K_{1:N,t} + \theta_{i,j,t}))$$ (10)

Where $y_{i,j,t}$ denotes the amount of resources that individual, $i$, transferred to individual, $j$, at time $t$, $RA_{i,t}$ is the amount of resources available that individual $i$ at time $t$ has for resource transfers, $\sigma$ is a softmax function that normalizes the values of $K$ and $\theta$ to be on the probability scale. $K_{1:N,t}$ is a vector with the length of the total population ($N$), at time $t$, that contains a 1 in the entry that corresponds to individual $i$ and 0 in all other entries (i.e. it is an indicator variable containing 0 or 1, and not probabilities). $\theta_{i,j,t}$ is a vector containing the stage-specific probabilities that individual $i$ transfers resources to other individual $j$, at time $t$.

The surplus of resources than an individual has for resource transfers ($RA_{i,t}$) is the maximum number of ties an individual can form in the iteration. The surplus of resources considers the costs of survival, reproduction, and life cycle stage transition so individuals prioritise their own survival and reproduction, together with their descendants, before engaging in sharing dynamics. It is defined as follows:

$$RA_{i,t} = RA_{i,t-1} + RP_{i,t} - MI_{i,t} - SC - RC$$ (11)

Where $RA_{i,t}$ is the amount of resources available for individual $i$ at time $t$, which defines the maximum number of ties an individual can form in the iteration (i.e. their maximum out-degree), $RA_{i,t-1}$ is the stored resources from the previous iteration, $RP_{i,t}$ and $MI_{i,t}$ are the amount of resources produced and maternal investment of individual $i$ at time $t$, respectively, and $SC$ and $RC$ are the survival and reproductive costs.

The vector $K_{1:N,t}$ is used to control for individual tendencies to keep resources for themselves, containing 0 or 1 as real numbers and not probabilities. The vector contains a 1 in the $i$th entry and 0 in all other entries. The length of the vector is defined by the population size ($N$) at time $t$. $K$ can be defined as:
have a 1 in the element that corresponds with the position of individual $i$ in the vector, and 0 elsewhere.

The stage-specific probabilities of an individual $i$ to transfer resources to another individual $j$ at time $t$ is defined as:

$$
\theta_{(i,j,t)} = B[s(i), s(j)]
$$

where the probability that individual $i$ in stage $s_i$ transfers a resource to another individual in stage $s_j$, at time $t$, is controlled by a corresponding entry in a square matrix, $B[{s(i), s(j)}]$.

We produce an $N \times N$ square matrix, $Y_{[i,j]}$, by binding all vectors produced by our resources transfers module, $y_{i,i,j,t}$. The matrix row and column labels are symmetric, denoting the identities all individuals in the population, and contains all transfers from individuals (the rows of the matrix) to all other individuals (the columns of the matrix). Each element of the matrix contains the total number of transfers that an individual, $i$, made to another individual, $j$ at time $t$. That is, the value contained in element $Y_{[i,j]}$ was, for instance, 2, it denotes that individual 4 shared two units of resources with individual 5. The sum of each row of the matrix represents is, therefore, the number of resources that individual $i$ sends to all other individuals (i.e. their out-degree($RT_{i,t}$)). The sum of the columns represent the number of resources that individual $j$ receives (i.e. in-degree ($RR_{i,t}$)). The out-degree and in-degree only considers the elements of $Y$ where $i \neq j$.

The amount of resources that an individual transfers to other individuals, or their out-degree, can be defined then as:

$$
RT_{i,t} = \sum_{j=1}^{n} x_{ij}
$$

Where $RT_{i,t}$ is the amount of resources transferred by individual $i$ at time $t$, $\sum_{j=1}^{n}$ is the sum from column $j$ to $n$, and $x_{ij}$ is element $x$ in row $i$ and column $j$ in the square matrix $Y_{[i,j]}$.

The amount of resources that an individual transfers to other individuals, or their out-degree, can be defined then as:

$$
RR_{i,t} = \sum_{i=1}^{n} x_{ij}
$$

Where $RR_{i,t}$ is the amount of resources transferred by individual $i$ at time $t$, $\sum_{j=1}^{n}$ is the sum from row $i$ to $n$, and $x_{ij}$ is element $x$ in row $i$ and column $j$ in the square matrix $Y_{[i,j]}$.

**Block matrix (Auxiliary variable):** The square matrix refers to the block matrix $B$, which sets the stage-specific probabilities of transferring resources. The block matrix is defined as:

$$
B = \begin{pmatrix}
\beta_{J\rightarrow J} & \beta_{J\rightarrow A} & \beta_{J\rightarrow RC} & \beta_{J\rightarrow PR} \\
\beta_{A\rightarrow J} & \beta_{A\rightarrow A} & \beta_{A\rightarrow RC} & \beta_{A\rightarrow PR} \\
\beta_{RC\rightarrow J} & \beta_{RC\rightarrow A} & \beta_{RC\rightarrow RC} & \beta_{RC\rightarrow PR} \\
\beta_{PR\rightarrow J} & \beta_{PR\rightarrow A} & \beta_{PR\rightarrow RC} & \beta_{PR\rightarrow PR}
\end{pmatrix}
$$

Where every value in the matrix ($\beta_{s\rightarrow s}$) is the probability that an individual $i$ transfers resources to individual $j$, depending on the life cycle stage of each of them ($s$). The probabilities of transferring resources within life cycle stages are on the diagonal of the matrix, while the off-diagonal elements of the matrix contain
\[ K_{(1: N,t)} = \begin{cases} 1 & K_x = i \\ 0 & K_x \neq i \end{cases} \]  

where \( K_x \) is the element \( x \) in the vector and \( i \) is the \( i \)th entry in the vector. Hence, the vector would have a 1 in the element that corresponds with the position of individual \( i \) in the vector, and 0 elsewhere.

The stage-specific probabilities of an individual \( i \) to transfer resources to another individual \( j \) at time \( t \) is defined as:

\[ \theta_{(i,i:j,t)} = B[s(i), s(j)] \]  

where the probability that individual \( i \) in stage \( s_i \) transfers a resource to another individual in stage \( s_j \), at time \( t \), is controlled by a corresponding entry in a square matrix, \( B[s(i), s(j)] \).

We produce an \( N \times N \) square matrix, \( Y_{[i,j]} \), by binding all vectors produced by our resources transfers module, \( y_{i,i:j,t} \). The matrix row and column labels are symmetric, denoting the identities all individuals in the population, and contains all transfers from individuals (the rows of the matrix) to all other individuals (the columns of the matrix). Each element of the matrix contains the total number of transfers that an individual, \( i \), made to another individual, \( j \) at time \( t \). That is, the value contained in element \( Y_{[4,5]} \) was, for instance, 2, it denotes that individual 4 shared two units of resources with individual 5. The sum of each row of the matrix represents, therefore, the number of resources that individual \( i \) sends to all other individuals in the population (i.e. their out-degree(\( RT_{i,t} \))). The sum of the columns represent the number of resources that individual \( j \) receives (i.e. in-degree (\( RR_{i,t} \))). The out-degree and in-degree only considers the elements of \( Y \) where \( i \neq j \).

The amount of resources that an individual transfers to other individuals, or their out-degree, can be defined then as:

\[ RT_{i,t} = \sum_{j=1}^{n} x_{ij} \]  

Where \( RT_{i,t} \) is the amount of resources transferred by individual \( i \) at time \( t \), \( \sum_{j=1}^{n} x_{ij} \) is the sum from column \( j \) to \( n \), and \( x_{ij} \) is element \( x \) in row \( i \) and column \( j \) in the square matrix \( Y_{[i,j]} \).

The amount of resources that an individual transfers to other individuals, or their out-degree, can be defined then as:

\[ RR_{i,t} = \sum_{i=1}^{n} x_{ij} \]  

Where \( RR_{i,t} \) is the amount of resources transferred by individual \( i \) at time \( t \), \( \sum_{j=1}^{n} x_{ij} \) is the sum from row \( i \) to \( n \), and \( x_{ij} \) is element \( x \) in row \( i \) and column \( j \) in the square matrix \( Y_{[i,j]} \).

