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## The role of resource dynamics in the distribution of life cycles within a female human population. Registered Report

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### November 10, 202<mark>3</mark>

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## May 11, 2024

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#### Abstract

The evolution of the female human life cycle, which is characterised by having a reproductive career 2 nested within juvenile and post-reproductive periods, has been linked to the surplus of adult resource 3 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-8 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, 10 and based on surpassing the thresholds for survival, reproduction, and life cycle stage transition costs. 11 12 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 13 will reveal possible mechanisms behind the demographic diversity observed in human populations, and 14 the extent to which the female life cycle varies in reaction to social and environmental changes. 15

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

#### 18 1 Introduction

1

The female human life cycle can be described as having a reproductive career nested between juvenile 19 and post reproductive periods. The life cycle has also being described with specific life history traits, 20 such as a long lifespan, high reproductive output, and short interbirth intervals, in comparison to other 21 primates (Kaplan et al., 2000; Kramer, 2010; Hawkes et al., 1998). This representation of the female 22 human life cycle is a common assumption in human life history theory, and is commonly observed in 23 hunter-gatherer populations (Kaplan et al., 2000). Evidence from other human populations suggests that 24 life history traits can exhibit large individual-level variation within human populations. The average life 25 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 27 can also differ in their age at first reproduction—as can be seen in Germany, where ages range from  $\sim 15$  to  $\sim$ 43 years old (Statistisches Bundesamt, 2023)). Evidence also suggests that reproductive inequality within 29 a population can be high, with estimates of up to 40% of women in several sub-Saharan Africa populations 30 being childless (Bailey and Aunger, 1995; Belsey, 1976). This variation in life cycles among women is crucial 31 for demographic change (Borgerhoff Mulder, 1998) and creating inequalities between individuals (Colleran 32 et al., 2015), but the source of this variation is not fully understood (Sear et al., 2016). Most potential 33 explanations are based on adaptive models that focus on variation in particular life history traits, ignoring 34 the potential role of stochasticity (Snyder and Ellner, 2018) and the allocation of resources not only between 35 different life history traits within individuals but also the redistribution of resources between individuals 36 (e.g., through sharing behaviours; Jones, 2015). Here, we develop a computational model to (1) determine 37 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 30 transfers between individuals might buffer the variations due to resource production and habitat quality. 40 The conditions under which a life cycle emerges can be understood by considering the environmental 41

<sup>41</sup> The conditions under which a life cycle emerges can be understood by considering the environmental <sup>42</sup> constraints experienced by individuals, and how individuals resolve these constraints through the allocation

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The evolution of the female human life cycle, which is characterised by having a reproductive career 2 nested within juvenile and post-reproductive periods, has been linked to the surplus of adult resource 3 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-8 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, 10 and based on surpassing the thresholds for survival, reproduction, and life cycle stage transition costs. 11 12 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 13 will reveal possible mechanisms behind the demographic diversity observed in human populations, and 14 the extent to which the female life cycle varies in reaction to social and environmental changes. 15

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#### 18 1 Introduction

1

The female human life cycle can be described as having a reproductive career nested between juvenile and 19 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 21 intervals (Kaplan et al., 2000; Kramer, 2010; Hawkes et al., 1998). This representation of the female human 22 life cycle is a common assumption in human life history theory, mainly based in populatinos of hunter-23 gatherers (Kaplan et al., 2000). However, within this general pattern, the various traits that constitute 24 the female human life cycle can exhibit a large individual-level variation. The average life expectancy 25 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  $\sim 15$  to  $\sim 43$  years 28 old (Statistisches Bundesamt, 2023)). Evidence also suggests that reproductive inequality within a female 29 population can be high, with estimates of up to 40% of women in several sub-Saharan Africa populations 30 being childless (Bailey and Aunger, 1995; Belsey, 1976). This variation in life cycles among women is 31 crucial for demographic change (Borgerhoff Mulder, 1998) and creating inequalities between individuals 32 (Colleran et al., 2015), but the sources of variability of life cycles between women are not fully understood 33 (Sear et al., 2016). Most potential explanations for the variability of life cycles between women are based 34 on adaptive models that focus on the variation of particular life history traits, the allocation of resources 35 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 40 human female life cycles might arise from stochasticity in resource production, (2) assess which life history 41 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 45 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 47 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 51 transfers" Lee (2003) advances that—under the assumption of adult surplus of resource production, and 52 transfer of this surplus towards juveniles—the potential for resource transfers at later ages can explain 53 selection on reduced mortality at later ages. This would result in an extended lifespan, while the cumulative 54 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 57 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 59 from parents to offspring, but that alloparenting from individuals of different generations reduces the load 60 of parental investment, and therefore allows the allocation of more resources towards reproduction and 61 growth (Kramer and Ellison, 2010). These models highlight that the key dynamics that constrain female 62 human life cycles appear to be related to how both the physical and the social environment influence how 63 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 65 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). 69

The evolutionary models that predict variability in life cycles within populations focus on how individual 70 differences in resource acquisition and allocation at different life cycle stages might result in differences in 71 fitness. One set of models predicts that differences in how many resources individuals receive during their 72 early life might have far reaching consequences for the whole life cycle. The "silver spoon model" predicts 73 that individuals who receive more resources early in life will have the highest fitness irrespective of the 74 adult environmental conditions (Pigeon et al., 2019; Lummaa and Clutton-Brock, 2002). In contrast, the 75 "adaptive developmental plasticity model" proposes that individuals whose experience in early life matches 76 what they experience later in life would develop a phenotype that allows a higher fitness than those that have 77 a mismatch between early and late life (Bateson et al., 2004; Nettle and Bateson, 2015). The "environmental 78 saturation model" expands these early life models to point out that differences between individuals should 79 be most visible in environments with intermediate conditions, because harsh environments would constrain 80 all individuals while abundant ones would permit individuals with a disadvantage to catch up (Engquist and 81 Reinhold, 2016). Another set of models focuses on the resources that adults have available for the trade-offs 82 between different life history traits (Van Noordwijk and de Jong, 1986). These models suggest that high 83 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 <sup>43</sup> how resource transfers between female individuals might influence the variability of the female human life
<sup>44</sup> 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 45 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 47 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 51 investment (i.e. resource transfers towards juveniles), and short interbirth intervals. Furthermore, long 52 juvenile periods relate to the amount of time needed to acquire the skills necessary to produce surplus, 53 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 57 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 59 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 61 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 71 occur from the differences among individuals within a population in their ability to acquire resources in a 72 given environment, as demonstrated by the theoretical model from Van Noordwijk and de Jong (1986).

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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 88 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 90 acquisition appears to indeed play an equal, or larger, role than resource allocation in explaining life cycle 91 differences between individuals (Laskowski et al., 2021; Haave-Audet et al., 2022). However, in all of these 92 evolutionary models, resource acquisition is the variable that is manipulated, which precludes that ability of 93 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 95 between parents and offspring), which diversifies the ways in which resources are acquired and distributed within a population. 97

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 99 some individuals at the cost of others. The benefits of sharing resources have been linked to two strategies 100 that matter in terms of variability in fitness: bet-hedging and cooperative breeding. In environments 101 where resource production might be unpredictable, flexible resource transfers that are based on surpluses 102 and need can be a way for individuals to hedge their bets (Carter et al., 2017). This redistribution of 103 resources is expected to lead to a decrease in the variance of life cycles between individuals. Therefore, 104 sharing behaviour might reduce the risk that the fitness of an individual will drop to zero in unpredictable 105 environmental conditions, increasing the long-term fitness of individuals exhibiting such a strategy within a 106 population (Cohen, 1966; Gillespie, 1974; Caswell, 1983; Starrfelt and Kokko, 2012). In primates, including 107 humans, life history strategies are characterised by delayed reproduction, reduced fertility, and extended 108 generation times. These strategies can be viewed as adaptive responses to highly unstable environments, 109 which leads to also high fluctuations in population size (i.e. non-equilibrium ecological conditions) (Jones, 110 2011). These strategies enable individuals to explore diverse environments over longer periods, thereby 111 enhancing the likelihood that their descendants will survive, and decreasing the influence of variability over 112 the mean fitness (Jones, 2011). Cooperative breeding has also been proposed as a bet-hedging strategy 113 Rubenstein (2011). However, in this case the idea is that dominant individuals maximise their fitness 114 because the contribution of the helpers reduces any environmentally-induced fecundity variance. This leads 115 to higher variability in life cycles between individuals in the group. Evidence in humans supports models 116 of bet-hedging, and speaks more closely to cooperative breeding (i.e. communal breeding), due to the 117 common practice of resources transfers between individuals of a population (e.g. alloparenting (Ivey, 2000; 118 Sear and Mace, 2008; Sear and Coall, 2011; Kramer and Veile, 2018) or food sharing (Gurven et al., 2000; 119 Gurven, 2004; Jaeggi and Gurven, 2013; Bird et al., 2002; Gettler et al., 2023; Ready and Power, 2018)). 120 However, there is also evidence showing that resource dynamics in humans is influenced by competitive 121 dynamics that occurs over limited social and material resources (Nitsch et al., 2013; Mace and Alvergne, 122 2012; Lahdenperä et al., 2012; Redhead and von Rueden, 2021; Redhead and Power, 2022). The mixed 123 evidence regarding the nature of resource transfers in human populations can be explained because such 124 dynamics can change depending on the genetic relatedness between individuals (Strassmann, 2011) or by 125 the amount of resource available (Borgerhoff Mulder, 2007). One common, but not exclusive, pattern 126 regarding sharing dynamics in human populations are inter-generational resource transfers that go from 127 older individuals in the population towards younger ones (i.e. downward resource transfers), in order to 128

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 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 91 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 97 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 100 within a population. 101

