

# Theoretical and methodological approaches to ecological changes, social behaviour and human intergroup tolerance 300,000 to 30,000 BP.

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## Abstract

Archaeological evidence suggests that important shifts were taking place in the character of human social behaviours 300,000 to 30,000 years ago. New artefact types appear and are disseminated with greater frequency; transfers of both raw materials and finished artefacts take place over increasing distances, implying larger scales of regional mobility and more frequent and friendlier interactions between different communities. Whilst these changes occur during a period of increasing environmental variability, the relationship between ecological changes and transformations in social behaviours has been elusive. Here we explore a possible theoretical approach and methodology for understanding how ecological contexts can influence selection pressures acting on intergroup social behaviours. We focus on the relative advantages and disadvantages of intergroup tolerance in different ecological contexts using agent-based modelling (ABM). We assess the relative costs and benefits of different 'tolerance' levels in between-group interactions on survival and resource exploitation in different environments. The results enable us to infer a potential relationship between ecological changes and proposed changes in between-group behavioural dynamics. We conclude that increasingly harsh environments may have driven changes in hormonal and emotional responses in humans leading to increasing intergroup tolerance, i.e. transformations in social behaviour associated with 'self domestication'. We argue that changes in intergroup tolerance is a more parsimonious explanation for the emergence of what has been seen as 'modern human behaviour' than changes in hard aspects of cognition or other factors such as cognitive adaptability or population size.

**Keywords: Modern human behaviour, tolerance, social connectivity, agent-based model, environmental change, Palaeolithic, self-domestication.**

## Introduction – approaches to the ‘modern human transition’

Of all the key transitions in human origins it is that which occurred between 300,000 and 30,000 years ago — *the modern human transition* — which is the focus of the most intense debate (Högberg and Lombard, this volume). It is during this period that we see the emergence of our own species *Homo sapiens*, otherwise referred to as anatomically and cognitively modern humans (ACMH).

Whilst there remains a consensus that after 300,000 years ago, and following the spread of modern humans out of Africa, the range and frequency of key elements of ‘modernity’ increases (French 2018), the broader mechanisms by which new biological forms of hominin and new types of technological and social behaviour emerge remain poorly understood (D’Errico & Banks 2013; Moncel & Schreve 2016). Modern human behaviour (defined as behaviours that indicate modern-level linguistic and cognitive abilities and identified archaeologically through the presence of, among others, deliberate burials, complex lithic and hafting technologies, personal ornamentation, pigment use and ‘symbolic’ art and artefacts (Henshilwood & Marean 2003; Mellars 2007)) clearly has earlier origins (Kissel & Fuentes 2018) with many elements of such behaviour also exhibited by archaic humans (e.g. Hoffmann et al. 2018; Joordens et al. 2015; Zilhão et al. 2010) and is far from unproblematic as a concept (Ames et al. 2013). Furthermore, prosocial motivations and behaviours including care for the ill and injured (Spikins et al. 2018), and collaborative hunting practices and food sharing (Agam & Barkai 2016; Domínguez-Rodrigo et al. 2014; Faurby et al., 2020), emerged relatively early in human evolution. Nonetheless, it is largely after 300,000 years ago that many complex social and cultural behaviours become widespread.

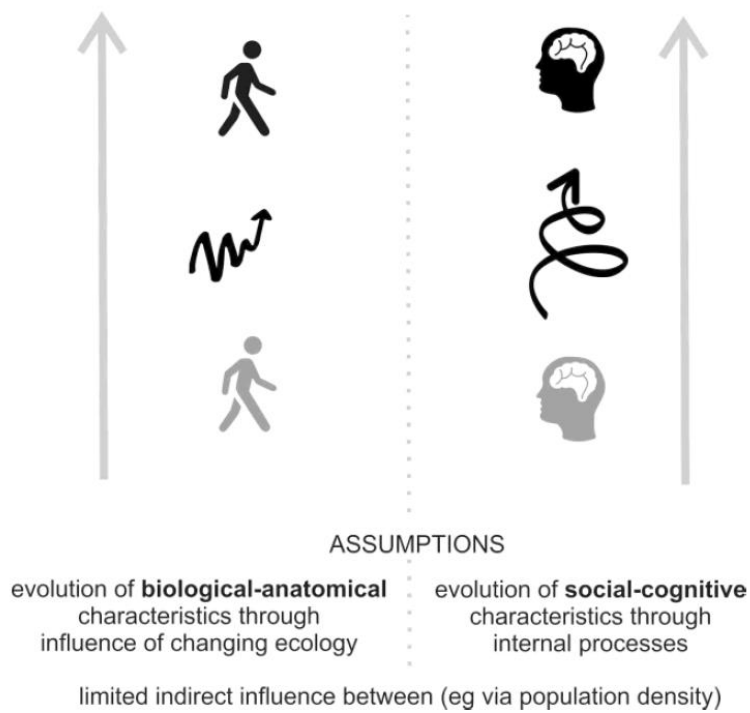
Certain particularly interesting patterns of change are evident in human social behaviours in Africa during the period 300,000 – 30,000 years ago. Alongside increased ecological variability in East Africa around 300,000 BP we see evidence of increased raw material transfer distances for example (Potts et al. 2018) indicating changes in patterns of group and intergroup mobility. From typically local raw material distance transfers of around 5 km we see new movements of obsidian of around 25 to 50 km, and up to 95 km in certain cases, implying interactions with neighbouring groups (Brooks et al. 2018). Middle Stone age populations in the Kalahari also import preferred silcrete raw material from up to 295 km, particularly during drier periods (Nash et al. 2013, 2016), well beyond the transfer distances typically recorded in previous periods. Greater patterns of large-scale regional mobility both within Africa and beyond are also evident from genetic data (Lamb et al. 2018; Petraglia et al., 2019; Rito et al. 2019; Timmermann & Friedrich 2016).

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Important anatomical changes associated with the emergence of anatomically modern humans also occur during the same period, with so-called craniofacial “feminisation” drawing the most attention (Cieri et al. 2014). From around 300,000 years ago certain populations in Africa display traits such as a reduction in brow ridges and other changes in facial form, as well as increased gracility associated with anatomically modern humans (Stringer & Galway-Witham 2017) with populations at Jebel Irhoud in Morocco dating to around 315,000 years ago being a particularly notable example (Hublin et al. 2017; Richter et al. 2017). Whilst archaic forms continue to be represented, crania such as that from Omo 1, dated to around 195,000 years ago or Herto, dated to 100-165,000 years ago are considered modern in appearance (Klein 2019). This is a period of both marked behavioural change and marked physiological and anatomical change.