**Block matrix (Auxiliary variable):** The square matrix refers to the block matrix \( B \), which sets the stage-specific probabilities of transferring resources. The block matrix is defined as:

\[
B = \begin{pmatrix}
\beta_{J\rightarrow J} & \beta_{J\rightarrow A} & \beta_{J\rightarrow RC} & \beta_{J\rightarrow PR} \\
\beta_{A\rightarrow J} & \beta_{A\rightarrow A} & \beta_{A\rightarrow RC} & \beta_{A\rightarrow PR} \\
\beta_{RC\rightarrow J} & \beta_{RC\rightarrow A} & \beta_{RC\rightarrow RC} & \beta_{RC\rightarrow PR} \\
\beta_{PR\rightarrow J} & \beta_{PR\rightarrow A} & \beta_{PR\rightarrow RC} & \beta_{PR\rightarrow PR}
\end{pmatrix}
\]
the probabilities of sending resources between different stages. For simplification purposes, we assume that
the probabilities in the block matrix follow a resource transfers pattern from older to younger stages. This
follows previous work on the role of sharing and the evolution of the female life cycle (Hooper et al., 2015;
Lee, 2003; Chu and Lee, 2006), which shows that juveniles are more likely to receive resources, while those
in later life cycle stages tend to send more resources—with a slight increase of receiving resources for those
in the post-reproductive stage.

The updated amount of resources available for individual $i$ at time $t$ after the resources transfers module
is defined as follows:

$$ RA_{i,t,m3} = RA_{i,t,m2} - RT_{i,t} + RR_{i,t} $$

(16)

where $RA_{i,t,m3}$ is the amount of resources available for individual $i$ at time $t$ after the resource transfer
module ($m3$), $RA_{i,t,m2}$ is the resources available from the previous module ($m2$), $RT_{i,t}$ is the amount of
resources transferred, and $RR_{i,t}$ is the amount of resources received by individual $i$ at time $t$.

Life history dynamics

Reproduction (State variable): Captures whether an individual produces one descendant (1) or not
(0) during a given iteration. Reproduction is deterministic. Therefore, it depends on whether an individual
has enough resources to surpass the reproductive threshold, and is in the adult or reproductive career stage.
We assume that individuals can produce only one descendant per reproductive event. Reproduction is
defined as:

$$ R_{i,t} = \begin{cases} 
1, & RA_{i,t} \geq RT_h \\
0, & RA_{i,t} < RT_h 
\end{cases} $$

(17)

Where $R_{i,t}$ is the reproductive output of individual $i$ at time $t$, $RA_{i,t}$ is the amount of resources available
for individual $i$ at time $t$, and $RT_h$ is the reproductive threshold. Individuals who are in other life cycle
stages than adult or reproductive career have a reproductive output of zero.

Reproductive threshold (Auxiliary variable): Is the minimum amount of resources that an individual
needs to have available to reproduce ($RT_h$). This reflects the notion that individuals need to be in a
minimum condition in order to successfully reproduce (Jasienska et al., 2017). The reproductive threshold
is set to be five times the reproductive cost (10 resources), resembling the amount of resources an individual
accumulates as a juvenile to reach sexual maturity and is able to start her reproductive career.

Reproductive cost (Auxiliary variable): Is the amount of resources that are discounted from the
resources available to produce a descendant ($RC$). It is set to be two times the survival cost (2 resources),
and represents the energetic costs of pregnancy and childbearing (Butte and King, 2005).

The amount of resources available ($RA_{i,t}$) is updated after the reproductive dynamics as:

$$ RA_{i,t,m4} = RA_{i,t,m3} - (RC \times R_{i,t}) $$

(18)

where $RA_{i,t,m4}$ is the amount of resources available for individual $i$ at time $t$ in the reproductive module
($m4$), $RA_{i,t,m3}$ is the amount of resources that individual $i$ has at time $t$ from the previous module ($m3$).
Where every value in the matrix \((\beta_{s \rightarrow s})\) is the probability that an individual \(i\) transfers resources to individual \(j\), depending on the life cycle stage of each of them \((s)\). The probabilities of transferring resources within life cycle stages are on the diagonal of the matrix, while the off-diagonal elements of the matrix contain the probabilities of sending resources between different stages. For simplification purposes, we assume that the probabilities in the block matrix follow a resource transfers pattern from older to younger stages. This follows previous work on the role of sharing and the evolution of the female life cycle [Hooper et al. 2015; Lee 2003; Chu and Lee 2006], which shows that juveniles are more likely to receive resources, while those in later life cycle stages tend to send more resources—with a slight increase of receiving resources for those in the post-reproductive stage.

The updated amount of resources available for individual \(i\) at time \(t\) after the resources transfers module is defined as follows:

\[
RA_{i,t,m3} = RA_{i,t,m2} - RT_{i,t} + RR_{i,t}
\]  

(16)

where \(RA_{i,t,m3}\) is the amount of resources available for individual \(i\) at time \(t\) after the resource transfer module \((m3)\), \(RA_{i,t,m2}\) is the resources available from the previous module \((m2)\), \(RT_{i,t}\) is the amount of resources transferred, and \(RR_{i,t}\) is the amount of resources received by individual \(i\) at time \(t\).

Life history dynamics

**Reproduction (State variable):** Captures whether an individual produces one descendant (1) or not (0) during a given iteration. Reproduction is deterministic. Therefore, it depends on whether an individual has enough resources to surpass the reproductive threshold, and is in the adult or reproductive career stage. We assume that individuals can produce only one descendant per reproductive event. Reproduction is defined as:

\[
R_{i,t} = \begin{cases} 
1, & RA_{i,t} \geq RTh \\
0, & RA_{i,t} < RTh
\end{cases}
\]

(17)

Where \(R_{i,t}\) is the reproductive output of individual \(i\) at time \(t\), \(RA_{i,t}\) is the amount of resources available for individual \(i\) at time \(t\), and \(RTh\) is the reproductive threshold. Individuals who are in other life cycle stages than adult or reproductive career have a reproductive output of zero.

**Reproductive threshold (Auxiliary variable):** Is the minimum amount of resources that an individual needs to have available to reproduce \((RTh)\). This reflects the notion that individuals need to be in a minimum condition in order to successfully reproduce [Jasienska et al. 2017]. The reproductive threshold is set to be five times the reproductive cost (10 resources), resembling the amount of resources an individual accumulates as a juvenile to reach sexual maturity and is able to start her reproductive career.

**Reproductive cost (Auxiliary variable):** Is the amount of resources that are discounted from the resources available to produce a descendant \((RC)\). It is set to be two times the survival cost (2 resources), and represents the energetic costs of pregnancy and childbearing [Butte and King 2005].

The amount of resources available \((RA_{i,t})\) is updated after the reproductive dynamics as:
\( R_{i,t} \) is the output from the “Reproduction” module, which can be either 1 or 0.

**Transition (State variable):** Is when an individual evaluates if she is able to move to the next life cycle stage (1) or not (0), depending on whether an individual has enough resources available to allocate towards the key event of transition.

\[
T_{R_i} = \begin{cases} 
T_{J \rightarrow A} = 1, & RA_{i,t,m4} - RC \geq SC + RTh \land AGE_{i,t} \geq 10 \lor AGE_{i,t} \leq 18 \\
T_{A \rightarrow RC} = 1, & RA_{i,t,m4} - RC \geq RTh \\
T_{A \rightarrow PR} = 1, & AGE_{i,t,m4} \geq 60 \\
T_{RC \rightarrow PR} = 1, & RA_{i,t,m4} - RC < RTh \land TLR_{i,t} \geq 10 \land AGE_{i,t} \geq 40 \lor AGE_{i,t} \geq 60 
\end{cases}
\] (19)

Where \( T_i \) is the transition output of an individual, \( i \). \( RA_{i,t,m4} \) is the amount of resources available from the previous module \((m4)\), \( RC \) is the reproductive cost, \( SC \) is the survival cost, \( RTh \) is the reproductive threshold, \( AGE_{i,t} \) is age, and \( TLR_{i,t} \) is the time since last reproduction of individual \( i \) at time \( t \). \( T_{J \rightarrow A} \), \( T_{A \rightarrow RC} \), \( T_{A \rightarrow PR} \), \( T_{RC \rightarrow PR} \) are the transitions from one life cycle stage to the next one. It is important to note that the reproductive cost has a different value than zero only in the transition from the reproductive career to the post reproductive stage \((T_{RC \rightarrow PR})\).

The transitions are defined as follow:

- **Age at sexual maturity** \((T_{J \rightarrow A})\): A juvenile female individual reaches menarche and transitions to adulthood once her resources available go above the reproductive threshold, and she is at least 10 years old. If the individual reaches 18 years old she is forced to reach sexual maturity, regardless of the amount of resources available. The minimum and maximum ages of sexual maturity are based on values presented in [Morabia et al. (1998)] and [Kramer and Lancaster (2010)]

- **Age at first reproduction** \((T_{A \rightarrow RC})\): An individual in the adult stage transitions to a reproductive career stage when she has her first descendant. The first descendant is born when the individual has enough resources to cover the survival and reproductive thresholds.