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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 131 on the influence of different resource dynamics and habitat quality. Extant models have focused on the 132 resource dynamics under which the female human life cycle evolved (e.g. embodied capital model (Kaplan, 133 1996) or resource transfer model (Chu and Lee, 2006)), while the model here advances the literature by 134 focusing on the mechanisms that drive the variability of life cycles within a population, rather than on the 135 emergence of a specific life cycle. Additionally, the model is more explicit in modelling resource dynamics 136 than previous models (Price and Jones, 2020; Kaplan, 1996; Chu and Lee, 2006; Lee, 2003; Kramer and 137 Ellison, 2010; Van Noordwijk and de Jong, 1986), as it assumes that networks of resource transfers follow 138 stage-structure. The model will focus on answering four research questions, which increase in complexity. 139 (1) How is the variability of life cycles within a female human population influenced by stochasticity in 140 individual resource production? Building upon Van Noordwijk and de Jong (1986), we expect that there 141 will be a higher variability of life cycles in a population under higher stochastic differences of resource 142 production between individuals due to larger individual differences in the amount of resources available 143 that can be allocated towards survival and reproduction. (2) How does the relationship between resource 144 production and life cycle variability change under different environmental conditions (i.e. habitat quality)? 145 We expect that the variability of life cycles within a female human population decreases as habitat quality 146 increases. With higher habitat quality, individuals can have a larger amount of resources available to 147 allocate towards survival and/or reproduction—buffering the individual differences in resource production 148 and, therefore, homogenising the life cycles in the population such that variability is reduced (Bolund, 149 2020). (3) How does stochastic variation in resource transfers influence the variability of life cycles within a 150 female human population? Considering the literature related to bet-hedging (Jones, 2011), we expect that 151 the redistribution of resources within the population will act as a buffer against environmental uncertainty, 152 and therefore decrease the variability of life cycles as the probabilities of individual resource transfers 153 increase. (4) How does the variability of life cycles within a population change due to the interplay between 154 individual resource dynamics and environmental conditions? We will look at the full interplay between 155 habitat quality, resource production and transfers to determine how their interaction may change the ways 156 in which resource availability influences the variability of life history traits within a human population (see 157 Fig. 1 for a graphical representation). 158

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 135 based on the influence of different resource dynamics and habitat quality. Extant models have focused 136 on the resource dynamics under which the female human life cycle evolved (e.g. embodied capital model 137 (Kaplan, 1996) or resource transfer model (Chu and Lee, 2006)), while the model here advances the literature 138 by focusing on the mechanisms that drive the variability of life cycles within a population, rather than 139 on the emergence of a specific life cycle. Additionally, the model is more explicit in modelling resource 140 dynamics than previous models (Price and Jones, 2020; Kaplan, 1996; Chu and Lee, 2006; Lee, 2003; 141 Kramer and Ellison, 2010; Van Noordwijk and de Jong, 1986), as it assumes that networks of resource 142 transfers follow stage-structure. The model will focus on answering four research questions, which increase 143 in complexity, following a generative inference approach (Kandler and Powell, 2018). Hence, the patterns 144 stated here are meant as possible scenarios that would emerge based on the assumptions and parameter 145 settings of the model. (1) How is the variability of life cycles within a female human population influenced 146 by stochasticity in individual resource production? Building upon Van Noordwijk and de Jong (1986), 147 it would be expected a higher variability of life cycles in a population under higher stochastic differences 148 of resource production between individuals due to larger individual differences in the amount of resources 149 available that can be allocated towards survival and reproduction. (2) How does the relationship between 150 resource production and life cycle variability change under different environmental conditions (i.e. habitat 151 quality)? The variability of life cycles within a female human population should decrease as habitat quality 152 increases. With higher habitat quality, individuals can have a larger amount of resources available to 153 allocate towards survival and/or reproduction—buffering the individual differences in resource production 154 and, therefore, homogenising the life cycles in the population such that variability is reduced (Bolund, 2020). 155 (3) How does stochastic variation in resource transfers influence the variability of life cycles within a female 156 human population? Considering the literature related to bet-hedging (Jones, 2011), the redistribution of 157 resources within the population should act as a buffer against environmental uncertainty, and therefore 158 decrease the variability of life cycles as the probabilities of individual resource transfers increase. (4)159 How does the variability of life cycles within a population change due to the interplay between individual 160 resource dynamics and environmental conditions? We will look at the full interplay between habitat quality, 161 resource production and transfers to determine how their interaction may change the ways in which resource 162 availability influences the variability of life history traits within a human population (see Fig. 1 for a 163 graphical representation). 164



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). This infographic will be updated in a later version of this manuscript, as it is currently improved by graphic designers.

In this registered report, we developed a computational framework to address these questions. This 159 framework includes the complexity of environmental conditions, resource dynamics, as well as life history 160 dynamics that might arise in different environmental and social conditions. By focusing on resource dy-161 namics, our framework can show the potential biological limits to life cycle variation. The framework will 162 be explored using an agent-based model. This is because agent based models have the capacity to address 163 complex phenomena from individual and population levels and because of its implicit way to incorporate 164 stochasticity by allowing agents to behave differently, despite being all under the same rules (Judson, 1994; 165 Wilensky and Rand, 2015). The key parameters in the model are: habitat quality, defined as the maximum 166 amount of resources available in the environment at any given time; production probability, which is the 1<mark>6</mark>7 probability that individuals successfully acquire resources from the environment at any given time; and 168 transfer probability, the probability that individuals will share resources with each other. In the follow-169 ing section, we describe the model following an ODD (Overview, Design concepts, Details) protocol, as a 170 standardised approach for clarifying the scope, assumptions, and parameters used to answer our research 171 questions (Grimm et al., 2006, 2020). For question 1, we will run the agent-based model without sharing, 172 setting the habitat quality to baseline, and change the production probabilities to range between 0.1 and 0.9, 173 producing a total of 41 values in our parameter sweep. For question 2, we will set sharing to zero, habitat 174 quality to high, and change the production probabilities to range between 0.1 and 0.9 (an additional 41175 values). For question 3, we set habitat quality to baseline, production probabilities to average, and change 176



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). This infographic will be updated in a later version of this manuscript, as it is currently improved by graphic designers.

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- $1\pi$  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
- $1_{100}$  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 181 range between 0.1 and 0.9, producing a total of 17 values in our parameter sweep. For question 2, we will set 182 sharing to zero, habitat quality to high, and change the production probabilities to range between 0.1 and 183 0.9 (an additional 17 values). For question 3, we set habitat quality to baseline, production probabilities 184 to average, and change the stage-specific sharing values to range between 0.05 and 0.95 (19 values, and 185 323 combinations), while maintaining the structure of the network. For question 4, we set habitat quality 186 to baseline and high, production probabilities to range between 0.1 and 0.9 (17 values), and change the 187 stage-specific values of sharing to range between 0.05 and 0.95 (19 values, and 323 combinations), leading 188 to a maximum of 10982 combinations in our final simulation regime (see Table 1 for a summary). The 189 total number of resulting combinations could be smaller than this maximum because populations die out if 190 certain combinations lead to too few resources being generated (e.g. in preliminary explorations we noticed 191 that populations with a habitat quality of 12 and a production probability of 0.3 will grow exponentially, 192 whereas populations with the same habitat quality and a production probability of 0.2 quickly go extinct). 193 We will repeat each unique combination 10 times. Afterwards, we will describe and compare the population 194 distributions of the different life history traits (e.g. longevity, lifetime reproductive output, age at sexual 195 maturity, first reproduction, and menopause) that result from each parameter sweep designed to answer 196 each research question. The model will allow us to understand the conditions and mechanisms that allow 197 higher variability of life history traits within a population. Furthermore, the results will help to understand 198 the demographic diversity observed among human populations, as well as offer a tool to further test the 199 complexity of the environmental and social components that link resource availability with the development 200 of life cycles. 201

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.

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

## <sup>190</sup> 2 Model description

#### <sup>191</sup> 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.

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

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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 199 through life related to survival, reproduction, and growth and development, is described by her longevity, 200 lifetime reproductive output, and the timing of life cycle stage transition. Longevity is the total number 201 of years that an individual is alive. Lifetime reproductive output refers to the total number of descendants 202 produced by the end of the life cycle of an individual. The timing of life cycle stage transition refers to the 203 age at which an individual transitions through four discrete stages (i.e. juvenile, adult, reproductive-career, 204 post-reproductive). Each transition represents a specific event in the life cycle of an individual: age at 205 sexual maturity, age at first reproduction, and age at menopause. 206

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 oppor-213 tunity to send resources to other individuals in the population. The maximum number of transfers that 214 an individual can send is determined by their surplus of available resources (i.e. amount of resources that 215 an individual has once they account for the costs of reproduction and survival). The number of trans-216 fers an individual sends is stochastically determined, where the maximum number of transfers provide an 217 upper limit. Who individuals choose to transfer resources to is probabilistically determined by the life-218 cycle-stage structure of the population. We use a variation of a stochastic block model to construct these 219 stage-structured resource transfers (Redhead et al., 2023; Ross et al., 2023; Lee and Wilkinson, 2019; Hol-220 land et al., 1983). Furthermore, we use a block matrix, as part of the social network model, to specify the 221 values for resource transfers within and between life cycle stages. This means that individuals of a given life 222 cycle stage are more, or less, likely to transfer resources to other individuals, based on the life cycle stage 223 that both individuals occupy. We use a block matrix, as part of the social network model, to specify the 224 values for resource transfers within and between life cycle stages. For instance, in certain regimes, adults 225 are more likely to share food with juveniles and post-reproductive individuals than other adults or those in 226 their reproductive career within the population. An example of such sharing pattern can be seen among the 227 Tsimane in Bolivian Amazonia, where parents, grandparents, and siblings provide significant net downward 228 transfers of food across generations (Hooper et al., 2015). 229

We expect that the patterns of life cycle variation will depend on the resource dynamics that individuals 230 experience. Therefore, changes in the probabilities of resource production and transfers, together with habi-231 tat quality, are predicted to produce individual differences of life history traits within the population (i.e. 232 longevity, lifetime reproductive output, age at menarche, age at first reproduction, and age at menopause). 233 First, an increase in the individual probabilities for resource production is expected to increase the average 234 timing of transitions and the average reproductive output, and should lead to an inverted U-shaped pattern 235 in the expected variation between individuals. These patterns would be expected because more resources 236 mean that, on average, individuals are more likely to survive and reproduce. Regarding variability, individ-237 uals would experience more homogeneous resource dynamics on the extreme individual probabilities (e.g. 238