These archaeological and anatomical changes are set against a backdrop of marked ecological challenges. Across the whole continent the expansion and contraction of the Sahara, basin structure and variable topography provide a unique environment (Foley 2018) in which distinct subdivided populations seem to have emerged and periodically connected (Scerri et al. 2018; Galway-Witham et al. 2019). Both southern and eastern Africa, are seen as key to the emergence of modern humans (Rito et al. 2019). Increasingly aridification from half a million years ago in East Africa placed particular pressures on the survival of many mammalian species and is associated with mammalian extinctions in the South Kenya Rift between 500-400 k BP (Owen et al. 2018). Alternating periods of arid and wetter conditions also affected southern African environments, placing particular pressures on human populations in arid periods and prompting dispersions along wetter corridors (Simon et al. 2015; Kutzbach et al. 2020). Whilst the precise conditions under which our species emerged remain unclear and much debated, distinctively spatially and chronologically variable and often increasingly resource poor environments appear to have been key to the complex patterns of evolutionary change taking place within both archaic and modern humans.

The mechanisms by which these ecological changes might lead to such notable changes in anatomy, physiological and behaviour remain to be explored. A particular challenge lies in understanding the relationship between biological/anatomical or social/cognitive change, and how these may relate to ecological context. All too often traditional disciplinary boundaries, alongside preconceptions about how evolutionary processes **ought to work**, further a distinction between changes in body (biological/anatomical change) assumed to be driven by ecological changes and changes in mind (social/cognitive change) assumed to be driven by internal social processes (*figure 1*).



**Fig. 1** Graphical illustration of assumed distinctions between evolutionary processes affecting mind and body Left: representation of assumed evolution of body shape through interactions with the environment, right: representation of assumed evolution of mind through internal social processes.

## Ecological changes and selection pressures on social tolerance

An understanding of how ecological contexts influence changes in *social emotional dispositions* may provide a pathway to link ecological-biological and social-cognitive

1 approaches, and contribute additional insights into the nature of key transformations occurring  
2 300,000-30,000 years ago.  
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4 Evolutionary transformations in emotional dispositions and responses are likely to have played  
5 an important role in key transitions in human evolution (Decety et al. 2012; Marsh 2019;  
6 Spikins 2021; Spikins et al. 2018). Variations in oxytocin responses for example have a  
7 notable influence on caring behaviours in modern human populations (Marsh, 2019), undergo  
8 significant changes in human evolution (Theofanopoulou et al. 2018) and are implicated in  
9 food sharing (Wittig et al. 2014), care for injured adults (Spikins et al. 2018) and also teaching  
10 and learning (Thornton & McAuliffe 2006) in other species. The transition into a new human  
11 niche involving greater levels of carnivory from around two million years ago (Domínguez-  
12 Rodrigo et al. 2014) is likely to have involved changes in collaborative emotional dispositions  
13 including those affected by oxytocin, facilitating food sharing, shared infant care and care for  
14 vulnerable and injured adults, much as seen in social carnivores.  
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23 Emotional dispositions also play a key role in social connectivity at a regional scale. Emotional  
24 reactions to 'outsiders' are influenced by hormonal responses affecting approach behaviours  
25 i.e. *friendliness*, through hormonal influences on fight or flight responses (affected by  
26 hormones such as cortisol) and willingness to explore (affected by hormones such as  
27 dopamine, Wilkins et al. 2014). Key changes in these hormone systems occur over the last  
28 300,000 years (Theofanopoulou et al. 2017; Theofanopoulou et al., 2017) and have also been  
29 implicated in the evolution of fully modern language (Thomas and Kirby 2018). Whilst it would  
30 be foolish to suggest that anything as complex as human regional social interactions is just  
31 about biology, the influence and constraints of emotional responses play an important role  
32 even in modern contexts (Sapolsky 2017).  
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## 44 **Ecological selection pressures on intergroup tolerance**

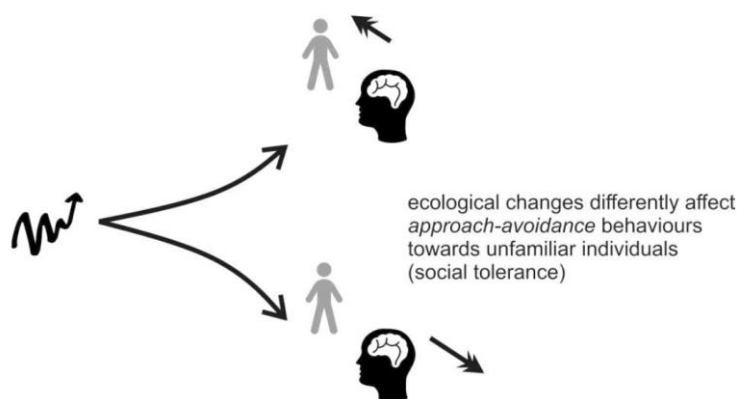
45 The relationship between ecological changes and selection pressures on intergroup tolerance  
46 may have played a significant role in changes in social connectivity and mobility occurring  
47 300,000-30,000 years ago. The relationship between ecology, resource distributions and  
48 intergroup tolerance in mammals in general and in primates specifically provide useful  
49 insights.  
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Even though unfamiliar individuals are typically a threat to territories or resources there are several factors which can promote rather than constrain tolerance towards unfamiliar or “outgroup” individuals. The most obvious and most important factor is that of access to resources. Tolerance enables exploitation of resources at boundaries whilst avoidance or aggression makes such exploitation impossible. The friendly interaction at boundaries recorded in bonobos (*Pan paniscus*) facilitates exploitation of boundary resources such as fruiting trees as well as small prey for example (Tan and Hare 2013; Tan et al. 2017; Hare and Yamamoto 2017; Lucchesi et al. 2020). Bonobos from different groups will willingly share food with non group members, and have been observed actively sharing with other groups at boundaries (Tan et al. 2017). In ecological contexts, where resources are highly clustered and critical for survival, tolerance may be particularly key to enabling access (Pisor & Surbeck 2019).

The advantages which tolerance may bring to resource exploitation is not the only factor promoting tolerant intergroup interactions. There are also other factors such as the potential for gathering information before the transfer of individuals within mating networks and for increased opportunities for extra group meeting, as well as collaborative defence (Pisor & Surbeck 2019). Collaboration between unrelated colonies has even been recorded in eusocial ants as a means of collaborative predator defence (Robinson & Barker 2017).

Clearly, ecological changes affecting resource availability and the distribution of resources, as well as other factors such as predation will influence selection pressures on tolerant, rather than avoidant, or aggressive, reactions to ‘outsiders’ (figure 2).