- **Age at menopause** \((T_{A \rightarrow PR} \text{ and } T_{RC \rightarrow PR})\): An individual reaches menopause once she has enough resources to cover the survival costs but has not reproduced in the last 10 iterations (years) due to insufficient resources—either because she does not acquire enough resources or because she has high maternal investment into her existing descendants, based on [Caro et al. (1995)]; [Towner et al. (2016)]. She will be forced to transition if she is 60 years old based on [Morabia et al. (1998)] and [Thomas et al. (2001)]

**Transition cost (Auxiliary variable):** Is the amount of resources that an individual uses to transition from one life cycle stage to another. There are two transitions that have a cost with a value different from zero, which are:

- **Age at sexual maturity**: Here the cost of transition is the reproductive cost, in order to resemble the sub fecundity associated with menarche [Wood (2017)]. This way, an individual who transitions from juvenile to adult will not reproduce immediately after reaching sexual maturity.
\[ RA_{i,t,m4} = RA_{i,t,m3} - (RC \times R_{i,t}) \]  
\[ (18) \]

where \( RA_{i,t,m4} \) is the amount of resources available for individual \( i \) at time \( t \) in the reproductive module \((m4)\), \( RA_{i,t,m3} \) is the amount of resources that individual \( i \) has at time \( t \) from the previous module \((m3)\), \( R_{i,t} \) is the output from the “Reproduction” module, which can be either 1 or 0.

**Transition (State variable):** Is when an individual evaluates if she is able to move to the next life cycle stage (1) or not (0), depending on whether an individual has enough resources available to allocate towards the key event of transition.

\[ Tr_i = \begin{cases} 
Tr_{J \rightarrow A} = 1, & RA_{i,t,m4} - RC \geq SC + RTh \land AGE_{i,t} \geq 10 \lor AGE_{i,t} \leq 18 \\
Tr_{A \rightarrow RC} = 1, & RA_{i,t,m4} - RC \geq RTh \\
Tr_{A \rightarrow PR} = 1, & AGE_{i,t,m4} \geq 60 \\
Tr_{RC \rightarrow PR} = 1, & RA_{i,t,m4} - RC < RTh \land TLRI_{i,t} \geq 10 \land AGE_{i,t} \geq 40 \lor AGE_{i,t} \geq 60 
\end{cases} \]
\[ (19) \]

Where \( T_{ji} \) is the transition output of an individual, \( i \). \( RA_{i,t,m4} \) is the amount of resources available from the previous module \((m4)\), \( RC \) is the reproductive cost, \( SC \) is the survival cost, \( RTh \) is the reproductive threshold, \( AGE_{i,t} \) is age, and \( TLRI_{i,t} \) is the time since last reproduction of individual \( i \) at time \( t \). \( T_{J \rightarrow A} \), \( T_{A \rightarrow RC} \), \( T_{A \rightarrow PR} \), \( T_{RC \rightarrow PR} \) are the transitions from one life cycle stage to the next one. It is important to note that the reproductive cost has a different value than zero only in the transition from the reproductive career to the post reproductive stage \((Tr_{RC \rightarrow PR})\).

The transitions are defined as follow:

- **Age at sexual maturity** \((Tr_{J \rightarrow A})\): A juvenile female individual reaches menarche and transitions to adulthood once her resources available go above the reproductive threshold, and she is at least 10 years old. If the individual reaches 18 years old she is forced to reach sexual maturity, regardless of the amount of resources available. The minimum and maximum ages of sexual maturity are based on values presented in Morabia et al. (1998) and Kramer and Lancaster (2010).

- **Age at first reproduction** \((Tr_{A \rightarrow RC})\): An individual in the adult stage transitions to a reproductive career stage when she has her first descendant. The first descendant is born when the individual has enough resources to cover the survival and reproductive thresholds.

- **Age at menopause** \((Tr_{A \rightarrow PR} \text{ and } Tr_{RC \rightarrow PR})\): An individual reaches menopause once she has enough resources to cover the survival costs but has not reproduced in the last 10 iterations (years) due to insufficient resources—either because she does not acquire enough resources or because she has high maternal investment into her existing descendants, based on Caro et al. (1995); Towner et al. (2016). She will be forced to transition if she is 60 years old based on Morabia et al. (1998) and Thomas et al. (2001).

**Transition cost (Auxiliary variable):** Is the amount of resources that an individual uses to transition from one life cycle stage to another. There are two transitions that have a cost with a value different from zero, which are:
• Age at first reproduction: Here the cost of transition is also the reproductive cost, but because the
individual produces her first descendant.

Therefore, the transition cost can be defined as:

\[
T_{RC} = \begin{cases} 
RC, & T_{rJ\rightarrow A} = 1 \\
RC, & T_{rA\rightarrow RC} = 1 \\
0, & T_{rA\rightarrow PR} = 1 \\
0, & T_{rRC\rightarrow PR} = 1 
\end{cases}
\]  (20)

Where \(T_{RC}\) is the transition cost, \(RC\) is the reproductive cost, and \(T_{rJ\rightarrow A}, T_{rA\rightarrow RC}, T_{rA\rightarrow PR}\), \(T_{rRC\rightarrow PR}\) are the transitions from one life cycle stage to the next one.

The amount of resources available \((RA_{i,t,m5})\) is updated after the transition dynamics as:

\[
RA_{i,t,m5} = RA_{i,t,m4} - (T_{RC} \cdot Tr_{i,t})
\]  (21)

where \(RA_{i,t,m5}\) is the amount of resources available for individual \(i\) at time \(t\) after the transition module \((m5)\), \(RA_{i,t,m4}\) the amount of resources available from the previous module \((m4)\), \(T_{RC}\) is the transition costs, and \(Tr_{i,t}\) is the output from the “Transition” module, which can be 1 or 0.

**Stage (State variable):** Is the life cycle stage in which the individual is at the moment \((s_{i})\). The stage changes if the individual fulfils the requirements to move to the next life cycle stage in the iteration \((Tr_{i})\). There are four stages (juvenile, adult, reproductive-career, post-reproductive), each with its own stage-specific resource dynamics.

**Survival (State variable):** Whether the individual survives (1) or not (0) to the next iteration depends on whether the individual has enough resources available to cover the survival cost. Survival is defined as:

\[
S_{i} = \begin{cases} 
1, & RA_{i,t} \geq SC \\
0, & RA_{i,t} < SC
\end{cases}
\]  (22)

Where \(S_{i}\) is the survival outcome of individual \(i\), \(RA_{i,t}\) is the amount of resources available for individual \(i\) at time \(t\), and \(SC\) is the survival cost.

**Survival cost (Auxiliary variable):** Is the amount of resources that are discounted from the resources available to ensure the survival of the individual \((SC)\). It is set to be equal to one resource unit.

The amount of resources available \((RA_{i,t})\) is updated after the survival dynamics as:

\[
RA_{i,t,m6} = RA_{i,t,m5} - (SC \cdot S_{i,t})
\]  (23)

where \(RA_{i,t,m6}\) is the amount of resources available for individual \(i\) at time \(t\) after the survival module, \(RA_{i,t,m5}\) the resources available from the previous module \((m5)\), \(SC\) is the survival cost, and \(S_{i,t}\) is the output from the “Survival” module, which can be 1 or 0.
• Age at sexual maturity: Here the cost of transition is the reproductive cost, in order to resemble the sub fecundity associated with menarche (Wood 2017). This way, an individual who transitions from juvenile to adult will not reproduce immediately after reaching sexual maturity.

• Age at first reproduction: Here the cost of transition is also the reproductive cost, but because the individual produces her first descendant.

Therefore, the transition cost can be defined as:

\[
T_{rC} = \begin{cases} 
RC, & T_{rJ \rightarrow A} = 1 \\
RC, & T_{rA \rightarrow RC} = 1 \\
0, & T_{rA \rightarrow PR} = 1 \\
0, & T_{rRC \rightarrow PR} = 1 
\end{cases} \tag{20}
\]

Where \(T_{rC}\) is the transition cost, \(RC\) is the reproductive cost, and \(T_{rJ \rightarrow A}, T_{rA \rightarrow RC}, T_{rA \rightarrow PR}, T_{rRC \rightarrow PR}\) are the transitions from one life cycle stage to the next one.