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 211 through life related to survival, reproduction, and growth and development, is described by her longevity, 212 lifetime reproductive output, and the timing of life cycle stage transition. Longevity is the total number 213 of years that an individual is alive. Lifetime reproductive output refers to the total number of descendants 214 produced by the end of the life cycle of an individual. The timing of life cycle stage transition refers to the 215 age at which an individual transitions through four discrete stages (i.e. juvenile, adult, reproductive-career, 216 post-reproductive). Each transition represents a specific event in the life cycle of an individual: age at 217 sexual maturity, age at first reproduction, and age at menopause (see Fig. 2 for a graphical representation 218 of the female human life cycle). 219

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 oppor-226 tunity to send resources to other individuals in the population. The maximum number of transfers that an 227 individual can send is determined by their surplus of available resources (i.e. amount of resources that an 228 individual has once they account for the costs of reproduction and survival). The number of transfers an 229 individual sends is stochastically determined, where the maximum number of transfers provide an upper 230 limit. Who individuals choose to transfer resources to is probabilistically determined by the life-cycle-stage 231 structure of the population. We assume a stochastic approach to remain agnostic regarding who transfers 232 resources to whom because the focus of our research is on the relationship between resource dynamics and 233 the variability of life history traits, and not the mechanisms behind the sharing dynamics. This assumption 234 is based on the evidence showing that the different mechanisms behind the sharing dynamics in human pop-235 ulations are quite diverse (e.g. genetic relatedness, need-based, reciprocity, costly signaling (Gurven, 2004; 236 Allen-Arave et al., 2008; Sear and Mace, 2008; Smith et al., 2019)), and therefore it would require a wider 237 number of parameters, and an increase of the parameter space, in order to test the different mechanisms. 238 Our aim here is to more generally understand if the presence of sharing dynamics in a population in general 239 has the potential to shift life history dynamics, rather than to account for the specific sharing dynamics 240 that might occur in different social and environmental contexts. 241

We use a variation of a stochastic block model to construct the stage-structured resource transfers 242 (Redhead et al., 2023; Ross et al., 2023; Lee and Wilkinson, 2019; Holland et al., 1983). We use a block 243 matrix, as part of the social network model, to specify the values for resource transfers within and between life 244 cycle stages. This means that individuals are more, or less, likely to transfer resources to other individuals, 245 based on the life cycle stage that both individuals occupy. We assume an downward inter-generational 246 resource transfer structure within the block matrix, meaning that individuals in younger stages of the 247 life cycle (e.g. juveniles) are more likely to receive resources from those in older stages (e.g. adult). 248 This assumption is based on previous theoretical work (Chu and Lee, 2006; Kramer and Ellison, 2010) 249 and empirical work (Hooper et al., 2015; Lee, 2020), which shows that it is a common pattern observed 250

- <sup>239</sup> 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
- <sup>242</sup> from her environment increases. Hence, the average life cycle would increase and the variability would show
- <sup>243</sup> 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
- <sup>245</sup> 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
- $_{247}$  life cycles (e.g. having no descendants or shorter lifespans) (see Table 2 and 1 for a summary). A graphical
- <sup>248</sup> 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 254 gives to her dependent descendants follows a need-base dynamic, providing sufficient resources to cover the 255 survival costs of the descendant if the mother has sufficient resources (Aktipis, 2016). Maternal dynamics 256 are defined separately from general resource transfers because they are governed by separate evolutionary 257 mechanisms (e.g. kin selection, parent-offspring conflict, reproductive conflict) from those that shape re-258 source transfers among other individuals (Hamilton, 1964; Godfray, 1995; Cant and Johnstone, 2008; Mace 259 and Alvergne, 2012). Hence, we assume it is a dynamic required for the development of the female human 260 life cycle that works separately from the sharing dynamics within a population. 261

We expect that the patterns of life cycle variation will depend on the resource dynamics that individuals 262 experience. Therefore, changes in the probabilities of resource production and transfers, together with habi-2**6**3 tat quality, are predicted to produce individual differences of life history traits within the population (i.e. 264 longevity, lifetime reproductive output, age at menarche, age at first reproduction, and age at menopause). 265 First, an increase in the individual probabilities for resource production is expected to increase the average 266 timing of transitions and the average reproductive output, and should lead to an inverted U-shaped pattern 267 in the expected variation between individuals. These patterns would be expected because more resources 268 mean that, on average, individuals are more likely to survive and reproduce. Regarding variability, individ-269 uals would experience more homogeneous resource dynamics on the extreme individual probabilities (e.g. 270 with low resource production everyone is poor whereas with high resource production everyone is rich), 271 reducing diversity in resource allocation towards survival and reproduction throughout their lives. Second, 272 the patterns described above should be more extreme if the amount of resources that an individual acquires 273 from her environment increases. Hence, the average life cycle would increase and the variability would show 274 a shape with higher kurtosis. Finally, the inclusion of resource transfers is predicted to have a buffering 275 effect, where the increase of the average life cycle and the inverted U-shaped pattern in variability would be 276 more smooth compared to the patterns described before. This buffering is caused by the redistribution of 277 resources within a population, which would reduce the probability that many individuals will show extreme 278 life cycles (e.g. having no descendants or shorter lifespans) (see Table 1 and 2 for a summary). A graphical 279 representation of how the distribution of life history traits can vary can be seen in Fig. 1, and the ways 280 that resource dynamics are expected to influence the life cycle is shown in Fig. 2. 281

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.

	II 1	A 1 : 1	T	
Question How is the variability of life cycles within a female human population influ- enced by individual re- source production?	Hypothesis There will be a higher variability of life cycles in a population under inter- mediate (but stochastic) differences of resource pro- duction between individu- als. This is due to larger individual differences in the amount of resources available to allocate to- wards survival and repro- duction	Analysis plan We will run a simu- lation regime using our agent-based model and fix the probability of resource transfers to 0 for all indi- viduals (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 be- tween 0.1 and 0.9 (across 41 values).	Interpretation Higher production prob- abilities allow, on aver- age, for more individuals to obtain resources, which support extended lifespan and increased reproduc- tion. Lower life cycle variability would happen under more extreme pro- duction probabilities as individuals would experi- ence similar conditions of scarcity or abundance.	A lack of variability of life cycles after changes in production probabili- ties could be explained if selection processes have optimised the female hu- man life cycle, allowing individuals to withstand fluctuations in resource production.
How does the relationship between resource produc- tion and life cycle vari- ability change under dif- ferent environmental con- ditions (i.e. habitat qual- ity)?	The variability of life cy- cles within a female hu- man population decreases as habitat quality in- creases. Under conditions of higher habitat qual- ity, individuals can have a larger amount of re- sources available to allo- cate towards life history traits, buffering the indi- vidual differences in re- source production and ho- mogenising the life cycles in the population	We will perform a simu- lation 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).	Habitat quality acts as a buffering effect as re- sources will be so abun- dant that individuals will be able to sustain them- selves, even though indi- viduals they may be more often unsuccessful in pro- duction. This will reduce the variability in life cycles within the population	If the increase in habi- tat quality leads to no changes in life cycle vari- ability, it could be that either phenotypic masking is happening or that vari- ability only shows in in- termediate levels of habi- tat quality (Van Noord- wijk and de Jong, 1986; Engqvist and Reinhold, 2016).
How does variation in the probabilities of resource transfers at the individ- ual level influence the vari- ability of life cycles within a female human popula- tion?	The redistribution of resources within the population will act as a buffer against environ- mental stochasticity, and therefore decrease the variability of life cycles as the probabilities of re- ceiving resource transfers increase.	We will perform a simulation regime where we set our habitat quality and production probabil- ities 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 be- tween 0.05 and 0.95 (656 values).	Resource transfers buffers the effects of fluctuations in resource production on the life cycles within a population. The redis- tribution of resources al- lows individuals who fail to produce their own re- sources to sustain them- selves and potentially re- produce, and therefore avoid extreme life cycles. On the other extreme, in- dividuals who are success- ful in producing resources would avoid extreme life cycles by decreasing their resource surplus via re- source transfers.	An increase in life cycle variability with higher re- source transfers could be explained because the re- distribution of limited re- sources could lead to other social behaviours that en- hance inequality between individuals.
How does the variability of life cycles within a popu- lation change due to the interplay of individual re- source dynamics and envi- ronmental conditions?	Scenarios where resource production is higher will display more extreme amounts of life cycle vari- ability. 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.	We will perform a simu- lation regime where habi- tat quality is set to base- line (4) and high (8). We will vary production prob- abilities 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). Over- all, this will produce a maximum of 3362 combi- nations of parameter val-	Production is the main driver of individual differ- ences in life cycles, while resource transfer near- 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.	If resource transfers have a higher impact on life cycle variability than produc- tion, then social dynam- ics would play a more fun- damental role than indi- vidual performance in de- termining life cycles. If habitat quality is the main driver of life cycle vari- ability, this would mean that the female human life cycle is more responsive to environmental changes than to individual re- source dynamics.

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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.