1 **Fig. 2** Graphical illustration how ecological changes affect tendencies to approach-avoidance  
2 behaviours towards unfamiliar individuals through evolved hormonal responses affecting social  
3 tolerance. Ecological changes (left) can have different evolutionary effects on brain and physiology from  
4 promoting more tolerant behaviours (upper right) to promoting less tolerant behaviours (lower right).  
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7 Archaic humans will have been particularly vulnerable to these changes due to their  
8 dependence on several types of resources, not only plant and animal foods, but also raw  
9 material for tool manufacture and other resources such as medicines (Hardy 2018). Modern  
10 ethnographically documented hunting and gathering populations demonstrate a high degree  
11 of intergroup interactions (Bird et al. 2019) and dependence on intergroup transfers (Pisor &  
12 Surbeck 2019). Intergroup collaboration allows access to widely distributed resources, such  
13 as salt, medicines, raw materials for toolmaking (Pisor & Surbeck 2019) and buffers resource  
14 unpredictability and shortfalls (Dyble et al. 2016; Wiessner 2002a). The classic example of  
15 Ju'houansi hxaro network, a system of distant allies able to provide support in times of  
16 resource shortfall, is perhaps the most well-known example of how intergroup tolerance and  
17 collaboration foster survival (Wiessner 2002b). Many other examples also exist. In Tierra del  
18 Fuego for example beached whales are exploited by different communities who reciprocate  
19 the opportunity by alerting others and allowing entry into their territory (Santos et al. 2015).  
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29 Attention has tended to be focused on the significance of multilevel networks in human  
30 evolution (Grove et al. 2012; Layton et al. 2012). However, a focus on changes in social  
31 tolerance *between foraging or kin groups* may be a more useful theoretical approach,  
32 particularly given that evidence for high levels of inbreeding (discussed below) is difficult to  
33 reconcile with what we know of multilevel networks. Whilst we have assumed that that the  
34 evolutionary origins of regional networks of connectivity lie predominantly in an increasingly  
35 complex cognition, physiological changes influencing social behaviour may have played a far  
36 more significant role than has previously been considered.  
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## 44 **Intergroup tolerance in archaic humans**

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47 There was almost certainly some level of regional population connectivity in archaic humans  
48 (Hovers & Belfer-Cohen, this volume), although evidence suggests that this social connectivity  
49 was subject to notable constraints. Evidence from skeletal abnormalities (Ríos et al. 2019;  
50 Ríos et al. 2015; Trinkaus 2018) and genetics (e.g. Castellano et al. 2014) support the notion  
51 of high rates of inbreeding throughout the Lower and Middle Palaeolithic for example, which  
52 would be unlikely to occur where social groups were fluid and connected. Across the archaic  
53 world there are limited connections beyond home ranges up until at least 500,000 years ago  
54 (Layton et al. 2012; Marwick 2003). In Eurasia, the long genetic history of close interbreeding  
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1 (equivalent to the half-sibling level) seen in the genome of the Altai Neanderthal (Prüfer et al.  
2 2014), contrasts with the evidence for the ACMH Sunghir burials II,III and IV, whose genome  
3 sequences indicate exogamous mating practices (Sikora et al. 2017) for example.  
4 Connections of some kind over a long distance exist. In Middle Palaeolithic Europe there are  
5 rare examples of long distance material movements (Féblot-Augustins 1999), and even rarer  
6 examples of distant raw materials even predominating where local materials are unsuitable as  
7 in southern Italy (Spinapolice 2012). However, as a whole there seems to be no good evidence  
8 for frequent social interaction between groups. The evidence for longer distance movements  
9 outside of a group's typical range is consistent with what we might expect when external social  
10 connections were not common (Djindjian 2012), perhaps limited to movements around mating  
11 patterns (which may have been constrained by patrilocality see Lalueza-Fox et al. 2011). Even  
12 what we might consider as the first stage of regional intergroup connectivity - resource  
13 exploitation at boundaries – is not always evident. In the Middle Palaeolithic of the Levant,  
14 detailed studies of the transport of flint materials to the site of 'Ein Qashish even suggest  
15 potential borders between groups where resources remain unexploited for example (Ekshtain  
16 et al. 2014, 2017; Hovers 2018). We can reasonably assume that archaic groups were capable  
17 of the kind of intergroup or landscape scale interactions recorded in bonobos, i.e. exploitation  
18 of resources between groups and some sharing of resources (not only on the basis of common  
19 ancestry but also on the basis of evidence from raw material transfers). However, the level of  
20 social tolerance which we often assume ought to have characterised human societies for much  
21 of our evolutionary past, i.e. frequent social connection and access to complementary  
22 resources as well as mating opportunities, is far more elusive than we might expect.  
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38 There is little doubt that transformations in connectivity 300,000-30,000 years ago significantly  
39 changed regional social relationships, laying the basis for fluid social and biological  
40 connections to emerge, as well as regular aggregations, and the spread of new innovations  
41 and ways of doing things (Coward 2015; French 2016, 2018; Gamble 2009). Physiological  
42 changes, in response to the influence of changing ecology on selection pressures towards  
43 intergroup social tolerance, are likely to have played a key role in these transformations.  
44 Whether 'self domestication' is an appropriate term to apply to changes in the human  
45 evolutionary past or not remains debated (see Sánchez- Villagra and van Schaik 2019).  
46 Nonetheless, it is clear that over the timeframe 300,000 and 30,000 years ago there have  
47 been transformations in physiology and anatomy in emerging modern human populations  
48 associated with changes in hormone function which are broadly associated with increased  
49 tolerance (Theofanopoulou et al. 2017). Analogies have been drawn between the changes  
50 observed in humans and those seen in other primates (such as distinctions between common  
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1 chimpanzees and bonobos) and other species less closely related to humans (such as wolves  
2 and free ranging dogs).

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4 Here we investigate the mechanisms behind these changes in social disposition which are  
5 often generalised within the term self domestication. To illustrate potential methods to better  
6 understand such changes we develop an agent-based model to simulate the potential effects  
7 of ecological changes on intergroup tolerance in archaic humans.  
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11 We simplify two different populations within the broad classification as being “avoidant” and  
12 “tolerant” in order to compare these different strategies in differing ecological contexts.  
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## 15 16 Method

### 17 18 **Model overview**

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20 We use a spatially-explicit, agent-based model (ABM) to simulate individuals attached to  
21 groups (or ‘bands’ within modern ethnographic contexts, Hill et al. 2014) of hunter-gatherers.  
22 Agent-based models are a widely-used tool for investigating complex systems (Railsback and  
23 Grimm 2019). They have long been used in archaeology to reveal how individuals interact  
24 with each other and their environment to produce emergent patterns (reviewed by Premo  
25 2005; Romanowska et al. 2019 and Cegielski and Rogers 2016). It has been shown that prey  
26 depletion across a landscape with interacting individuals is best addressed using a simulation  
27 model (Křivan and Eisner 2003). Brantingham (2003) used a model of individuals moving  
28 around a spatially heterogeneous landscape encountering, collecting and processing  
29 resources to provide a null model of the diversity of stone sources that would be found in a  
30 tool-kit.  
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34 Here we model individual humans moving around a dynamic landscape hunting resources  
35 (similar to Janssen and Hill 2014, but with more abstract animal populations). Our focus is on  
36 the effect of the nature of inter-group interactions and whether food resources are shared  
37 when groups meet. Individuals foray from their group foci to acquire resources and to interact  
38 with other groups, and they also age and may reproduce. The model is implemented in C#,  
39 compiled and run on a PC using Microsoft Visual Studio 2019.  
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43 Like every model, this simulation cannot represent the full extent of all social interactions  
44 among archaic humans, therefore it simplifies some of the aspect to allow us to explore the  
45 key questions. We use a series of assumptions based on a simplification of what is known  
46 about the social behaviour of archaic humans.  
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- We assume that archaic humans belong to groups distributed across a landscape, and that these groups can move around and interact with other groups.
- Groups may interact with the probability of interactions higher when group foci are closer (that each groups are not *seeking each other out*, but interacting randomly).
- Social interactions may be “avoidant” or “tolerant”, with the latter allowing for potential transfers of resources from a group with excess resources to one with a deficit (resource sharing).
- Resources (in this case hunted food, though foraged plant foods would function in the same way) are tracked in landscape cells. Food is needed for maintenance and excess food is needed for successful reproduction.
- Animal populations increase following logistic growth and successful hunting removes animals from the landscape and adds food to a group’s supply.
- Individuals age and mature females can reproduce (when the group has sufficient resources) and suffer age-dependent mortality.