The amount of resources available \((RA_{i,t,m5})\) is updated after the transition dynamics as:

\[
RA_{i,t,m5} = RA_{i,t,m4} - (T_{rC} \cdot T_{r,i,t}) \tag{21}
\]

where \(RA_{i,t,m5}\) is the amount of resources available for individual \(i\) at time \(t\) after the transition module \((m5)\), \(RA_{i,t,m4}\) the amount of resources available from the previous module \((m4)\), \(T_{rC}\) is the transition costs, and \(T_{r,i,t}\) is the output from the “Transition” module, which can be 1 or 0.

**Stage (State variable):** Is the life cycle stage in which the individual is at the moment \(s_i\). The stage changes if the individual fulfils the requirements to move to the next life cycle stage in the iteration \((T_{r,i})\). There are four stages (juvenile, adult, reproductive-career, post-reproductive), each with its own stage-specific resource dynamics.

**Survival (State variable):** Whether the individual survives (1) or not (0) to the next iteration depends on whether the individual has enough resources available to cover the survival cost. Survival is defined as:

\[
S_i = \begin{cases} 
1, & RA_{i,t} \geq SC \\
0, & RA_{i,t} < SC 
\end{cases} \tag{22}
\]

Where \(S_i\) is the survival outcome of individual \(i\), \(RA_{i,t}\) is the amount of resource available by individual \(i\) at time \(t\), and \(SC\) is the survival cost.

**Survival cost (Auxiliary variable):** Is the amount of resources that are discounted from the resources available to ensure the survival of the individual \((SC)\). It is set to be equal to one resource unit.

The amount of resources available \((RA_{i,t})\) is updated after the survival dynamics as:

\[
RA_{i,t,m6} = RA_{i,t,m5} - (SC \cdot S_i) \tag{23}
\]
**Age (State variable):** Is the sum of iterations where individual $i$ is alive, since birth ($t_0$) until death ($T$). Age increases by one after each iteration, reflection one year. It can be defined as:

$$AGE_{i,t} = \sum_{t_0}^{T} S_{i,t}$$

Where $AGE_{i,t}$ is the age of individual $i$ at time $t$, $\sum_{t_0}^{T}$ is the sum of iterations from birth ($t_0$) until death ($T$), and $S_{i,t}$ is the survival output for individual $i$ at time $t$.

**Lifetime reproductive output (State variable):** Is the total number of descendants produced ($LRO$). The reproductive output increases by one if the individual reproduces in the iteration. It can be defined as follows:

$$LRO_{i,t} = \sum_{t_0}^{T} R_{i,t}$$

Where $LRO_{i,t}$ is the lifetime reproductive output of individual $i$ at time $t$, $\sum_{t_0}^{T}$ is the sum of iterations from birth ($t_0$) until death ($T$), and $R_{i,t}$ is the reproductive output for individual $i$ at time $t$.

### 2.3 Process overview and scheduling

The following process describes the life cycle of an individual while she transitions from one stage to another. In the juvenile stage, an individual goes through production, resource transfer, and survival modules each year until she reaches sexual maturity, transitioning to the adult stage. In the adult stage, an individual goes through production, resource transfer, and survival modules until she either has her first descendant, transitioning to the reproductive career, or until she reaches menopause and transitions to become post-reproductive. If an adult transitions to the reproductive-career stage, she goes through the production, maternal investment, and resource transfer modules followed by the reproduction and survival modules until she reaches menopause. After an individual transitions to the post-reproductive stage, she only goes through production, resource transfer, and survival stage-specific modules. Each year, the individual increases her age and updates the amount of resources that she has stored. Her lifetime reproductive output is also updated if she reproduces in that iteration. During each transition, the individual updates her stage variable.

The scheduling of the process starts with the production module, followed by the maternal investment module if an individual is in the reproductive-career stage. The first decrease of resources available occurs if an individual needs to invest resources in her descendants. This is followed by the resource transfer module, which results in updating the amount of resources available for all individuals after accounting for the amount of resources that are given and received. The life history modules follow, which allows for a clear understanding on how resources are acquired and how they are allocated towards reproduction, survival, and transition. Furthermore, the surplus of resources considered for the modules of maternal investment and resource transfers is defined in order to ensure the reproduction and survival of an individual, and her descendants. The life history modules begin with reproduction, followed by stage transition, and survival modules. Finally, the storage module evaluates if there are resources that can be passed to the next year. See in Algorithm 3 a full description of the process through one iteration.
where $RA_{i,t,m}$ is the amount of resources available for individual $i$ at time $t$ after the survival module, $RA_{i,t,m}$ the resources available from the previous module ($m$), $SC$ is the survival cost, and $S_{i,t}$ is the output from the “Survival” module, which can be 1 or 0.

**Age (State variable):** Is the sum of iterations where individual $i$ is alive, since birth ($t_0$) until death ($T$). Age increases by one after each iteration, reflection one year. It can be defined as:

$$AGE_{i,t} = \sum_{t_0}^{T} S_{i,t}$$  \hspace{1cm} (24)

Where $AGE_{i,t}$ is the age of individual $i$ at time $t$, $\sum_{t_0}^{T}$ is the sum of iterations from birth ($t_0$) until death ($T$), and $S_{i,t}$ is the survival output for individual $i$ at time $t$.

**Lifetime reproductive output (State variable):** Is the total number of descendants produced ($LRO$). The reproductive output increases by one if the individual reproduces in the iteration. It can be defined as follows:

$$LRO_{i,t} = \sum_{t_0}^{T} R_{i,t}$$  \hspace{1cm} (25)

Where $LRO_{i,t}$ is the lifetime reproductive output of individual $i$ at time $t$, $\sum_{t_0}^{T}$ is the sum of iterations from birth ($t_0$) until death ($T$), and $R_{i,t}$ is the reproductive output for individual $i$ at time $t$.

### 2.3 Process overview and scheduling

The following process describes the life cycle of an individual while she transitions from one stage to another. In the juvenile stage, an individual goes through production, resource transfer, and survival modules each year until she reaches sexual maturity, transitioning to the adult stage. In the adult stage, an individual goes through production, resource transfer, and survival modules until she either has her first descendant, transitioning to the reproductive career, or until she reaches menopause and transitions to become post-reproductive. If an adult transitions to the reproductive-career stage, she goes through the production, maternal investment, and resource transfer modules followed by the reproduction and survival modules until she reaches menopause. After an individual transitions to the post-reproductive stage, she only goes through production, resource transfer, and survival stage-specific modules. Each year, the individual increases her age and updates the amount of resources she has stored. Her lifetime reproductive output is also updated if she reproduces in that iteration. During each transition, the individual updates her stage variable.

The scheduling of the process starts with the production module, followed by the maternal investment module if an individual is in the reproductive-career stage. The first decrease of resources available occurs if an individual needs to invest resources in her descendants. This is followed by the resource transfer module, which results in updating the amount of resources available for all individuals after accounting for the amount of resources that are given and received. The life history modules follow, which allows for a clear understanding on how resources are acquired and how they are allocated towards reproduction, survival, and transition. Furthermore, the surplus of resources considered for the modules of maternal investment and resource transfers is defined in order to ensure the reproduction and survival of an individual, and her
2.4 Design concepts

2.4.1 Basic principles

The model aims to understand how the variability of life cycles within a population changes as a function of resource dynamics and habitat quality. Existing models have focused on the conditions under which the female human life cycle evolved (e.g. embodied capital model [Kaplan 1996] or resource transfer model [Chu and Lee 2006]), while the model presented here focuses on the mechanisms that explain the variability of life cycles within a population. Additionally, our model more explicitly incorporates a network of resource transfers, which more directly examines resource dynamics that are reflective of real-world resource sharing than previous models (Price and Jones 2020; Kaplan 1996; Chu and Lee 2006; Lee 2003; Kramer and Ellison 2010; Van Noordwijk and de Jong 1986). First, resource transfers are defined more generally, and not bounded to specific relationships between individuals (e.g. parent-offspring transfers as in Kaplan 1996 or downward adult-juvenile transfers as in Chu and Lee 2006). Second, resource transfers are modelled with a stochastic component, and not just as an immediate byproduct of other resource dynamics (e.g. giving as a positive outcome from resource production and consumption, and receiving as a negative one, as in Lee 2003; Chu and Lee 2006). Hence, our model makes it possible to track the unique contributions of resource production and transfers, allowing us to disentangle what resource dynamics are behind possible phenotypic masking effects, as highlighted in Van Noordwijk and de Jong 1986. Finally, the model is driven by mechanistic processes, as individuals survive, reproduce, and transition through the life cycle depending on the amount of available resources that she has. Therefore, individuals have deterministic behaviours in relation to the allocation of resources towards survival and reproduction, whereas resource acquisition and sharing is more stochastic.