Question	Hypothesis	Analysis plan	Interpretation	Contested Theory
How is the variability of life cycles within a female	There will be a higher variability of life cycles in	We will run a simu- lation regime using our	Higher production prob- abilities allow, on aver-	A lack of variability of life cycles after changes
human population influ-	a population under inter-	agent-based model and fix	age, for more individuals	in production probabili-
enced by individual re-	mediate (but stochastic)	the probability of resource	to obtain resources, which	ties could be explained
source production?	differences of resource pro-	transfers to 0 for all indi-	support extended lifespan	if selection processes have
	duction between individu-	viduals (i.e., there will be	and increased reproduc-	optimised the female hu-
	als. This is due to larger	no sharing dynamics). We	tion. Lower life cycle	man life cycle, allowing
	individual differences in	will set our habitat quality	variability would happen	individuals to withstand
	the amount of resources	parameter to baseline $(4)$ ,	under more extreme pro-	fluctuations in resource
	available to allocate to-	and vary the parameter	duction probabilities as	production.
	duction	that controls production	individuals would experi-	
	duction	tween 0.1 and 0.9 (across	scarcity or abundance	
		41 values).	bearenty of abaliaties.	
How does the relationship	The variability of life cy-	We will perform a simu-	Habitat quality acts as	If the increase in habi-
between resource produc-	cles within a female hu-	lation regime where the	a buffering effect as re-	tat quality leads to no
tion and life cycle vari-	man population decreases	probability of resource	sources will be so abun-	changes in life cycle vari-
ability change under dif-	as habitat quality in-	transfers is set to 0 for all	dant that individuals will	ability, it could be that
ferent environmental con-	creases. Under conditions	individuals (i.e., there will	be able to sustain them-	either phenotypic masking
ditions (i.e. habitat qual-	of higher habitat qual-	be no sharing dynamics).	selves, even though indi-	is happening or that vari-
ity):	a larger amount of ro	to high $(8)$ and perform a	often unsuccessful in pro	tormodiate levels of habi
	sources available to allo-	parameter sweep over the	duction This will reduce	tat quality (Van Noord-
	cate towards life history	production probabilities.	the variability in life cycles	wijk and de Jong, 1986:
	traits, buffering the indi-	ranging between 0.1 and	within the population	Engquist and Reinhold,
	vidual differences in re-	0.9 (41 values).		2016).
	source production and ho-			
	mogenising the life cycles			
How does variation in the	in the population	We will perform a sim	Pasauraa transfora huffora	An increase in life quale
probabilities of resource	resources within the	ulation regime where we	the effects of fluctuations	variability with higher re-
transfers at the individ-	population will act as a	set our habitat quality	in resource production on	source transfers could be
ual level influence the vari-	buffer against environ-	and production probabil-	the life cycles within a	explained because the re-
ability of life cycles within	mental stochasticity, and	ities set to baseline (4	population. The redis-	distribution of limited re-
a female human popula-	therefore decrease the	and 0.5, respectively), and	tribution of resources al-	sources could lead to other
tion?	variability of life cycles	equally vary the values of	lows individuals who fail	social behaviours that en-
	as the probabilities of re-	the block matrix for the	to produce their own re-	hance inequality between
	incrosso	resource transfers, while	solves and potentially re-	individuals.
	increase.	structure to range be-	produce and therefore	
		tween $0.05$ and $0.95$ (656	avoid extreme life cycles.	
		values).	On the other extreme, in-	
			dividuals who are success-	
			ful in producing resources	
			would avoid extreme life	
			cycles by decreasing their	
			resource surplus via re-	
How does the variability of	Scenarios where resource	We will perform a simu-	Production is the main	If resource transfers have a
life cycles within a popu-	production is higher will	lation regime where habi-	driver of individual differ-	higher impact on life cycle
lation change due to the	display more extreme	tat quality is set to base-	ences in life cycles, while	variability than produc-
interplay of individual re-	amounts of life cycle vari-	line $(4)$ and high $(8)$ . We	resource transfer near-	tion, then social dynam-
source dynamics and envi-	ability. This is because	will vary production prob-	always acts as a buffer.	ics would play a more fun-
ronmental conditions?	higher probabilities of	abilities to range between	Habitat quality can act	damental role than indi-
	resource transfers, and	0.1 and 0.9 (41 values),	as a buffer only when	vidual performance in de-
	richer habitat quality,	and change the values of	there is enough resource	termining life cycles. If
	against larger amounts	maintaining the structure	to compensate for years	driver of life cycle yeri
	of life cycle variation	of the sharing network to	or iterations, where they	ability, this would mean
	between individuals.	range between 0.05 and	are unsuccessful.	that the female human life
		0.95 (656 values). Over-		cycle is more responsive
		all, this will produce a		to environmental changes

maximum of 3362 combinations of parameter val-

ues.

than to individual resource dynamics.



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 to 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.



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#### 250 2.2 Entities, variables, and scale

#### 251 2.2.1 Entities

An individual represents a female in a single-sex population. A single-sex population is a simplifying 252 assumption that is commonly used in the field that operates under the assumption that the female population 25<mark>3</mark> evolves independent of a male counterpart (Wood, 2017). Individuals are considered juveniles from birth 254 until they reach menarche. Adults are individuals that are sexually mature but have not yet produced their 255 first descendant, or reached menopause. Adults transition to a reproductive-career stage once they have 256 their first reproduction, and remain in this stage until they reach menopause. From menopause onward, 257 individuals are considered post-reproductive. An individual only dies if she has not enough resources to 258 cover the survival costs. The population is run for about 10 generations (300 years) to assess the overall 259 population dynamics produced by these assumptions, without inheritance from individuals towards their 260 descendants, nor changes between generations in the strategies that individuals can follow, because we only 261 record the reactions of individuals to the given conditions. 262

#### 263 2.2.2 Scale

Each iteration in the model represents one year. One resource unit is non-divisible, and therefore values 264 are rounded so resources are always natural numbers. Resource production is generated by sampling from 265 a binomial distribution, which is informed by parameters controlling a stage-specific maximum amount 266 of resource that can be produced  $(n_{i,s})$  and a parameter controlling production probability  $(p_{i,s})$ . That 267 is, the amount of resources and probability that an individual produces are stage-specific. During the 268 resource transfer stage of our model, the number of resources transferred can range from zero (i.e. no 269 receiving/giving) to a maximum based on the surplus of resources available for all individuals  $(RTS_{i,t})$ . 270 At the individual-level, individuals can therefore decide to transfer 0 resources to others—and keep the 271 resources for themselves—or transfer resources up to the amount of resources that they have available at 272 that stage of the iteration. We simulate resources transfers from a multinomial distribution. Intuitively, the 273 probability of an individual transferring one unit of their available resources to others within population is 274 structured by life cycle stage; there are different probabilities assigned to resource transfers based on the 275 stage that the deciding individual occupies and the stage in which the other individuals in the population 276 occupy. The total amount of resources that an individual transfers is typically referred to as their out-277 degree, whereas the total amount that an individual receives denotes their in-degree. Life history dynamics 278 are evaluated after the resource dynamics, starting with reproduction, followed by stage transition, and 279 finishing with survival. Finally, the amount of resources available by the end of the iteration is stored and 280 passed from one year to the next. 281

#### 282 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

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#### <sup>291</sup> 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:

$$n_{i,s} = HQ * n_s \tag{3}$$

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).

#### 323 **Resource dynamics**

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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 RCUpdate  $RA_{i,t}$ else Do not reproduce end if if s = J, older than 10 yo and  $RA_{i,t} \ge RTh$  OR s = J and older than 18 yo then Transition to adult stage (A) and discount RCelse if stage = A and  $RA_t \ge RTh$  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 vo 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.

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**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 postreproductive 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:

$$p_{i,s} = \max(p) * p_s \tag{4}$$

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 indivitual.

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 4 336 resource units, and the stage-specific resource production  $(n_s)$  is set at 0.7. Then, the maximum amount of 337 resource production of an individual  $(n_{i,s})$  would be 3 resource units, since resource units are non-divisible, 338 and therefore they are rounded to be natural numbers. If the maximum production probability  $(\max(p))$  is 339 set at 0.8, and the stage-specific production probability  $(p_s)$  is set at 0.7, then the production probability 340 of an individual  $(p_{i,s})$  would be 0.56. Now that the maximum amount of resource production (3) and 341 the production probability (0.56) are defined, then it is possible to say that the amount of resources an 342 individual can produce in one iteration  $RP_{i,t}$  would range from producing between 0 and 3 resources with 343 a probability of 0.56, based on a binomial probability distribution. 344

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 (*m*1),  $RA_{i,t-1}$  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  $(n_s)$ .

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$$MI_{i,t} = \begin{cases} RA_{i,t} - \sum DN_{j,i} &, RA_{i,t} \ge \sum DN_{j,i} \\ 0 &, RA_{i,t} < \sum DN_{j,i} \end{cases}$$
(6)

<sup>357</sup> Where  $MI_{i,t}$  is the amount of maternal investment of individual *i* at time *t*,  $RA_{i,t}$  is the amount of <sup>358</sup> resources available an individual *i* at time *t* has for maternal investment, and  $DN_{j,i}$  is the amount of <sup>359</sup> resources that descendant *j* needs from individual *i*.

<sup>360</sup> The amount of resource surplus for maternal investment is defined as:

$$RA_{i,t} = RA_{i,t-1} + RP_{i,t} - SC \tag{7}$$

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:

$$DN_{j,i} = \begin{cases} 0 & SC - RA_{j,t} \le 0\\ SC - RA_{j,t} & SC - RA_{j,t} > 0 \end{cases}$$
(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 4 373 resource units, and the stage-specific resource production  $(n_s)$  is set at 0.7. Then, the maximum amount of 374 resource production of an individual  $(n_{i,s})$  would be 3 resource units, since resource units are non-divisible, 375 and therefore they are rounded to be natural numbers. If the maximum production probability  $(\max(p))$  is 376 set at 0.8, and the stage-specific production probability  $(p_s)$  is set at 0.7, then the production probability 377 of an individual  $(p_{i,s})$  would be 0.56. Now that the maximum amount of resource production (3) and 378 the production probability (0.56) are defined, then it is possible to say that the amount of resources an 379 individual can produce in one iteration  $RP_{i,t}$  would range from producing between 0 and 3 resources with 380 a probability of 0.56, based on a binomial probability distribution. 381

<sup>382</sup> 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 (*m*2),  $RA_{i,t,m1}$  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:

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

<sup>394</sup> The amount of resource surplus for maternal investment is defined as:

$$RA_{i,t} = RA_{i,t-1} + RP_{i,t} - SC \tag{7}$$

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:

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$$DN_{j,i} = \begin{cases} 0 & SC - RA_{j,t} \le 0\\ SC - RA_{j,t} & SC - RA_{j,t} > 0 \end{cases}$$
(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 4 407 resource units, and the stage-specific resource production  $(n_s)$  is set at 0.7. Then, the maximum amount of 408 resource production of an individual  $(n_{i,s})$  would be 3 resource units, since resource units are non-divisible, 409 and therefore they are rounded to be natural numbers. If the maximum production probability  $(\max(p))$  is 410 set at 0.8, and the stage-specific production probability  $(p_s)$  is set at 0.7, then the production probability 411 of an individual  $(p_{i,s})$  would be 0.56. Now that the maximum amount of resource production (3) and 412 the production probability (0.56) are defined, then it is possible to say that the amount of resources an 413 individual can produce in one iteration  $RP_{i,t}$  would range from producing between 0 and 3 resources with 414 a probability of 0.56, based on a binomial probability distribution. 415