Our use of ‘tolerance’ in this context implies a positive interaction with members of other groups, leading to the possibility of resource transfers to those in need from those with available resources, in accordance with sharing as observed in modern ethnographically documented contexts (Lavi & Friesem 2019; Spikins 2019).

## **Model operation**

### **Initialisation**

At initialisation there are 160 group foci placed randomly in continuous space within the landscape. The starting population of humans is 3000 individuals randomly assigned to a group and starting at the group focus. Individuals have a random age [1, 50] and sex [even chance] assigned at the start of the simulation. Animal populations are set independently for each grid cell and initially have a random value [1, 100].

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3 **Model flow**  
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5 There are several phases within a model year:  
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8 Hunting. Individuals each start from their group focus point and, if old enough to hunt, take a  
9 series of step moves with hunting attempted at the end of each step. A successful hunt adds  
10 a unit of resource to the group's stock. Details are in supplementary materials.  
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14 Inter-group interactions. Pairs of groups are selected at random and may meet for an  
15 intergroup interaction where, if tolerant, resources may be exchanged. Details are in  
16 supplementary materials.  
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20 Maintenance. Individuals eat food from the group's supply for subsistence.  
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23 Ageing, birth and death. All individuals age each year and there is an age-specific probability  
24 of death. Adult females in groups with excess resources may have offspring.  
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27 Group fission and loss. Groups of size 50 and above split, those below size 4 are lost.  
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30 Animal population growth. Details in supplementary materials.  
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33 **Elements and variables of the model**  
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36 The elements and variables used in the model are described in table 1.  
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Element	Explanation
Landscape	The landscape is represented by a regular grid of 100x100 landscape cells (the side length referred to as a 'grid unit'). Each landscape cell supports an independent animal population.
Individual	An individual human located in continuous space within the landscape. An individual's sex, age and group affiliation is tracked.
Group	Individuals are assigned to groups. Each group has a focal point or 'camp', located in continuous space, that remains fixed for a season. Groups are assumed to pool hunted resources and successful hunting adds to the group's stock.
Hunting	All individuals older than 10 are assumed to move in forays through the landscape and hunt resources (detailed description in supplementary materials and see flowchart in supplementary section).
Maintenance and starvation	Each group loses 1 unit of food for each group member to provide subsistence. If there is insufficient food to cover this maintenance individuals may starve (detailed description in supplementary materials).
Birth and death	Females between ages 16 and 39 have offspring if there is sufficient food after maintenance to cover the birth cost. There is age-dependent death applied following (Gurven & Kaplan, 2007; Hill et al., 2007; Kelly, 2013) in addition to death from starvation.

Group loss and group fission	Any group with fewer than four members is dissolved and all remaining group members are assumed to have died. Any group with 50 or more members will split into two. At group fission all individuals in the current group are randomly assigned to one of the two daughter groups. One group will have its focus in a new location (details in supplementary materials).
Animal population growth	Each landscape grid square has an independent animal population and at the end of each year populations can increase following logistic growth (details in supplementary materials).
'Harshness' of environment	Harshness of the environment is varied by varying the cost of births. Here we use a range of costs of reproduction from 26 to 35.
Tolerance (potential for resource transfer)	With a simulation run all groups are either 'avoidant' or 'tolerant'. If groups avoid each other no food will be transferred, when groups are tolerant food will be transferred (shared) if one has a surplus and the other a deficit.
Storage of resources	There is no long-term storage of resources and groups start each hunting season with no stored food.

**Table 1** Explanation of elements and variables used in the model

### Model realisations

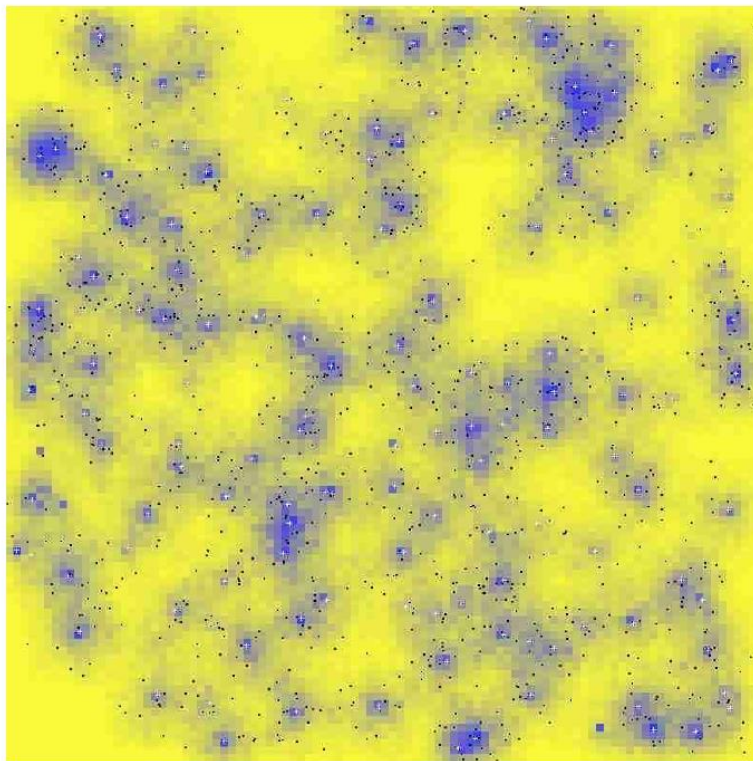
For each model realisation here we focus on the total population size as a measure of success. In all simulations, the population size reported is the mean total population within a realisation between timesteps 901 and 1000.