2.4.2 Emergence

Variability of life cycles between individuals emerges from the dynamics in acquiring resources from production and transfers (see Fig. 1 Resource production changes depending on habitat quality and the stage-specific probability of production, making it stochastic. Resource transfers depend on the surplus of resources available to individuals in the population, changes in the demographic composition of the population, and the stage-specific probabilities of transfers, therefore making it stochastic. Allocation towards reproduction, stage transition, and survival are deterministic, but also depend on events in previous years, such as whether an individual already has given birth or not. The aim of this study is to understand how the resource dynamics (i.e. production and transfers) experienced by individuals within a population cause different amounts of variation in key components of the female human life cycle (i.e. longevity, age at menarche, age at first reproduction, number of descendants, age at last reproduction, age at menopause).

2.4.3 Adaptation

The rules that govern the behaviour of individuals do not change depending on experience, changes in circumstances, or over time. Accordingly, individuals do not flexibly adapt their behaviour according to their circumstances. In addition, there is also no adaptation across generations as the rules equally apply to all individuals, and there is no heritability of behaviour.
descendants. The life history modules begin with reproduction, followed by stage transition, and survival modules. Finally, the storage module evaluates if there are resources that can be passed to the next year. See in Algorithm 3 a full description of the process through one iteration.

2.4 Design concepts

2.4.1 Basic principles

The model aims to understand how the variability of life cycles within a population changes as a function of resource dynamics and habitat quality. Existing models have focused on the conditions under which the female human life cycle evolved (e.g. embodied capital model \cite{Kaplan1996} or resource transfer model \cite{Chu2006}), while the model presented here focuses on the mechanisms that explain the variability of life cycles within a population. Additionally, our model more explicitly incorporates a network of resource transfers, which more directly examines resource dynamics that are reflective of real-world resource sharing than previous models \cite{Price2020,Kaplan1996,Chu2006,Le2003,Kramer2010,VanNoordwijk1986}. First, resource transfers are defined more generally, and not bounded to specific relationships between individuals (e.g. parent-offspring transfers as in \cite{Kaplan1996} or downward adult-juvenile transfers as in \cite{Chu2006}). Second, resource transfers are modelled with a stochastic component, and not just as an immediate byproduct of other resource dynamics (e.g. giving as a positive outcome from resource production and consumption, and receiving as a negative one, as in \cite{Lee2003,Chu2006}). Hence, our model makes it possible to track the unique contributions of resource production and transfers, allowing us to disentangle what resource dynamics are behind possible phenotypic masking effects, as highlighted in \cite{VanNoordwijk1986}. Finally, the model is driven by mechanistic processes, as individuals survive, reproduce, and transition through the life cycle depending on the amount of available resources that she has. Therefore, individuals have deterministic behaviours in relation to the allocation of resources towards survival and reproduction, whereas resource acquisition and sharing is more stochastic.

2.4.2 Emergence

Variability of life cycles between individuals emerges from the dynamics in acquiring resources from production and transfers (see Fig. 1). Resource production changes depending on habitat quality and the stage-specific probability of production, making it stochastic. Resource transfers depend on the surplus of resources available to individuals in the population, changes in the demographic composition of the population, and the stage-specific probabilities of transfers, therefore making it stochastic. Allocation towards reproduction, stage transition, and survival are deterministic, but also depend on events in previous years, such as whether an individual already has given birth or not. The aim of this study is to understand how the resource dynamics (i.e. production and transfers) experienced by individuals within a population cause different amounts of variation in key components of the female human life cycle (i.e. longevity, age at menarche, age at first reproduction, number of descendants, age at last reproduction, age at menopause).

2.4.3 Adaptation

The rules that govern the behaviour of individuals do not change depending on experience, changes in circumstances, or over time. Accordingly, individuals do not flexibly adapt their behaviour according to
2.4.4 Learning

There is no learning process for the individuals in the population because the model focuses on the environmental constraints and resource dynamics under which the female human life cycle varies.

2.4.5 Expectations

We expect that the variability of life cycles within the population will be higher under scenarios where individuals differ more in the amount of available resources that they have. We have such an expectation because of the stochastic nature of how resource dynamics are defined in the model, while the life history outcomes are deterministic. Therefore, and following our research questions (Table 2), we expect that (1) there will be larger life cycle variability as stochastic differences in resource production increase, and that (2) life cycle variability will decrease as habitat quality increases. This is because individuals that are less lucky in resource production would be able to compensate by acquiring larger amounts of resources when successful. We also expect that (3) life cycle variability should decrease as the probabilities of resource transfer increase, as the redistribution of resources within the population would have a buffering effect on individual differences. Finally, we predict that (4) resource production is the main driver of individual differences in life cycles, followed by the buffering effect of resource transfers. We expect that habitat quality will only play a role if resources are abundant enough for individuals can compensate for unsuccessful production years. Hence, the variability of life cycles within a female human population would depend on the individual production of resources, the social structure of resource transfers, and the environmental richness where individuals develop.

2.4.6 Sensing

Individuals are assumed to know their life cycle stage, which resource and life history dynamics (e.g. the probabilities of producing resources, and if they can reproduce in the iteration or not) depend upon. They also know the amount of resources available, and surplus, to determine the amount of resources used in maternal investment and resource transfers. Furthermore, they are assumed to know the amount of resources available after the resource dynamics, which are used to allocate them to reproduction, life cycle stage transition, and/or survival. Finally, they are assumed to know the amount of resources left at the end of the iteration to store them and carry them to the next iteration. We do not include any implementation error in the knowledge of individuals of any of the deterministic rules specified in our model—that is, individuals have perfect knowledge of the system and always behave in a way that maximises their life history traits.

2.4.7 Interaction

Not apply.

2.4.8 Stochasticity

Resource dynamics are stochastic in the model as they are based on probability distributions. Individuals produce resources within an iteration based on randomly sampling a value from a binomial distribution with an upper bound based on the stage-specific maximum resource production and probability. The sharing dynamics are also stochastic because the number of times and with whom resources are transferred are also
their circumstances. In addition, there is also no adaptation across generations as the rules equally apply to all individuals, and there is no heritability of behaviour.

2.4.4 Learning

There is no learning process for the individuals in the population because the model focuses on the environmental constraints and resource dynamics under which the female human life cycle varies.

2.4.5 Expectations

We expect that the variability of life cycles within the population will be higher under scenarios where individuals differ more in the amount of available resources that they have. We have such an expectation because of the stochastic nature of how resource dynamics are defined in the model, while the life history outcomes are deterministic. Therefore, and following our research questions (Table 2), we expect that (1) there will be larger life cycle variability as stochastic differences in resource production increase, and that (2) life cycle variability will decrease as habitat quality increases. This is because individuals that are less lucky in resource production would be able to compensate by acquiring larger amounts of resources when successful. We also expect that (3) life cycle variability should decrease as the probabilities of resource transfer increase, as the redistribution of resources within the population would have a buffering effect on individual differences. Finally, we predict that (4) resource production is the main driver of individual differences in life cycles, followed by the buffering effect of resource transfers. We expect that habitat quality will only play a role if resources are abundant enough for individuals can compensate for unsuccessful production years. Hence, the variability of life cycles within a female human population would depend on the individual production of resources, the social structure of resource transfers, and the environmental richness where individuals develop.

2.4.6 Sensing

Individuals are assumed to know their life cycle stage, which resource and life history dynamics (e.g. the probabilities of producing resources, and if they can reproduce in the iteration or not) depend upon. They also know the amount of resources available, and surplus, to determine the amount of resources used in maternal investment and resource transfers. Furthermore, they are assumed to know the amount of resources available after the resource dynamics, which are used to allocate them to reproduction, life cycle stage transition, and/or survival. Finally, they are assumed to know the amount of resources left at the end of the iteration to store them and carry them to the next iteration. We do not include any implementation error in the knowledge of individuals of any of the deterministic rules specified in our model—that is, individuals have perfect knowledge of the system and always behave in a way that maximises their life history traits.

2.4.7 Interaction

Not apply.
based on probability distributions specified from a stage-structured multinomial distribution. Individuals survive, reproduce, and transition from one life stage to another by reaching a certain amount of resources. Therefore, the resource dynamics of an individual are stochastic, whereas resource allocation is deterministic.

### 2.4.9 Collectives

Not apply

### 2.4.10 Observation

The purpose of the model is to identify which combinations of resource dynamics and habitat quality influence variation in the timing of life stage transitions, longevity, and reproductive timing and output of individuals. Therefore, the different resource dynamics (i.e. production and transfers) and the timing and output of the different components of the life cycle are recorded for each individual. At the population level, distributions of each trait of the female human life cycle as well as resource dynamics are produced based on the individual data.