<sup>416</sup> 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 387 to others within the population at during each iteration. Every transfer that an individual makes within 388 the population represents the sharing of one resource unit to another individual. Therefore, an individual 389 will transfer can transfer up to the maximum number of resources that she has available. The probability 390 of transfers is stage-structured through use of the principles of a stochastic block model. That is, resource 391 transfers are assumed to be a network, and this network assumed to be partitioned by life cycle stage—with 392 individuals in a given stage having the same probability of transferring resources to any individual occupying 393 another specific stage (e.g. all individuals in reproductive career stage have the same probability of making 394 resource transfers to all individuals in the juvenile stage). These probabilities vary based on the stages 395 in which both the deciding individual and the target individual occupy (e.g., adult individuals are more 396 likely to transfer resources to juveniles than they are to transfer resources to post-reproductive individuals). 397 Resource transfers occur after maternal investment, and are therefore not guided by relatedness (e.g. genetic 398 relatedness). The social network module is described as follows: 399

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

Where  $y_{i,j}$  denotes the amount of resources that individual, *i*, transferred to individual, *j*, at time *t*, *RA*<sub>*i*,*t*</sub> 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 *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:

$$K_{(1:N,t)} = \begin{cases} 1 & K_x = i \\ 0 & K_x \neq i \end{cases}$$
(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 (*m*2),  $RA_{i,t,m1}$  are the resources available for individual *i* from the previous module (*m*1),  $MI_{i,t}$  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 421 to others within the population at during each iteration. Every transfer that an individual makes within 422 the population represents the sharing of one resource unit to another individual. Therefore, an individual 423 will transfer can transfer up to the maximum number of resources that she has available. The probability 424 of transfers is stage-structured through use of the principles of a stochastic block model. That is, resource 425 transfers are assumed to be a network, and this network assumed to be partitioned by life cycle stage—with 426 individuals in a given stage having the same probability of transferring resources to any individual occupying 427 another specific stage (e.g. all individuals in reproductive career stage have the same probability of making 428 resource transfers to all individuals in the juvenile stage). These probabilities vary based on the stages 429 in which both the deciding individual and the target individual occupy (e.g., adult individuals are more 430 likely to transfer resources to juveniles than they are to transfer resources to post-reproductive individuals). 431 Resource transfers occur after maternal investment, and are therefore not guided by relatedness (e.g. genetic 432

relatedness). The social network module is described as follows:

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

<sup>434</sup> Where  $y_{i,j}$  denotes the amount of resources that individual, *i*, transferred to individual, *j*, at time *t*, <sup>435</sup> *RA*<sub>*i*,*t*</sub> is the amount of resources available that individual *i* at time *t* has for resource transfers,  $\sigma$  is a softmax <sup>436</sup> function that normalizes the values of *K* and  $\theta$  to be on the probability scale.  $K_{(1:N,t)}$  is a vector with the <sup>437</sup> length of the total population (*N*), at time *t*, that contains a 1 in the entry that corresponds to individual <sup>438</sup> *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 <sup>439</sup> a vector containing the stage-specific probabilities that individual *i* transfers resources to other individual <sup>440</sup> *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 tis defined as:

$$\theta_{(i,i:j,t)} = B[s_{(i)}, s_{(j)}]$$
(13)

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 NXN square matrix,  $Y_{[i,j]}$ , by binding all vectors produced by our resources transfers 424 module,  $y_{i,i:j,t}$ . The matrix row and column labels are symmetric, denoting the identities all individuals in 425 the population, and contains all transfers from individuals (the rows of the matrix) to all other individuals 426 (the columns of the matrix). Each element of the matrix contains the total number of transfers that an 427 individual, i, made to another individual, j at time t. That is, the value contained in element  $Y_{[4,5]}$  was, 428 for instance, 2, it denotes that individual 4 shared two units of resources with individual 5. The sum of 429 each row of the matrix represents is, therefore, the number of resources that individual *i* sends to all other 430 individuals in the population (i.e. their out-degree  $(RT_{i,t})$ ). The sum of the columns represent the number 431 of resources that individual j receives (i.e. in-degree  $(RR_{i,t})$ ). The out-degree and in-degree only considers 432 the elements of Y where  $i \neq j$ . 433

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

$$RT_{i,t} = \sum_{j=1}^{n} x_{ij} \tag{14}$$

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 *xij* 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:

$$RR_{i,t} = \sum_{i=1}^{n} x_{ij} \tag{15}$$

Where  $RT_{i,t}$  is the amount of resources transferred by individual i at time  $t, \sum_{j=1}^{n} i$  is the sum from row i to n, and xij 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:

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

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Where every value in the matrix  $(\beta_{s \to s})$  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

$$K_{(1:N,t)} = \begin{cases} 1 & K_x = i \\ 0 & K_x \neq i \end{cases}$$
(12)

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 tis defined as:

$$\theta_{(i,i:j,t)} = B[s_{(i)}, s_{(j)}]$$
(13)

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 NXN square matrix,  $Y_{[i,j]}$ , by binding all vectors produced by our resources transfers 458 module,  $y_{i,i:j,t}$ . The matrix row and column labels are symmetric, denoting the identities all individuals in 459 the population, and contains all transfers from individuals (the rows of the matrix) to all other individuals 460 (the columns of the matrix). Each element of the matrix contains the total number of transfers that an 461 individual, i, made to another individual, j at time t. That is, the value contained in element  $Y_{[4,5]}$  was, 462 for instance, 2, it denotes that individual 4 shared two units of resources with individual 5. The sum of 463 each row of the matrix represents is, therefore, the number of resources that individual i sends to all other 464 individuals in the population (i.e. their out-degree  $(RT_{i,t})$ ). The sum of the columns represent the number 465 of resources that individual j receives (i.e. in-degree  $(RR_{i,t})$ ). The out-degree and in-degree only considers 466 the elements of Y where  $i \neq j$ . 467

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

$$RT_{i,t} = \sum_{j=1}^{n} x_{ij} \tag{14}$$

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 *xij* 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:

$$RR_{i,t} = \sum_{i=1}^{n} x_{ij} \tag{15}$$

Where  $RT_{i,t}$  is the amount of resources transferred by individual *i* at time  $t, \sum_{j=1}^{n} i$  is the sum from row *i* to *n*, and *xij* 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:

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

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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 (*m*3),  $RA_{i,t,m2}$  is the resources available from the previous module (*m*2),  $RT_{i,t}$  is the amount of resources transferred, and  $RR_{i,t}$  is the amount of resources received by individual *i* at time *t*.

## 459 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:

$$R_{i,t} = \begin{cases} 1, & RA_{i,t} \ge RTh \\ 0, & RA_{i,t} < RTh \end{cases}$$
(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:

$$RA_{i,t,m4} = RA_{i,t,m3} - (RC * R_{i,t})$$
(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  $(\beta_{s\to s})$  is the probability that an individual *i* transfers resources to 479 individual j, depending on the life cycle stage of each of them (s). The probabilities of transferring resources 480 within life cycle stages are on the diagonal of the matrix, while the off-diagonal elements of the matrix contain 481 the probabilities of sending resources between different stages. For simplification purposes, we assume that 482 the probabilities in the block matrix follow a resource transfers pattern from older to younger stages. This 483 follows previous work on the role of sharing and the evolution of the female life cycle (Hooper et al., 2015; 484 Lee, 2003; Chu and Lee, 2006), which shows that juveniles are more likely to receive resources, while those 485 in later life cycle stages tend to send more resources—with a slight increase of receiving resources for those 486 in the post-reproductive stage. 487

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 (*m*3),  $RA_{i,t,m2}$  is the resources available from the previous module (*m*2),  $RT_{i,t}$  is the amount of resources transferred, and  $RR_{i,t}$  is the amount of resources received by individual *i* at time *t*.

## <sup>493</sup> 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:

$$R_{i,t} = \begin{cases} 1, & RA_{i,t} \ge RTh \\ 0, & RA_{i,t} < RTh \end{cases}$$
(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.

$$Tr_{i} = \begin{cases} Tr_{J \to A} = 1, & RA_{i,t,m4} - RC \ge SC + RTh \land AGE_{i,t} \ge 10 \lor AGE_{i,t} \le 18 \\ Tr_{A \to RC} = 1, & RA_{i,t,m4} - RC \ge RTh \\ Tr_{A \to PR} = 1, & AGE_{i,t,m4} \ge 60 \\ Tr_{RC \to PR} = 1, & RA_{i,t,m4} - RC < RTh \land TLR_{i,t} \ge 10 \land AGE_{i,t} \ge 40 \lor AGE_{i,t} \ge 60 \end{cases}$$
(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 (*m*4), *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*.  $T_{J\to A}$ ,  $T_{A\to RC}$ ,  $T_{A\to PR}$ ,  $T_{RC\to PR}$  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 ( $Tr_{RC\to PR}$ ).

<sup>489</sup> The transitions are defined as follow:

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- Age at sexual maturity  $(Tr_{J\to A})$ : 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  $(Tr_{A\to RC})$ : 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<sub>A→PR</sub> and Tr<sub>RC→PR</sub>): 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.

$$RA_{i,t,m4} = RA_{i,t,m3} - (RC * R_{i,t})$$
(18)

where  $RA_{i,t,m4}$  is the amount of resources available for individual *i* at time *t* in the reproductive module (*m*4),  $RA_{i,t,m3}$  is the amount of resources that individual *i* has at time *t* from the previous module (*m*3).  $R_{i,t}$  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.

$$Tr_{i} = \begin{cases} Tr_{J \to A} = 1, & RA_{i,t,m4} - RC \ge SC + RTh \land AGE_{i,t} \ge 10 \lor AGE_{i,t} \le 18 \\ Tr_{A \to RC} = 1, & RA_{i,t,m4} - RC \ge RTh \\ Tr_{A \to PR} = 1, & AGE_{i,t,m4} \ge 60 \\ Tr_{RC \to PR} = 1, & RA_{i,t,m4} - RC < RTh \land TLR_{i,t} \ge 10 \land AGE_{i,t} \ge 40 \lor AGE_{i,t} \ge 60 \end{cases}$$
(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 (*m*4), *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*.  $T_{J\to A}$ ,  $T_{A\to RC}, T_{A\to PR}, T_{RC\to PR}$  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 ( $Tr_{RC\to PR}$ ).