Populations within a simulation are either 'avoidant' where there are no intergroup interactions (other than indirectly through exploitation competition) or 'tolerant' where positive intergroup

1 interactions (food sharing) are possible. We vary the 'harshness' of the environment by  
2 changing the cost of offspring from 26 (benign) to 35 (harsh). There are 200 replicate  
3 simulations of each tolerance / environment combination.  
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6 We then repeated the simulations with temporal environmental heterogeneity. This was  
7 achieved by adding variation in the cost of reproduction between years to simulate a mix of  
8 good and bad years with the same mean. Each year we added a value to the cost of  
9 reproduction value drawn as a random uniform integer  $[-7,7]$ , mean 0, standard deviation of  
10 4.7. Variation was added independently each year and there was no temporal autocorrelation.  
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15 An illustration of the model in operation is shown in *figure 3*.  
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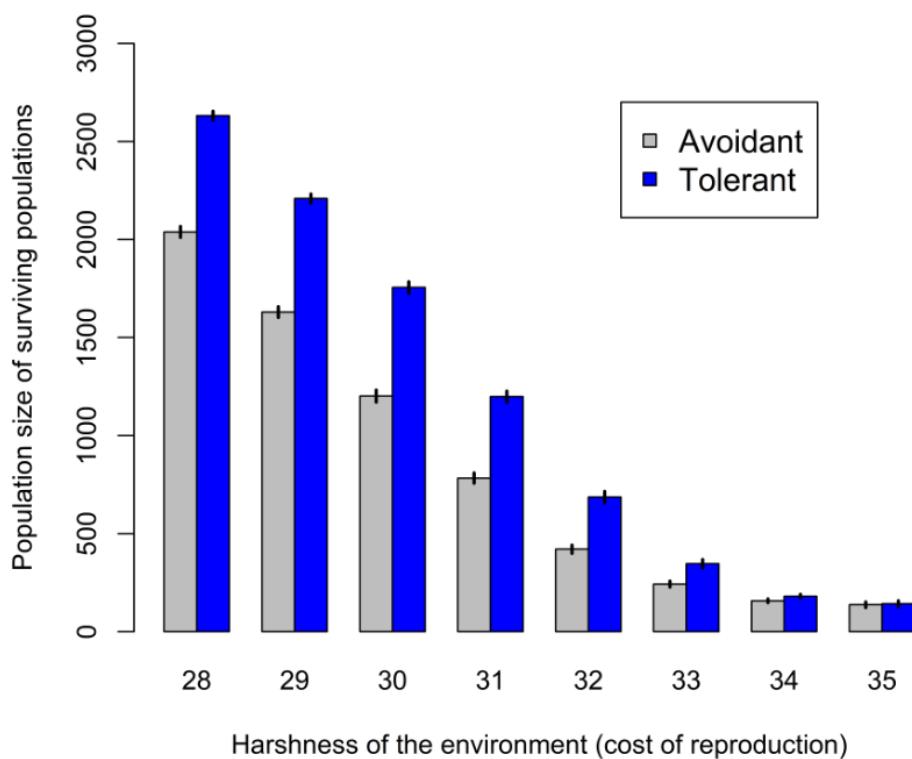
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**Fig. 3** A snapshot of the model in action. Blue dots are individual foragers, white crosses are group foci  
46 or 'camps', dark blue to yellow shading in landscape cells indicates the level of available resource from  
47 low to high. The effect of depletion of resources near camps is clear  
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## 51 **Results**

52 The model outputs allow us to make observations about the advantages or disadvantages of  
53 strategies of tolerance or avoidance of other groups under different environmental conditions.  
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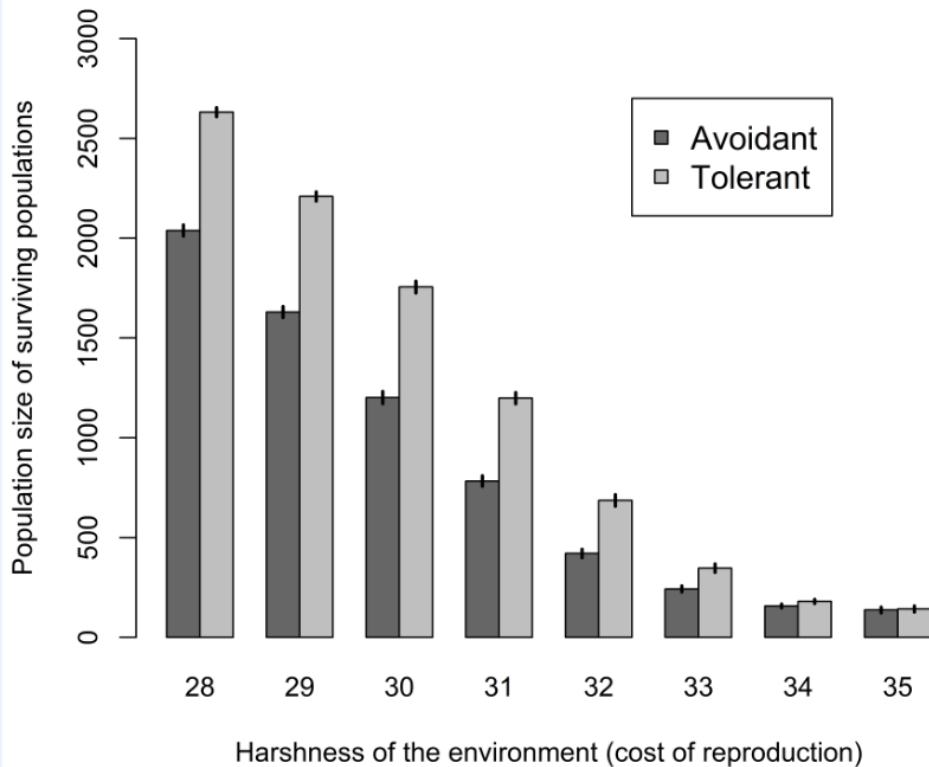
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Unsurprisingly, the harshness of the environment has a notable effect on the population size, *figure 4*, with harsher environments supporting smaller populations. Intriguingly, this effect is much more pronounced for avoidant than tolerant strategies i.e. sharing food resources across borders is advantageous, leading to higher population density and greater probability of survival. Sharing can still be costly nonetheless, and interestingly the benefits of sharing become less evident in the harshest environments as the costs of sharing become more significant in relation to resources quired for immediate survival.