### 2.5 Initialisation

At initialisation, the population will be composed of equal number of individuals per life cycle stage. Juveniles will start with age zero. Individuals in the adult stage will start with an age of 10 years old, whereas those in the reproductive career stages will start with 15 years old. Finally, those in the post-reproductive stage will start with an age of 45 years old. These values are based on cross-cultural values for human populations [Kramer and Lancaster 2010, Morabia et al. 1998, Thomas et al. 2001]. Finally, the values used for all the auxiliary variables are set at initialisation.

### 2.6 Input Data

Not apply

### 2.7 Sub models

Not apply

### 3 Model Analysis

The model analysis consists of exploring the impact of different parameter settings for habitat quality, the probability of resource production, and the probability of transferring resources. First, we will run the computational model to understand the influence of changes in resource production on the variability of life cycles. The model will not have resource transfers, the habitat quality will be set to baseline, and we will explore the impact of changing values of production probabilities from 0.1 to 0.9 (41 values). Second, we will run the computational model to understand the influence of habitat quality on the variability of life cycles. The model will not have resource transfers, the values of production will range from 0.1 to 0.9, and the habitat quality will be doubled to recreate a rich environment (82 values). We will compare the output of these model settings with those from the setting of the first regime. Third, the model will be set up to explore the role of resource transfers in the variability of life cycles. The parameters for
2.4.8 Stochasticity

Resource dynamics are stochastic in the model as they are based on probability distributions. Individuals produce resources within an iteration based on randomly sampling a value from a binomial distribution with an upper bound based on the stage-specific maximum resource production and probability. The sharing dynamics are also stochastic because the number of times and with whom resources are transferred are also based on probability distributions specified from a stage-structured multinomial distribution. Individuals survive, reproduce, and transition from one life stage to another by reaching a certain amount of resources. Therefore, the resource dynamics of an individual are stochastic, whereas resource allocation is deterministic.

2.4.9 Collectives

Not apply

2.4.10 Observation

The purpose of the model is to identify which combinations of resource dynamics and habitat quality influence variation in the timing of life stage transitions, longevity, and reproductive timing and output of individuals. Therefore, the different resource dynamics (i.e. production and transfers) and the timing and output of the different components of the life cycle are recorded for each individual. At the population level, distributions of each trait of the female human life cycle as well as resource dynamics are produced based on the individual data.

2.5 Initialisation

At initialisation, the population will be composed of equal number of individuals per life cycle stage. Juveniles will start with age zero. Individuals in the adult stage will start with an age of 10 years old, whereas those in the reproductive career stages will start with 15 years old. Finally, those in the post-reproductive stage will start with an age of 45 years old. These values are based on cross-cultural values for human populations [Kramer and Lancaster 2010, Morabia et al. 1998, Thomas et al. 2001]. Finally, the values used for all the auxiliary variables are set at initialisation.

2.6 Input Data

Not apply

2.7 Sub models

Not apply

3 Model Analysis

The model analysis consists of exploring the impact of different parameter settings for the probability of resource production, habitat quality, and the probability of resource transfers. The allocation of resources towards survival, reproduction, and maternal investment are not changed during the model analysis because they are deterministic parameters meant to clarify the link between resource dynamics and life history.
resource production and habitat quality will be set at baseline, while the values in the block matrix, which
defines the social network structure of the resource transfers, will range from 0.05 to 0.95 (656 values) while
keeping the downward pattern. Finally, we will run simulations to understand how the interplay between
resource production, transfers, and habitat quality influence the variability of life cycles within a population.
Accordingly, we will set habitat quality as baseline and then as high, production probabilities will range
from 0.1 to 0.9, and resource transfers between 0.05 and 0.95, leading to a maximum of 3362 combinations.
We will repeat each unique combination 10 times (see Table 1 for a summary).

We will calculate the longevity, lifetime reproductive output, and the timing of stage transitions for all
individuals in each combination of resource dynamics to analyse the variability of life cycles. Specifically,
we will analyse the coefficient of variation of different life history traits among all individuals born between
years 100 and 200 to cover one full generation (birth to death) of a large sample of individuals. This means
we should have no (or very few) of the initial individuals in the analysis population and all individuals in
the sample should have completed their life cycle by the end of the simulation (year 300). This way, we are
able to analyse how the variability of life cycles within a female human population changes under different
combinations of resource production, transfers, and habitat quality.

Finally, we will perform sensitivity analyses on population size, and also the costs of survival and
reproduction. These sensitivity analyses will assess the robustness of the results that we will obtain from
the analyses detailed above. We will analyse population size because evidence suggests that, via changes in
the reproductive output within a population, the importance of variance in fitness decreases as populations
become larger, which suggests possible changes in our results if we increase the initial population (Gillespie,
1974; Rubenstein, 2011; Lehmann and Balloux, 2007). We will also analyse the robustness of our results
under different combinations of survival and reproductive costs. The baseline is set so that an individual
survives with one resource and reproduces with two times the survival cost. The reproductive threshold
is set to be five times the reproductive cost, resembling the resources an individual needs to start her
reproductive career. Life history traits related to survival can decrease if the costs of survival increase, and
the same with reproduction, according to how the mechanics of our model work. Furthermore, changes
in the costs of reproduction and survival could also increase the influence of certain resource dynamics in
the life history dynamics that individuals face. An intuitive example could be that if the costs of survival
are higher than what a juvenile can produce, her chances of surviving until the next iteration will always
depend on maternal investment and resource transfers. Therefore, analysing the sensitivity of our results
under different population sizes, and survival and reproductive costs, can show how the importance of
resource dynamics might vary under different demographic and life history scenarios.

4 Level of bias control

We declare that our registered report has a Level 2 in terms of bias control, following the scale provided by
PCIRRR. In order to complete the design of the agent-based model, and ensure that the different mechanisms
of resource and life history dynamics worked correctly, it was necessary to generate data, access it, and
observe parts of it. This procedure included the exploration of a small set of combinations of parameter
values to identify a reasonable range for our analyses. Furthermore, we describe in the next section (Model
insights) the influence that such exploration had in the design of the model.

We can ensure that the level of bias in our registered report does not compromise the results and their
interpretation because, (1) it is necessary to explore the full range of values to make a robust conclusion on
traits. For this, we will analyse the role of each parameter separately (i.e. scenario one, two, and three), then combinations of two of them (i.e. scenario four, five, and six), and finally a combination of the three together (i.e. scenario seven), which translates in defining seven scenarios. **Scenario 1**, we will run the computational model to understand the influence of changes in resource production on the variability of life cycles. The model will not have resource transfers, the habitat quality will be set to baseline, and we will explore the impact of changing values of production probabilities from 0.1 to 0.9 (17 values). **Scenario 2**, we will run the computational model to understand the influence of changes in the habitat quality. For this, the model will not have resource transfers, the values of production will be set to baseline, and we will explore the influence of habitat quality by doubling its value, and recreate a rich environment. **Scenario 3**, we will set up the model to explore the role of resource transfers in the variability of female human life cycles. Therefore, the values of resource production and habitat quality will be set to baseline, while the values in the block matrix, which defines the social network structure of the resource transfers, will range from 0.05 to 0.95 (19 values, and 323 combinations) while keeping the downward pattern. **Scenario 4** will explore the variability of life cycles by the combination of resource production and habitat quality. For this, we will explore the values of production probabilities from 0.1 to 0.9 with habitat quality set to double the baseline, and no resource transfers (17 values). **Scenario 5** will explore the variability of life cycles by the combination of habitat quality and resource transfers. For this, we will explore the values in the block matrix from 0.05 to 0.95 with habitat quality set to double the baseline, and production probabilities set to baseline (19 values, and 323 combinations). **Scenario 6** will explore the combination of resource production and resource transfers. The model will be set up with habitat quality as baseline, while production probabilities will range from 0.1 to 0.9 (17 values) and the values in the block matrix will range from 0.05 to 0.95 (19 values, and 323 combinations). Finally, **Scenario 7** will run simulations to understand how the interplay between resource production, transfers, and habitat quality influence the variability of life cycles within a population. Accordingly, we will set habitat quality as high, production probabilities will range from 0.1 to 0.9, and resource transfers between 0.05 and 0.95, leading to a maximum of 10982 combinations. We will repeat each unique combination 10 times (see Table 1 for a summary).