523 The transitions are defined as follow:

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- Age at sexual maturity  $(Tr_{J\to A})$ : 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  $(Tr_{A \to RC})$ : 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<sub>A→PR</sub> and Tr<sub>RC→PR</sub>): 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.
- <sup>512</sup> Therefore, the transition cost can be defined as:

$$TrC = \begin{cases} RC, & Tr_{J \to A} = 1 \\ RC, & Tr_{A \to RC} = 1 \\ 0, & Tr_{A \to PR} = 1 \\ 0, & Tr_{RC \to PR} = 1 \end{cases}$$
(20)

Where TrC is the transition cost, RC is the reproductive cost, and  $Tr_{J\to A}$ ,  $Tr_{A\to RC}$ ,  $Tr_{A\to PR}$ ,  $Tr_{RC\to PR}$  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:

$$RA_{i,t,m5} = RA_{i,t,m4} - (TrC * Tr_{i,t})$$
(21)

where  $RA_{i,t,m5}$  is the amount of resources available for individual *i* at time *t* after the transition module (*m*5),  $RA_{i,t,m4}$  the amount of resources available from the previous module (*m*4), TrC 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:

$$S_i = \begin{cases} 1, & RA_{i,t} \ge SC \\ 0, & RA_{i,t} < SC \end{cases}$$
(22)

<sup>526</sup> Where  $S_i$  is the survival outcome of individual i,  $RA_{i,t}$  is the amount of resourced available by individual i<sup>527</sup> 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:

$$RA_{i,t,m6} = RA_{i,t,m5} - (SC * S_{i,t})$$
(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 (*m*5), *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.
- <sup>546</sup> Therefore, the transition cost can be defined as:

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$$TrC = \begin{cases} RC, & Tr_{J \to A} = 1 \\ RC, & Tr_{A \to RC} = 1 \\ 0, & Tr_{A \to PR} = 1 \\ 0, & Tr_{RC \to PR} = 1 \end{cases}$$
(20)

Where TrC is the transition cost, RC is the reproductive cost, and  $Tr_{J\to A}$ ,  $Tr_{A\to RC}$ ,  $Tr_{A\to PR}$ ,  $Tr_{RC\to PR}$  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:

$$RA_{i,t,m5} = RA_{i,t,m4} - (TrC * Tr_{i,t})$$
(21)

where  $RA_{i,t,m5}$  is the amount of resources available for individual *i* at time *t* after the transition module (*m*5),  $RA_{i,t,m4}$  the amount of resources available from the previous module (*m*4), TrC 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.

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$$S_i = \begin{cases} 1, & RA_{i,t} \ge SC \\ 0, & RA_{i,t} < SC \end{cases}$$
(22)

Where  $S_i$  is the survival outcome of individual i,  $RA_{i,t}$  is the amount of resourced available by individual iat 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:

$$RA_{i,t,m6} = RA_{i,t,m5} - (SC * S_{i,t})$$
(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:

$$AGE_{i,t} = \sum_{t_0}^T S_{i,t} \tag{24}$$

Where  $AGE_{i,t}$  is the age of individual *i* at time  $t, \sum_{0}^{T}$  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:

$$LRO_{i,t} = \sum_{t_0}^T R_{i,t} \tag{25}$$

Where  $LRO_{i,t}$  is the lifetime reproductive output of individual i at time t,  $\sum_{0}^{T}$  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.

## <sup>543</sup> 2.3 Process overview and scheduling

The following process describes the life cycle of an individual while she transitions from one stage to another. 544 In the juvenile stage, an individual goes through production, resource transfer, and survival modules each 545 year until she reaches sexual maturity, transitioning to the adult stage. In the adult stage, an individual 546 goes through production, resource transfer, and survival modules until she either has her first descendant, 547 transitioning to the reproductive career, or until she reaches menopause and transitions to become post-5**4**8 reproductive. If an adult transitions to the reproductive-career stage, she goes through the production, 549 maternal investment, and resource transfer modules followed by the reproduction and survival modules 550 until she reaches menopause. After an individual transitions to the post-reproductive stage, she only 551 goes through production, resource transfer, and survival stage-specific modules. Each year, the individual 552 increases her age and updates the amount of resources that she has stored. Her lifetime reproductive output 553 is also updated if she reproduces in that iteration. During each transition, the individual updates her stage 554 variable. 555

The scheduling of the process starts with the production module, followed by the maternal investment 556 module if an individual is in the reproductive-career stage. The first decrease of resources available occurs 557 if an individual needs to invest resources in her descendants. This is followed by the resource transfer 558 module, which results in updating the amount of resources available for all individuals after accounting for 559 the amount of resources that are given and received. The life history modules follow, which allows for a clear 560 understanding on how resources are acquired and how they are allocated towards reproduction, survival, 561 and transition. Furthermore, the surplus of resources considered for the modules of maternal investment 562 and resource transfers is defined in order to ensure the reproduction and survival of an individual, and her 563 descendants. The life history modules begin with reproduction, followed by stage transition, and survival 564 modules. Finally, the storage module evaluates if there are resources that can be passed to the next year. 565 See in Algorithm 3 a full description of the process through one iteration. 566

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 (*m*5), *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:

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Where  $AGE_{i,t}$  is the age of individual *i* at time  $t, \sum_{0}^{T}$  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*.

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Where  $LRO_{i,t}$  is the lifetime reproductive output of individual i at time t,  $\sum_{0}^{T}$  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.

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The scheduling of the process starts with the production module, followed by the maternal investment 590 module if an individual is in the reproductive-career stage. The first decrease of resources available occurs 591 if an individual needs to invest resources in her descendants. This is followed by the resource transfer 592 module, which results in updating the amount of resources available for all individuals after accounting for 593 the amount of resources that are given and received. The life history modules follow, which allows for a clear 59 understanding on how resources are acquired and how they are allocated towards reproduction, survival, 595 and transition. Furthermore, the surplus of resources considered for the modules of maternal investment 596 and resource transfers is defined in order to ensure the reproduction and survival of an individual, and her 597

## 567 2.4 Design concepts

## 568 2.4.1 Basic principles

The model aims to understand how the variability of life cycles within a population changes as a function 569 of resource dynamics and habitat quality. Existing models have focused on the conditions under which the 570 female human life cycle evolved (e.g. embodied capital model (Kaplan, 1996) or resource transfer model 571 (Chu and Lee, 2006)), while the model presented here focuses on the mechanisms that explain the variability 572 of life cycles within a population. Additionally, our model more explicitly incorporates a network of resource 573 transfers, which more directly examines resource dynamics that are reflective of real-world resource sharing 574 than previous models (Price and Jones, 2020; Kaplan, 1996; Chu and Lee, 2006; Lee, 2003; Kramer and 575 Ellison, 2010; Van Noordwijk and de Jong, 1986). First, resource transfers are defined more generally, and 576 not bounded to specific relationships between individuals (e.g. parent-offspring transfers as in Kaplan (1996) 577 or downward adult-juvenile transfers as in Chu and Lee (2006)). Second, resource transfers are modelled 578 with a stochastic component, and not just as an immediate byproduct of other resource dynamics (e.g. 579 giving as a positive outcome from resource production and consumption, and receiving as a negative one, as 580 in Lee (2003); Chu and Lee (2006)). Hence, our model makes it possible to track the unique contributions 581 of resource production and transfers, allowing us to disentangle what resource dynamics are behind possible 582 phenotypic masking effects, as highlighted in Van Noordwijk and de Jong (1986). Finally, the model is 583 driven by mechanistic processes, as individuals survive, reproduce, and transition through the life cycle 584 depending on the amount of available resources that she has. Therefore, individuals have deterministic 585 behaviours in relation to the allocation of resources towards survival and reproduction, whereas resource 586 acquisition and sharing is more stochastic. 587

## 588 2.4.2 Emergence

Variability of life cycles between individuals emerges from the dynamics in acquiring resources from pro-589 duction and transfers (see Fig. 1. Resource production changes depending on habitat quality and the 590 stage-specific probability of production, making it stochastic. Resource transfers depend on the surplus of 591 resources available to individuals in the population, changes in the demographic composition of the popu-592 lation, and the stage-specific probabilities of transfers, therefore making it stochastic. Allocation towards 593 reproduction, stage transition, and survival are deterministic, but also depend on events in previous years, 594 such as whether an individual already has given birth or not. The aim of this study is to understand how 595 the resource dynamics (i.e. production and transfers) experienced by individuals within a population cause 596 different amounts of variation in key components of the female human life cycle (i.e. longevity, age at 597 menarche, age at first reproduction, number of descendants, age at last reproduction, age at menopause). 598

## 599 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.

## <sup>601</sup> 2.4 Design concepts

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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

## 504 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.

#### <sup>607</sup> 2.4.5 Expectations

We expect that the variability of life cycles within the population will be higher under scenarios where 608 individuals differ more in the amount of available resources that they have. We have such an expectation 609 because of the stochastic nature of how resource dynamics are defined in the model, while the life history 610 outcomes are deterministic. Therefore, and following our research questions (Table 2), we expect that (1) 611 there will be larger life cycle variability as stochastic differences in resource production increase, and that 612 (2) life cycle variability will decrease as habitat quality increases. This is because individuals that are less 613 lucky in resource production would be able to compensate by acquiring larger amounts of resources when 614 successful. We also expect that (3) life cycle variability should decrease as the probabilities of resource 615 transfer increase, as the redistribution of resources within the population would have a buffering effect on 616 individual differences. Finally, we predict that (4) resource production is the main driver of individual 617 differences in life cycles, followed by the buffering effect of resource transfers. We expect that habitat 618 quality will only play a role if resources are abundant enough for individuals can compensate for unsuccessful 619 production years. Hence, the variability of life cycles within a female human population would depend on 620 the individual production of resources, the social structure of resource transfers, and the environmental 621 richness where individuals develop. 622

## <sup>623</sup> 2.4.6 Sensing

624 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 625 also know the amount of resources available, and surplus, to determine the amount of resources used 626 in maternal investment and resource transfers. Furthermore, they are assumed to know the amount of 627 resources available after the resource dynamics, which are used to allocate them to reproduction, life cycle 628 stage transition, and/or survival. Finally, they are assumed to know the amount of resources left at the end 629 of the iteration to store them and carry them to the next iteration. We do not include any implementation 630 error in the knowledge of individuals of any of the deterministic rules specified in our model—that is, 631 individuals have perfect knowledge of the system and always behave in a way that maximises their life 632 history traits. 633

### <sup>634</sup> 2.4.7 Interaction

<sup>635</sup> Not apply.