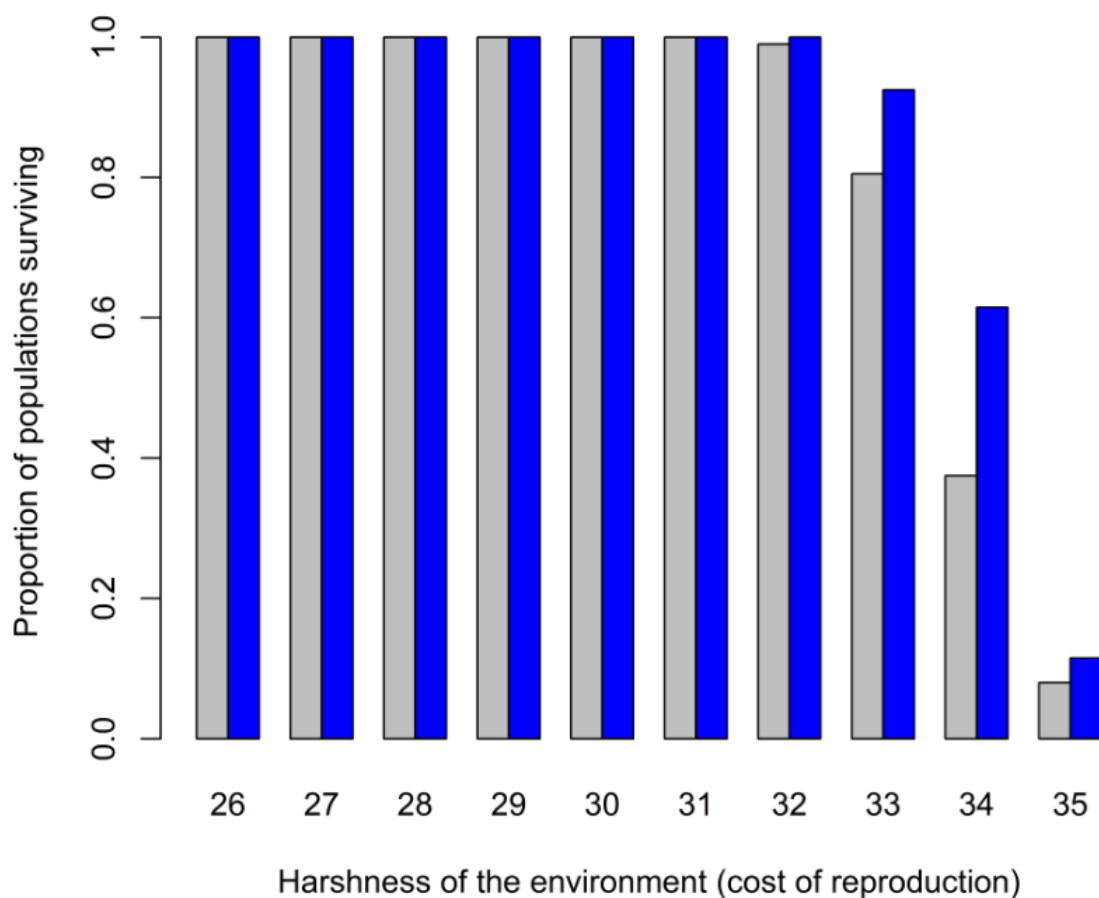
**Fig. 4 (colour)** A range of costs of reproduction with avoidant (grey, left column) and tolerant (blue, right column) simulations. Data shown are the mean population size at the end of the simulation from up to 200 replicates for each bar (fewer in more harsh environments where there are extinctions). Error bars show 95% confidence intervals





**Fig. 4** (black and white). A range of costs of reproduction with avoidant (dark tone, left column) and tolerant (light tone, right column) simulations. Data shown are the mean population size at the end of the simulation from up to 200 replicates for each bar (fewer in more harsh environments where there are extinctions). Error bars show 95% confidence intervals

The relative probability of populations surviving or failing to secure enough resources for survival under different strategies of avoidance or tolerance to other groups also show interesting patterns. In benign environments all populations persist, but again unsurprisingly, as we see from *figure 5*, harsh environments (where reproduction is costly) reduce population survival. However, interestingly, tolerant populations (which are able to share resources) are less affected by increasingly harsh environments i.e. a tolerant population not only has a higher population size than an avoidant population, as we see from *figure 4*, but a tolerant population is more likely to survive in a harsh environment, *figure 5* and less likely therefore to become locally extinct (i.e. where a total population falls to zero).



**Fig. 5.** Proportion of simulations with population over zero at the end (i.e. survival). 200 simulations for each bar with avoidant (grey) and tolerant (blue) simulations

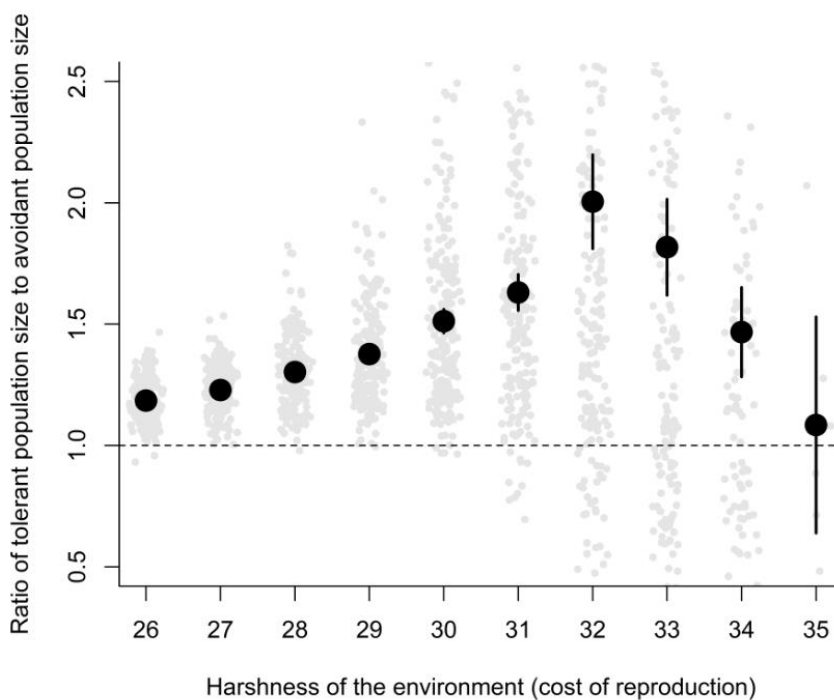
**Fig. 5** (black and white version). Proportion of simulations with population over zero at the end (i.e. survival). 200 simulations for each bar with avoidant (dark grey) and tolerant (light grey) simulations.

Statistical analysis supports these observations. An ANOVA with population size as the response variable and tolerance and cost of reproduction as predictors shows, unsurprisingly, very strongly significant effects of both as well as a highly significant interaction. Effect sizes, as measured by  $\eta^2$ , cost of reproduction: 0.94, tolerance: 0.27, interaction: 0.01, with all p values <0.001, although significance levels for simulation models should be treated with some caution (White et al. 2014). To investigate the form of the interaction between tolerance and

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cost of reproduction (environmental harshness) we expressed the results as tolerant population size / avoidant population size. Tolerance (food sharing) has a positive effect (ratio > 1) throughout, but the scale of the effect varies with environmental harshness.

As we see from figure 6 whilst tolerance is a generally advantageous strategy, this advantage is most pronounced where environments are neither extremely benign (where sharing becomes less necessary for reproduction and survival) nor extremely harsh (as the costs of sharing become more significant in relation to the resources needed to reproduce and survive).