We will calculate for each scenario the longevity, lifetime reproductive output, and the timing of stage transitions for all individuals in each combination of resource dynamics to analyse the variability of life cycles. Specifically, we will analyse how the full distributions of the different life history traits among all individuals born between years 100 and 200 to cover one full generation (birth to death) change in response to varying the parameters. Focusing on individuals born within this time frame means we should have no (or very few) of the initial individuals in the analysis population and all individuals in the sample should have completed their life cycle by the end of the simulation (year 300).

Following the research questions stated in Table 2, we will be able to answer our first research question, regarding the role of resource production in the female human life cycle, by analysing the distribution of the different life history traits of **Scenario 1**. The second research question about habitat quality will be answered by analysing the outcomes of **Scenario 2**, the comparison of **Scenario 1** and **Scenario 4**, and the comparison of **Scenario 3** and **Scenario 5**. The third resource question regarding the role of resource transfers will be answered once we analyse the distribution of longevity, lifetime reproductive output, and timing of life cycle stage transition from **Scenario 3**, the comparison of **Scenario 2** and **Scenario 5**, and the comparison of **Scenario 1** and **Scenario 6**. Finally, our fourth research answer will be answered when we analyse the outcomes of **Scenario 7** and compare them with the ones from **Scenario 6**. This way, we are able to analyse how the variability of life cycles within a female human population changes under
different combinations of resource production, transfers, and habitat quality (see Fig. 4 for a graphical representation).

Figure 4: Graphical description of the model analysis. There is the development of seven scenarios with different combinations of parameters configuration. Each scenario has on top the setting for resource production, in the middle the setting for habitat quality, and on the bottom the setting for resource transfer. In the different scenarios we define whether for resource production and transfers either we do a parameters swipe (PS), we set a parameter at baseline (B), or null (N). In the case of habitat quality, we set it either as poor (P) or rich (R). For each scenario we calculate as an outcome the distribution of longevity (LNG), lifetime reproductive output (LRO), age at sexual maturity (ASM), age at first reproduction (AFR), and age at menopause (AMe) to characterise the diversity of female life cycles within the population in each scenario. Finally, we compare the different scenarios to answer the research questions for which we develop the model. We explore the outcome of Scenario 1 for the first research question (RQ 1) about the role of resource production. We compare Scenario 1 with Scenario 4, and Scenario 3 with Scenario 5, to address our second research question (RQ 2) about the role of habitat quality. We analyse the output of Scenario 3, and compare Scenario 2 with Scenario 5, and Scenario 1 with Scenario 6, in order to answer the third research question (RQ 3) about the role of resource transfers. Finally, we compare Scenario 6 with Scenario 7 in order to answer our fourth research question (RQ 4) regarding the interplay of resource production, habitat quality, and resource transfers.

Finally, we will check the robustness of our results by changing population size, and also the costs of survival and reproduction. These robustness checks will assess the strength of the results that we will obtain from the analyses detailed above. We will analyse population size because evidence suggests that, via changes in the reproductive output within a population, the importance of variance in fitness decreases as populations become larger, which suggests possible changes in our results if we increase the initial population ([Gillespie 1974, Rubenstein 2011, Lehmann and Balloux 2007]). We will also analyse the robustness of our results under different combinations of survival and reproductive costs. The baseline is set so that an individual survives with one resource and reproduces with two times the survival cost. The reproductive
the role of resource production, transfers, and habitat quality in the variability of life cycles (Table 1), and
(2) we have not extracted information on the key variables of interest for our research questions, which is
the variability of different life history traits (i.e. coefficients of variation).

5 Model insights

During the design and building of the baseline model, there were certain assumptions that we made after
some initial exploration of the mechanics of the model. Given the complexity of our modelling framework,
this was a necessity. The exploratory analyses were not meant as a systematic revision of parameter values,
but as a way to decide upon certain processes for which there is no consensus in the literature as well as
to more deeply understand how any assumption that we make may influence any downstream component
of our model. The insights that we gained from this exploratory exercise are related to the definition and
implications of resource surplus for resource transfers and habitat quality, the mechanisms behind resource
transfers, and the importance of maternal investment.

Currently, the definition of resource surplus for resource transfers is the amount of resources an individual
has after going through resource production and maternal investment, while also accounting for the costs
of survival and reproduction. Hence, the amount of resources that an individual transfers during a given
iteration is limited to her remaining available resources once she has ensured her reproduction as well as the
survival of herself and her descendants. Therefore, individuals would follow a sharing behaviour closer to
communal breeding, where individuals share resources in the population to secure food and help with child
rearing (Federico et al., 2020). However, we also wanted to examine how our model behaved with a different
definition for the resources available for transfer. Once we excluded the reproductive cost from the definition
of resource surplus, individuals would show a behaviour that is closer to cooperative breeding (Federico et al.,
2020), where individuals shared resources even if that meant they themselves could not reproduce. Here, it
is very difficult for individuals to accumulate enough resources to reproduce, with reproduction essentially
being restricted to individuals who, by chance, receive many resource transfers at once in a given year,
leading to a very high proportion of individuals being childless. The change is essentially from individuals
being first selfish before sharing in the communal breeding scenario, to individuals being forced to always
share even if it is detrimental to their self interests. We decided to define the sharing behaviour closer
to communal breeding because the simulated population appeared to more closely resemble the behaviour
observed in human populations (Hrdy, 2007; Kramer and Veile, 2018).

Regarding habitat quality, we explored possible values that could have a more logical justification for
our baseline model while also fitting with the dynamics of the model. We decided to set habitat quality
so that an individual can produce sufficient resources to survive and reproduce in one iteration. Therefore,
an individual can reproduce in a year even if she does not have stored resources or receives any from
other members of the population. The reasoning behind this is that reproduction can be considered quite
stochastic and opportunistic (van Daalen and Caswell, 2017). In a rich environment, having a “lucky” year
would mean that an individual could get enough resources to compensate for previous years and minimise the
costs of survival and reproduction. An alternative setting would be to set up a forced obligate cooperative
breeding scenario, where women can only reproduce if they receive resources from others. Again, we decided
to set the habitat quality to facilitate behaviour that reflects communal breeding.

After running the baseline model to check that the resource and life history dynamics work, we realised
that the observed patterns of resource transfers can be explained by three components. First, the stage-
threshold is set to be five times the reproductive cost, resembling the resources an individual needs to start her reproductive career. Life history traits related to survival can decrease if the costs of survival increase, and the same with reproduction, according to how the mechanics of our model work. Furthermore, changes in the costs of reproduction and survival could also increase the influence of certain resource dynamics in the life history dynamics that individuals face. An intuitive example could be that if the costs of survival are higher than what a juvenile can produce, her chances of surviving until the next iteration will always depend on maternal investment and resource transfers. Therefore, analysing the robustness of our results under different population sizes, and survival and reproductive costs, can show how the importance of resource dynamics might vary under different demographic and life history scenarios.

4 Level of bias control

We declare that our registered report has a Level 2 in terms of bias control, following the scale provided by PCIRR. In order to complete the design of the agent-based model, and ensure that the different mechanisms of resource and life history dynamics worked correctly, it was necessary to generate data, access it, and observe parts of it. This procedure included the exploration of a small set of combinations of parameter values to identify a reasonable range for our analyses. Furthermore, we describe in the next section (Model insights) the influence that such exploration had in the design of the model.

We can ensure that the level of bias in our registered report does not compromise the results and their interpretation because, (1) it is necessary to explore the full range of values to make a robust conclusion on the role of resource production, transfers, and habitat quality in the variability of life cycles (Table 1), and (2) we have not extracted information on the key variables of interest for our research questions, which is the variability of different life history traits (i.e. coefficients of variation).

5 Model insights

During the design and building of the baseline model, there were certain assumptions that we made after some initial exploration of the mechanics of the model. Given the complexity of our modelling framework, this was a necessity. The exploratory analyses were not meant as a systematic revision of parameter values, but as a way to decide upon certain processes for which there is no consensus in the literature as well as to more deeply understand how any assumption that we make may influence any downstream component of our model. The insights that we gained from this exploratory exercise are related to the definition and implications of resource surplus for resource transfers and habitat quality, the mechanisms behind resource transfers, and the importance of maternal investment.