### **536** 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.

## <sup>638</sup> 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.

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Individuals are assumed to know their life cycle stage, which resource and life history dynamics (e.g. the 658 probabilities of producing resources, and if they can reproduce in the iteration or not) depend upon. They 659 also know the amount of resources available, and surplus, to determine the amount of resources used 660 in maternal investment and resource transfers. Furthermore, they are assumed to know the amount of 661 resources available after the resource dynamics, which are used to allocate them to reproduction, life cycle 662 stage transition, and/or survival. Finally, they are assumed to know the amount of resources left at the end 663 of the iteration to store them and carry them to the next iteration. We do not include any implementation 664 error in the knowledge of individuals of any of the deterministic rules specified in our model—that is, 665 individuals have perfect knowledge of the system and always behave in a way that maximises their life history traits. 667

#### 668 2.4.7 Interaction

669 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.

#### 644 2.4.9 Collectives

645 Not apply

#### 646 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.

## 553 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 postreproductive 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

661 Not apply

## <sup>662</sup> 2.7 Sub models

663 Not apply

## **3** Model Analysis

The model analysis consists of exploring the impact of different parameter settings for habitat quality, the 665 probability of resource production, and the probability of transferring resources. First, we will run the 666 computational model to understand the influence of changes in resource production on the variability of 667 life cycles. The model will not have resource transfers, the habitat quality will be set to baseline, and we 668 will explore the impact of changing values of production probabilities from 0.1 to 0.9 (41 values). Second, 669 we will run the computational model to understand the influence of habitat quality on the variability of 670 life cycles. The model will not have resource transfers, the values of production will range from 0.1 to 671 0.9, and the habitat quality will be doubled to recreate a rich environment (82 values). We will compare 672 the output of these model settings with those from the setting of the first regime. Third, the model will 673 be set up to explore the role of resource transfers in the variability of life cycles. The parameters for 674

## 670 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.

## 678 2.4.9 Collectives

679 Not apply

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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.

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## <sup>594</sup> 2.6 Input Data

695 Not apply

## <sup>696</sup> 2.7 Sub models

697 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 wil; 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 682 individuals in each combination of resource dynamics to analyse the variability of life cycles. Specifically, 683 we will analyse the coefficient of variation of different life history traits among all individuals born between 684 years 100 and 200 to cover one full generation (birth to death) of a large sample of individuals. This means 685 we should have no (or very few) of the initial individuals in the analysis population and all individuals in 686 the sample should have completed their life cycle by the end of the simulation (year 300). This way, we are 687 able to analyse how the variability of life cycles within a female human population changes under different 688 combinations of resource production, transfers, and habitat quality. 689

Finally, we will perform sensitivity analyses on population size, and also the costs of survival and 690 reproduction. These sensitivity analyses will assess the robustness of the results that we will obtain from 691 the analyses detailed above. We will analyse population size because evidence suggests that, via changes in 692 the reproductive output within a population, the importance of variance in fitness decreases as populations 693 become larger, which suggests possible changes in our results if we increase the initial population (Gillespie, 694 1974; Rubenstein, 2011; Lehmann and Balloux, 2007). We will also analyse the robustness of our results 695 under different combinations of survival and reproductive costs. The baseline is set so that an individual 696 survives with one resource and reproduces with two times the survival cost. The reproductive threshold 697 is set to be five times the reproductive cost, resembling the resources an individual needs to start her 698 reproductive career. Life history traits related to survival can decrease if the costs of survival increase, and 699 the same with reproduction, according to how the mechanics of our model work. Furthermore, changes 700 in the costs of reproduction and survival could also increase the influence of certain resource dynamics in 701 the life history dynamics that individuals face. An intuitive example could be that if the costs of survival 702 are higher than what a juvenile can produce, her chances of surviving until the next iteration will always 703 depend on maternal investment and resource transfers. Therefore, analysing the sensitivity of our results 704 under different population sizes, and survival and reproductive costs, can show how the importance of 705 resource dynamics might vary under different demographic and life history scenarios. 706

# <sup>707</sup> 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

traits. For this, we will analyse the role of each parameter separately (i.e. scenario one, two, and three), 703 then combinations of two of them (i.e. scenario four, five, and six), and finally a combination of the three 704 together (i.e. scenario seven), which translates in defining seven scenarios. Scenario 1, we will run the 705 computational model to understand the influence of changes in resource production on the variability of 706 life cycles. The model will not have resource transfers, the habitat quality will be set to baseline, and we 707 will explore the impact of changing values of production probabilities from 0.1 to 0.9 (17 values). Scenario 708 2, we will run the computational model to understand the influence of changes in the habitat quality. For 709 this, the model will not have resource transfers, the values of production will be set to baseline, and we will 710 explore the influence of habitat quality by doubling its value, and recreate a rich environment. Scenario 711 **3**, we will set up the model to explore the role of resource transfers in the variability of female human life 712 cycles. Therefore, the values of resource production and habitat quality will be set to baseline, while the 713 values in the block matrix, which defines the social network structure of the resource transfers, will range 714 from 0.05 to 0.95 (19 values, and 323 combinations) while keeping the downward pattern. Scenario 4 will 715 explore the variability of life cycles by the combination of resource production and habitat quality. For this, 716 we will explore the values of production probabilities from 0.1 to 0.9 with habitat quality set to double the 717 baseline, and no resource transfers (17 values). Scenario 5 will explore the variability of life cycles by the 718 combination of habitat quality and resource transfers. For this, we will explore the values in the block matrix 719 from 0.05 to 0.95 with habitat quality set to double the baseline, and production probabilities set to baseline 720 (19 values, and 323 combinations). Scenario 6 will explore the combination of resource production and 721 resource transfers. The model will be set up with habitat quality as baseline, while production probabilities 722 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 (19 723 values, and 323 combinations). Finally, Scenario 7 will run simulations to understand how the interplay 724 between resource production, transfers, and habitat quality influence the variability of life cycles within a 725 population. Accordingly, we will set habitat quality as high, production probabilities will range from 0.1 to 726 0.9, and resource transfers between 0.05 and 0.95, leading to a maximum of 10982 combinations. We will 727 repeat each unique combination 10 times (see Table 1 for a summary). 728

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, 736 regarding the role of resource production in the female human life cycle, by analysing the distribution of 737 the different life history traits of **Scenario 1**. The second research question about habitat quality will be 738 answered by analysing the outcomes of Scenario 2, the comparison of Scenario 1 and Scenario 4, and 739 the comparison of **Scenario 3** and **Scenario 5**. The third resource question regarding the role of resource 740 transfers will be answered once we analyse the distribution of longevity, lifetime reproductive output, and 741 timing of life cycle stage transition from Scenario 3, the comparison of Scenario 2 and Scenario 5, and 742 the comparison of Scenario 1 and Scenario 6. Finally, our fourth research answer will be answered when 743 we analyse the outcomes of Scenario 7 and compare them with the ones from Scenario 6. This way, 744 we are able to analyse how the variability of life cycles within a female human population changes under 745

different combinations of resource production, transfers, and habitat quality (see Fig. 4 for a graphicalrepresentation).



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 748 of survival and reproduction. These robustness checks will assess the strength of the results that we will 749 obtain from the analyses detailed above. We will analyse population size because evidence suggests that, via 750 changes in the reproductive output within a population, the importance of variance in fitness decreases as 751 populations become larger, which suggests possible changes in our results if we increase the initial population 752 (Gillespie, 1974; Rubenstein, 2011; Lehmann and Balloux, 2007). We will also analyse the robustness of 753 our results under different combinations of survival and reproductive costs. The baseline is set so that an 754 individual survives with one resource and reproduces with two times the survival cost. The reproductive 755

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).

## $_{719}$ 5 Model insights

During the design and building of the baseline model, there were certain assumptions that we made after 720 some initial exploration of the mechanics of the model. Given the complexity of our modelling framework, 721 this was a necessity. The exploratory analyses were not meant as a systematic revision of parameter values, 722 but as a way to decide upon certain processes for which there is no consensus in the literature as well as 723 to more deeply understand how any assumption that we make may influence any downstream component 724 of our model. The insights that we gained from this exploratory exercise are related to the definition and 725 implications of resource surplus for resource transfers and habitat quality, the mechanisms behind resource 726 transfers, and the importance of maternal investment. 727

Currently, the definition of resource surplus for resource transfers is the amount of resources an individual 7<mark>2</mark>8 has after going through resource production and maternal investment, while also accounting for the costs 729 of survival and reproduction. Hence, the amount of resources that an individual transfers during a given 730 iteration is limited to her remaining available resources once she has ensured her reproduction as well as the 731 survival of herself and her descendants. Therefore, individuals would follow a sharing behaviour closer to 732 communal breeding, where individuals share resources in the population to secure food and help with child 733 rearing (Federico et al., 2020). However, we also wanted to examine how our model behaved with a different 734 definition for the resources available for transfer. Once we excluded the reproductive cost from the definition 735 of resource surplus, individuals would show a behaviour that is closer to cooperative breeding (Federico et al., 736 2020), where individuals shared resources even if that meant they themselves could not reproduce. Here, it 737 is very difficult for individuals to accumulate enough resources to reproduce, with reproduction essentially 738 being restricted to individuals who, by chance, receive many resource transfers at once in a given year, 739 leading to a very high proportion of individuals being childless. The change is essentially from individuals 740 being first selfish before sharing in the communal breeding scenario, to individuals being forced to always 741 share even if it is detrimental to their self interests. We decided to define the sharing behaviour closer 742 to communal breeding because the simulated population appeared to more closely resemble the behaviour 743 observed in human populations (Hrdy, 2007; Kramer and Veile, 2018). 744