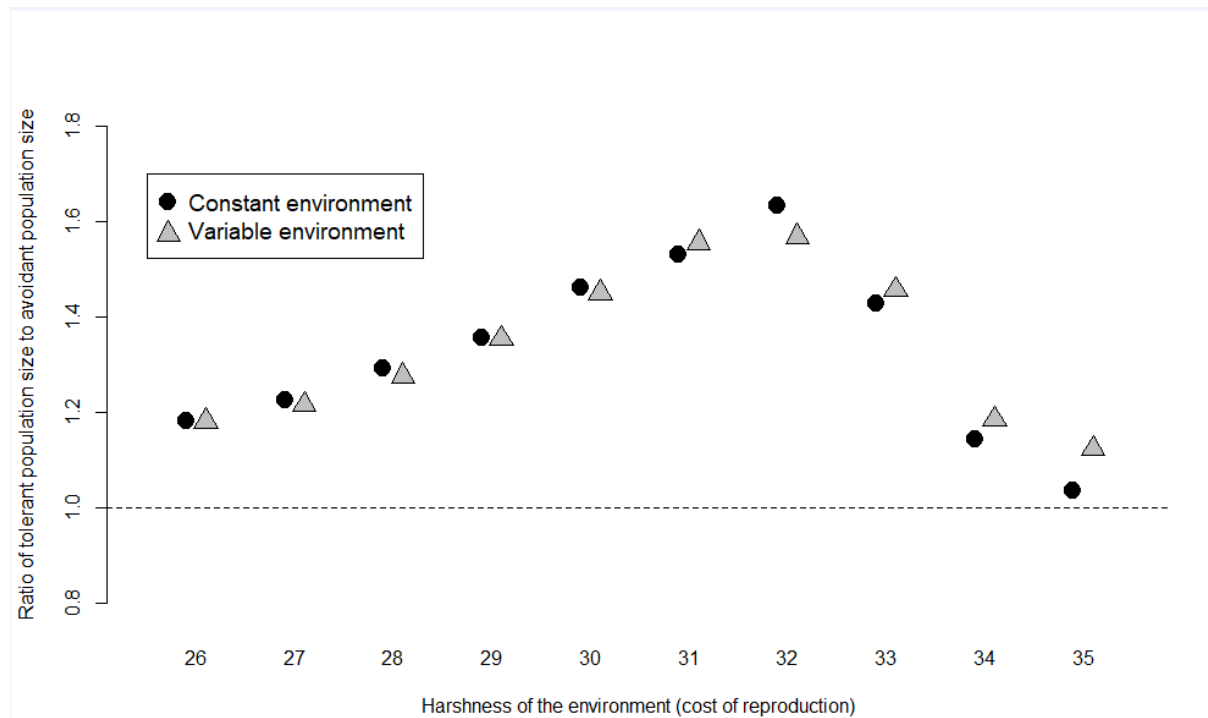


**Fig. 6.** Population size of tolerant simulations / avoidant simulations, means are filled black circles. A value of 1 (shown with a dashed horizontal line) will result if there is no effect of resource sharing, values over 1 indicate tolerant populations are larger, a value of 1.5 showing 50% larger. 200 pairs of simulations (1 avoidant, 1 tolerant) were run for each level of environmental harshness, raw data for the ratio in each pair are shown in light grey circles. Ratios are only available when both populations in the pair of simulations persisted to the end of the simulation. 95% confidence intervals are shown (note that for low values of environmental harshness these are within the circle showing the mean)

The effect of adding environmental variability through inter-annual variability in cost of reproduction is shown in Figure 7. It confirms the pattern in figure 6, indicating a clear peak for the benefit of food sharing at harshness of 32, but that the drop from there as conditions become harsher is larger in a constant environment than a variable one. Tolerance is even

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more beneficial to overall population success in a harsh (over level 33) and variable environment than when environments are more productive and stable. However, this pattern is much less pronounced than the overall effect within harsh rather than benign environments



**Fig. 7** Interaction between tolerance and cost of reproduction for a constant environment (black circles) and variable environment (grey triangles). Each point is the mean tolerant population size / mean avoidant population size (dashed horizontal line indicates equal population sizes for tolerant and avoidant strategies). There were 200 realisations of each strategy for each level of cost of reproduction for both constant and variable environments. All realisations below cost of reproduction 32 persisted. Simulations where the population died out were discarded, see figure 5

## Discussion

### The relationship between ecology and human intergroup tolerance

The model outlined here considers the implications of tolerant or avoidant strategies on forager success and survival when encountering other groups under different environmental conditions.

1 Our simulations demonstrate that intergroup tolerance, allowing the exchange or sharing of  
2 resources between groups, has a significant effect on populations survival in 'harsh' or difficult  
3 environments. Populations which share resources are likely to be more successful (i.e.  
4 increase in population) and are more likely to survive harsh environments where extinctions  
5 occur than those populations which do not share across borders. This finding supports  
6 arguments made on the basis of ethnographically documented resource transfers at times of  
7 famine (see for example Wiessner 2002b).  
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12 We also demonstrate novel patterns within the broader advantages of tolerance. Firstly the  
13 effects of intergroup tolerance are most significant in moderately harsh environments. In the  
14 harshest environments population density becomes too low to support interactions (the cost  
15 of interactions are high compared to the resources needed to survive, groups have little  
16 resources to spare to share and survival becomes critical). In the most benign environments  
17 however, the benefits of sharing become marginal (as resources for reproduction and survival  
18 are not threatened). Secondly, overall harshness has a far greater effect on the selection  
19 pressures promoting social tolerance than ecological variability, though ecological variability  
20 does have some effect.  
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29 The most significant finding in terms of broader debates over changes in the period 300,000  
30 to 30,000 bp is that tolerance towards other groups and intergroup collaboration becomes  
31 advantageous as environments become harsher (though in extremely harsh environments it  
32 becomes difficult to maintain the level of intergroup contact required to make collaboration  
33 possible) and tolerance also becomes more advantageous as environments become more  
34 variable. Although to date there has been some understanding of why intergroup collaboration  
35 might make communities more resilient, there has been little understanding of the ecological  
36 factors which might influence this or the limitations of collaborative strategies in certain  
37 ecological contexts. This finding therefore does provide some support for suggestions that  
38 environmental variability may have played a role in social changes in recent human evolution  
39 (Potts 2013; Potts et al. 2018). However, the effects of environmental variability on the  
40 selective advantages of intergroup tolerance are much less pronounced than the overall effect  
41 within harsh rather than benign environments. This result is perhaps surprising given the  
42 emphasis in the literature on environmental variability as a driver for human evolutionary  
43 changes rather than environmental harshness per se. Whilst variability is clearly an influence  
44 on selective pressures the potentially elevated significance of environmental harshness on  
45 intergroup interaction provides an important avenue for further research.  
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## Implications

The simulations provide useful insights which may further our understanding of the archaeological record documenting key human transformations taking place 300,000 to 30,000 years ago.