In our final model, the definition of resource surplus for resource transfers is the amount of resources an individual has after going through resource production and maternal investment, while also accounting for the costs of her own survival and reproduction. Therefore, the number of resource transfers that an individual performs during a given iteration has an upper limit defined by her remaining resources available once she has ensured her reproduction as well as the survival of herself and her descendants. This definition of surplus resembles what is assumed when individuals follow a sharing behaviour of communal breeding (Federico et al., 2020). However, we also wanted to examine how our model behaved with a different definition for the resources available for transfer, closer to what sometimes has been conceptualised as cooperative breeding (Federico et al., 2020) where individuals share resources even if this would impact
structured transfer probabilities coupled with the definition of resource surplus decreases the amount of resources available to transfer to individuals in their adult and reproductive career stages. Therefore, the definition of resource surplus can be considered as the trade-off individuals face regarding resource allocation. Second, the age distribution of individuals per life cycle stage influence because there are different dynamics happening for each of them that influence the interaction of the block matrix and the resource surplus. An example about the influence of the age distribution would be that individuals who transition to their post-reproductive stage will have a higher amount of resources available for transfers (i.e. resource surplus) than those individuals that have been longer in the post-reproductive stage. This situation would happen because an individual who just reaches menopause would have more resources stored due to the higher resource production and reproductive dynamics from the previous stage (i.e. adult or reproductive career). Hence, she would have a higher surplus than older post-reproductive individuals, which would lead to her transferring more sources within the population. In conclusion, there are social, individual, and demographic components in the model that influence the patterns that can be observed regarding resource transfers. Accordingly, rather than initialising the simulation with all individuals being of the same age, the initial population now consists of the same number of individuals per life cycle stage (i.e. 25 juveniles, adults, reproductive career, and post-reproductive individuals, which sum to an initial population of 100 individuals), and we only analyse data after the population is likely to have shifted towards a more balanced composition (i.e. those individuals born between years 100 and 200, to cover one full generation of individuals who do not belong to the initial population).

we will analyse the coefficient of variation of different life history traits among all individuals born between years 100 and 200 to cover one full generation (birth to death) of a large sample of individuals. This means we should have no (or very few) of the initial individuals in the analysis population and all individuals in the sample should have completed their life cycle by the end of the simulation (year 300). This way, we are able to analyse how the variability of life cycles within a female human population changes under different combinations of resource production, transfers, and habitat quality.

Finally, we define maternal investment as being independently to resource transfers dynamics for two reasons. First, even though parental investment is a form of resource transfer, it has a specific mechanisms that govern the transfer (e.g. kin selection, parent-offspring conflict) (Hamilton, 1964; Godfray, 1995). Second, we realised while building the baseline model that if individuals only produce resources but do not loose resources from sharing, as in our first research question, then they do not transition to a post-reproductive stage unless they are forced to do so. This is because they produce and store enough resources to keep reproducing until very late in life. However, when including maternal investment such that mothers cover the need her descendants for survival, women will transition to menopause if they have a large number of children. Such a pattern is consistent with the idea that reproductive conflict between women of different ages would turn into downward cooperation from older individuals in the case where they are mother and descendant—causing older women stop their reproduction career, and reach menopause, earlier (Cant and Johnstone, 2008; Mace and Alvergne, 2012). In conclusion, we defined maternal investment as a separate dynamic rather than it being part of the resource transfers because (a) they work under different evolutionary dynamics (e.g. kin selection, parent-offspring conflict, reproductive conflict), and because (b) maternal investment might be necessary so individuals transition to a post-reproductive stage, based on the resource and life history dynamics defined in our model.
their own reproduction. The difference is essentially from individuals being selfish before sharing in the communal breeding scenario, to individuals being forced to always share even if it is detrimental to their self interests. We observed in our model exploration that a sharing behaviour closer to cooperative breeding ended up with levels of childlessness that were higher than the ones observed in human populations (Bailey and Aunger 1995, Belsey 1976). This patterns was because of the difficulties for individuals to accumulate enough resources to reproduce, with reproduction essentially being restricted to individuals who, by chance, receive many resource transfers at once in a given year. In addition to leading to demographic patterns that do not resemble human populations, there are also conceptual reasons why a model that assumes reproductive costs of sharing resources is unlikely to represent the human pattern. Studies looking at the relationship between sharing and own reproduction, such as Kramer and Veile (2018), show that allocare does not have an effect on interbirth intervals and number of surviving children in a hunter-gatherer and a horticultural populations (Pumé and Maya, respectively), supporting the idea that resource sharing might not come at costs of the reproduction of an individual. These observations aligns with evidence in other species that show that even in cooperative breeders sharing resources is conditional on having no effect on the fitness of individuals (e.g. meerkats (Clutton-Brock et al., 2001), kookaburras (Legge, 2000), and crows (Canestrari et al., 2010)). Based on these observations, and our model exploration, we decided to define the amount of resources available for resource transfers closer to communal breeding, and therefore define the surplus of resources available for transfers after an individuals accounts for her own reproduction as well as the survival of herself and her descendants.

Regarding habitat quality, we explored possible values that could have a more logical justification for our baseline model while also fitting with the dynamics of the model. We decided to set habitat quality so that an individual can produce sufficient resources to survive and reproduce in one iteration. Therefore, an individual can reproduce in a year even if she does not have stored resources or receives any from other members of the population. The reasoning behind this is that reproduction can be considered quite stochastic and opportunistic van Daalen and Caswell (2017). In a rich environment, having a “lucky” year would mean that an individual could get enough resources to compensate for previous years and minimise the costs of survival and reproduction. An alternative setting would be to set up a forced obligate cooperative breeding scenario, where women can only reproduce if they receive resources from others. Again, we decided to set the habitat quality to facilitate behaviour that reflects communal breeding.

After running the baseline model to check that the resource and life history dynamics work, we realised that the observed patterns of resources transfers can be explained by three components. First, the stage-structured transfer probabilities coupled with the definition of resource surplus decreases the amount of resources available to transfer to individuals in their adult and reproductive career stages. Therefore, the definition of resource surplus can be considered as the trade-off individuals face regarding resource allocation. Second, the age distribution of individuals per life cycle stage influence because there are different dynamics happening for each of them that influence the interaction of the block matrix and the resource surplus. An example about the influence of the age distribution would be that individuals who transition to their post-reproductive stage will have a higher amount of resources available for transfers (i.e. resource surplus) than those individuals that have been longer in the post-reproductive stage. This situation would happen because an individual who just reaches menopause would have more resources stored due to the higher resource production and reproductive dynamics from the previous stage (i.e. adult or reproductive career). Hence, she would have a higher surplus than older post-reproductive individuals, which would lead to her transferring more sources within the population. In conclusion, there are social,
6 Funding

The authors thank the Max Planck Society for funding this work.

References


individual, and demographic components in the model that influence the patterns that can be observed regarding resource transfers. Accordingly, rather than initialising the simulation with all individuals being of the same age, the initial population now consists of the same number of individuals per life cycle stage (i.e., 25 juveniles, adults, reproductive career, and post-reproductive individuals, which sum to an initial population of 100 individuals), and we only analyse data after the population is likely to have shifted towards a more balanced composition (i.e., those individuals born between years 100 and 200, to cover one full generation of individuals who do not belong to the initial population).

we will analyse the coefficient of variation of different life history traits among all individuals born between years 100 and 200 to cover one full generation (birth to death) of a large sample of individuals. This means we should have no (or very few) of the initial individuals in the analysis population and all individuals in the sample should have completed their life cycle by the end of the simulation (year 300). This way, we are able to analyse how the variability of life cycles within a female human population changes under different combinations of resource production, transfers, and habitat quality.

Finally, we define maternal investment as being independently to resource transfers dynamics for two reasons. First, even though parental investment is a form of resource transfer, it has a specific mechanisms that govern the transfer (e.g., kin selection, parent-offspring conflict) (Hamilton, 1964; Godfray, 1995). Second, we realised while building the baseline model that if individuals only produce resources but do not lose resources from sharing, as in our first research question, then they do not transition to a post-reproductive stage unless they are forced to do so. This is because they produce and store enough resources to keep reproducing until very late in life. However, when including maternal investment such that mothers cover the need for descendants for survival, women will transition to menopause if they have a large number of children. Such a pattern is consistent with the idea that reproductive conflict between women of different ages would turn into downward cooperation from older individuals in the case where they are mother and descendant—causing older women stop their reproduction career, and reach menopause, earlier (Cant and Johnstone, 2008; Mace and Alvergne, 2012). In conclusion, we defined maternal investment as a separate dynamic rather than it being part of the resource transfers because (a) they work under different evolutionary dynamics (e.g., kin selection, parent-offspring conflict, reproductive conflict), and because (b) maternal investment might be necessary so individuals transition to a post-reproductive stage, based on the resource and life history dynamics defined in our model.

6 Funding

The authors thank the Max Planck Society for funding this work.

References


34