Regarding habitat quality, we explored possible values that could have a more logical justification for 745 our baseline model while also fitting with the dynamics of the model. We decided to set habitat quality 746 so that an individual can produce sufficient resources to survive and reproduce in one iteration. Therefore, 747 an individual can reproduce in a year even if she does not have stored resources or receives any from 748 other members of the population. The reasoning behind this is that reproduction can be considered quite 749 stochastic and opportunistic van Daalen and Caswell (2017). In a rich environment, having a "lucky" year 750 751 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 752 breeding scenario, where women can only reproduce if they receive resources from others. Again, we decided 753 to set the habitat quality to facilitate behaviour that reflects communal breeding. 754

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 stage756 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, 757 and the same with reproduction, according to how the mechanics of our model work. Furthermore, changes 758 in the costs of reproduction and survival could also increase the influence of certain resource dynamics in the 759 life history dynamics that individuals face. An intuitive example could be that if the costs of survival are 760 higher than what a juvenile can produce, her chances of surviving until the next iteration will always depend 761 on maternal investment and resource transfers. Therefore, analysing the robustness of our results under 762 different population sizes, and survival and reproductive costs, can show how the importance of resource 763 dynamics might vary under different demographic and life history scenarios. 764

# <sup>765</sup> 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).

# $_{777}$ 5 Model insights

During the design and building of the baseline model, there were certain assumptions that we made after 778 some initial exploration of the mechanics of the model. Given the complexity of our modelling framework, 779 this was a necessity. The exploratory analyses were not meant as a systematic revision of parameter values, 780 but as a way to decide upon certain processes for which there is no consensus in the literature as well as 781 to more deeply understand how any assumption that we make may influence any downstream component 782 of our model. The insights that we gained from this exploratory exercise are related to the definition and 783 implications of resource surplus for resource transfers and habitat quality, the mechanisms behind resource 784 transfers, and the importance of maternal investment. 785

In our final model, the definition of resource surplus for resource transfers is the amount of resources 786 an individual has after going through resource production and maternal investment, while also accounting 787 for the costs of her own survival and reproduction. Therefore, the number of resource transfers that an 788 individual performs during a given iteration has an upper limit defined by her remaining resources available 789 once she has ensured her reproduction as well as the survival of herself and her descendants. This definition 790 of surplus resembles what is assumed when individuals follow a sharing behaviour of communal breeding 791 (Federico et al., 2020). However, we also wanted to examine how our model behaved with a different 792 definition for the resources available for transfer, closer to what sometimes has been conceptualised as 793 cooperative breeding (Federico et al., 2020) where individuals share resources even if this would impact 794

structured transfer probabilities coupled with the definition of resource surplus decreases the amount of 757 resources available to transfer to individuals in their adult and reproductive career stages. Therefore, 758 the definition of resource surplus can be considered as the trade-off individuals face regarding resource 759 allocation. Second, the age distribution of individuals per life cycle stage influence because there are 760 different dynamics happening for each of them that influence the interaction of the block matrix and the 761 resource surplus. An example about the influence of the age distribution would be that individuals who 762 transition to their post-reproductive stage will have a higher amount of resources available for transfers 763 (i.e. resource surplus) than those individuals that have been longer in the post-reproductive stage. This 764 situation would happen because an individual who just reaches menopause would have more resources stored 765 due to the higher resource production and reproductive dynamics from the previous stage (i.e. adult or 766 reproductive career). Hence, she would have a higher surplus than older post-reproductive individuals, 767 which would lead to her transferring more sources within the population. In conclusion, there are social, 768 individual, and demographic components in the model that influence the patterns that can be observed 769 regarding resource transfers. Accordingly, rather than initialising the simulation with all individuals being 770 of the same age, the initial population now consists of the same number of individuals per life cycle stage 771 (i.e. 25 juveniles, adults, reproductive career, and post-reproductive individuals, which sum to an initial 772 population of 100 individuals), and we only analyse data after the population is likely to have shifted 773 towards a more balanced composition (i.e. those individuals born between years 100 and 200, to cover one 774 full generation of individuals who do not belong to the initial population). 775

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 782 reasons. First, even though parental investment is a form of resource transfer, it has a specific mechanisms 783 that govern the transfer (e.g. kin selection, parent-offspring conflict) (Hamilton, 1964; Godfray, 1995). 784 Second, we realised while building the baseline model that if individuals only produce resources but do 785 not loose resources from sharing, as in our first research question, then they do not transition to a post-786 reproductive stage unless they are forced to do so. This is because they produce and store enough resources 787 to keep reproducing until very late in life. However, when including maternal investment such that mothers 788 cover the need her descendants for survival, women will transition to menopause if they have a large 789 number of children. Such a pattern is consistent with the idea that reproductive conflict between women 790 of different ages would turn into downward cooperation from older individuals in the case where they are 791 mother and descendant—causing older women stop their reproduction career, and reach menopause, earlier 792 (Cant and Johnstone, 2008; Mace and Alvergne, 2012). In conclusion, we defined maternal investment as a 793 separate dynamic rather than it being part of the resource transfers because (a) they work under different 794 evolutionary dynamics (e.g. kin selection, parent-offspring conflict, reproductive conflict), and because (b) 795 maternal investment might be necessary so individuals transition to a post-reproductive stage, based on the 796

resource and life history dynamics defined in our model.

their own reproduction. The difference is essentially from individuals being selfish before sharing in the 795 communal breeding scenario, to individuals being forced to always share even if it is detrimental to their 796 self interests. We observed in our model exploration that a sharing behaviour closer to cooperative breeding 797 ended up with levels of childlessness that were higher than the ones observed in human populations (Bailey 798 and Aunger, 1995; Belsey, 1976). This patterns was because of the difficulties for individuals to accumulate 799 enough resources to reproduce, with reproduction essentially being restricted to individuals who, by chance, 800 receive many resource transfers at once in a given year. In addition to leading to demographic patterns 801 that do not resemble human populations, there are also conceptual reasons why a model that assumes 802 reproductive costs of sharing resources is unlikely to represent the human pattern. Studies looking at the 803 relationship between sharing and own reproduction, such as Kramer and Veile (2018), show that allocare 804 does not have an effect on interbirth intervals and number of surviving children in a hunter-gatherer and a 805 horticultural populations (Pumé and Maya, respectively), supporting the idea that resource sharing might 806 not come at costs of the reproduction of an individual. These observations aligns with evidence in other 807 species that show that even in cooperative breeders sharing resources is conditional on having no effect on 808 the fitness of individuals (e.g. meerkats (Clutton-Brock et al., 2001), kookaburras (Legge, 2000), and crows 809 (Canestrari et al., 2010)). Based on these observations, and our model exploration, we decided to define the 810 amount of resources available for resource transfers closer to communal breeding, and therefore define the 811 surplus of resources available for transfers after an individuals accounts for her own reproduction as well as 812 the survival of herself and her descendants. 813

Regarding habitat quality, we explored possible values that could have a more logical justification for 814 our baseline model while also fitting with the dynamics of the model. We decided to set habitat quality 815 so that an individual can produce sufficient resources to survive and reproduce in one iteration. Therefore, 816 an individual can reproduce in a year even if she does not have stored resources or receives any from 817 other members of the population. The reasoning behind this is that reproduction can be considered quite 818 stochastic and opportunistic van Daalen and Caswell (2017). In a rich environment, having a "lucky" year 819 would mean that an individual could get enough resources to compensate for previous years and minimise the 820 costs of survival and reproduction. An alternative setting would be to set up a forced obligate cooperative 821 breeding scenario, where women can only reproduce if they receive resources from others. Again, we decided 822 to set the habitat quality to facilitate behaviour that reflects communal breeding. 823

After running the baseline model to check that the resource and life history dynamics work, we realised 824 that the observed patterns of resources transfers can be explained by three components. First, the stage-825 structured transfer probabilities coupled with the definition of resource surplus decreases the amount of 826 resources available to transfer to individuals in their adult and reproductive career stages. Therefore, 827 the definition of resource surplus can be considered as the trade-off individuals face regarding resource 828 allocation. Second, the age distribution of individuals per life cycle stage influence because there are 829 different dynamics happening for each of them that influence the interaction of the block matrix and the 830 resource surplus. An example about the influence of the age distribution would be that individuals who 831 transition to their post-reproductive stage will have a higher amount of resources available for transfers 832 (i.e. resource surplus) than those individuals that have been longer in the post-reproductive stage. This 833 situation would happen because an individual who just reaches menopause would have more resources stored 834 due to the higher resource production and reproductive dynamics from the previous stage (i.e. adult or 835 reproductive career). Hence, she would have a higher surplus than older post-reproductive individuals, 836 which would lead to her transferring more sources within the population. In conclusion, there are social, 837

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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 851 reasons. First, even though parental investment is a form of resource transfer, it has a specific mechanisms 852 that govern the transfer (e.g. kin selection, parent-offspring conflict) (Hamilton, 1964; Godfray, 1995). 853 Second, we realised while building the baseline model that if individuals only produce resources but do 854 not loose resources from sharing, as in our first research question, then they do not transition to a post-855 reproductive stage unless they are forced to do so. This is because they produce and store enough resources 856 to keep reproducing until very late in life. However, when including maternal investment such that mothers 857 cover the need her descendants for survival, women will transition to menopause if they have a large 858 number of children. Such a pattern is consistent with the idea that reproductive conflict between women 859 of different ages would turn into downward cooperation from older individuals in the case where they are 860 mother and descendant—causing older women stop their reproduction career, and reach menopause, earlier 861 (Cant and Johnstone, 2008; Mace and Alvergne, 2012). In conclusion, we defined maternal investment as a 862 separate dynamic rather than it being part of the resource transfers because (a) they work under different 863 evolutionary dynamics (e.g. kin selection, parent-offspring conflict, reproductive conflict), and because (b) 864 maternal investment might be necessary so individuals transition to a post-reproductive stage, based on the 865 resource and life history dynamics defined in our model. 866

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