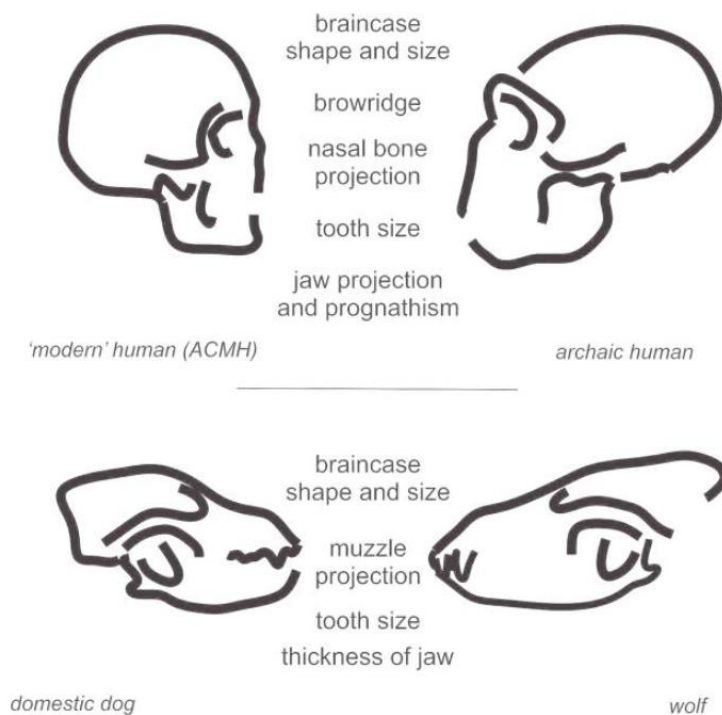
Archaic humans in this period were uniquely *pre-adapted* to being able to benefit from increasing social tolerance through their capacity to transfer resources to buffer shortfalls, as well as uniquely *susceptible* to ecological pressures due to their increasing reliance on many different resources (plant and animals resources for food, plant resources for medicines, raw materials (such as flint) for tool production).

Simulation modelling explains why specific ecological conditions occurring in certain contexts in Africa after 300,000 years ago, a time of increasing aridification and increasingly variable environments, may have provided the conditions in which elevated selection pressures on intergroup social tolerance might have emerged, leading to the passing of a threshold point beyond which intergroup collaboration became a normal stable state.

Particularly elevated selection pressures would have characterised certain African populations due to a unique combination of body form, ecological context and geography. Gracile or more slightly built humans (i.e. emerging modern humans in contrast to more heavily built or 'robust' archaic species), have lower energy requirements, and when living in equatorial contexts with high productivity would exist at higher population densities than robust forms. For this reason, early modern human African populations in many regions would be buffered from low population densities at which intergroup interactions become impossible. Moreover, such populations would be uniquely situated within a geographical situation in which large regional scale connectivity was possible. Increased friendly interactions and collaboration between groups will also enhance the spread of innovations, regardless of population size or density, thus further enabling greater adaptability to change.

The model also explains why anatomical features of 'self domestication' associated with increasing tolerance are visible in African population after 300,000 years ago. Self domestication represents an extreme form of social tolerance, affecting physiology, anatomy

1 and behaviour, most probably through the action of changes in neural crest cells and their  
 2 effect on the hypothalamic-pituitary-adrenal (HPA) axis (Wilkins et al. 2014). Whether the term  
 3 'self domestication' is appropriate within human evolution or not (Sánchez- Villagra and van  
 4 Schaik 2019; Shilton et al. 2020) both selective pressures on increased social tolerance and  
 5 associated anatomical changes provide an explanation for the similarities seen in cranial and  
 6 facial forms of ACMH compared to archaic species to changes seen between domestic dogs  
 7 and wolves (*figure 8*). Whereas domestication occurs through human influence within  
 8 artificially 'domesticated' species, ecological conditions are an influencing factor where  
 9 increasing levels of intergroup tolerance emerge in "wild" contexts (Pisor and Surbeck 2019)  
 10 (as described by Hare et al., 2012 for bonobos). Although explanations for this process in  
 11 humans have to date largely drawn on internal social process (Hare 2017; Wrangham, 2014;  
 12 Wrangham, 2019) we argue here that ecological context will have had an important role to  
 13 play in changing social tolerance and 'self-domestication' in humans.



**Fig. 8.** Similarities in cranio-facial changes seen between modern and archaic humans and between dogs and wolves (re-drawn after Theofanopoulou et al., 2017).

Increased intergroup tolerance thus provides an alternative explanation to that of population size or density (Langley et al. 2008; Shennan 2001) for transformations in the occurrence of

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innovation and cumulative evolution during this period. However, it complements models that link these transformations to increases in population connectivity (e.g. Powell et al. 2009), and, as demonstrated by our model, increased intergroup tolerance, can also lead to population increase. Moreover, explanations for ‘modern human behaviour’ based on changes brought about through increased intergroup tolerance do not depend on the questionable concept of an increasingly sophisticated cognition (e.g. Klein 2000).

## Limitations

Simulation models allow us to test out the implications of different scenarios and the relationships between many different variables. Our ABM allows an exploration of how particular processes (human intergroup behaviours) may have been affected by changes in certain variables (ecological changes). Like every model this simulation cannot represent the full extent of all social interactions among archaic humans, therefore it simplifies some of the aspects to allow us to explore how different strategies of avoidance of other groups or tolerance with the potential for sharing are affected by ecological context.

There is clearly far more to the emergence of hunter-gatherer intergroup tolerance and sharing than emotional dispositions, even though they play an important role (Spikins 2019). For this reason any model provides us with a starting point and not an end. For example, the level of ecological variability we modelled played only a minor role in influencing the advantages or disadvantages of sharing. However, this may be limited by only modelling only ‘simple’ one step interactions, and not accommodating uniquely human emotions such as gratitude, which may play a key role in maintaining generalised reciprocity (Ma et al. 2017; Nowak & Roch 2007; Smith et al. 2017) nor cultural behaviours such as gift giving (Coward 2015). Future models might address such issues.

## Further Research

The model described here is based at the level of the individual, and considered the success of different strategies when compared against each other. This could be developed further in several ways. For example it would be possible to add an evolutionary component ie to enable individuals to evolve across successive generations. This additional complexity would allow



1 questions about evolutionary mechanisms e.g. group selection to be addressed. Sharing of  
2 knowledge could be an additional element which would enable cultural evolution, potentially  
3 occurring differently within different groups (see Powell et al. 2009 regarding the relationship  
4 between population density and knowledge transfer Vaesen et al 2016 for a counter argument,  
5 and also Luchessi et al. 2020 regarding sharing knowledge of unfamiliar environments  
6 between groups amongst bonobos). Differences in memory capacities might also be  
7 incorporated into further models (see Cox et al. 1999).  
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## 13 **Research contribution within agent-based models in** 14 **archaeology** 15 16 17 18

19 As well as contributing to the key research question outlined here i.e. our understanding of  
20 changes taking place 300,000 to 30,000 years ago, and in particular in the factors influencing  
21 the proliferation of regional social networks and increased regional mobility this research  
22 contributes broadly to existing agent-based models which have been used to better  
23 understand how resource characteristics influence foraging behaviours. Janssen and Hill  
24 (2014) for example develop a model of foraging behaviour based on actualistic studies of the  
25 Hadza, and have developed this model to demonstrate that as hunted resources become more  
26 clumped the movement distances of hunters reduced (Janssen and Hill 2016). However, this  
27 model specifically focuses on the relatively under researched topic of food sharing between  
28 groups. Premo (2005) has developed a preliminary model to consider the evolution of food  
29 sharing. However, models considering inter-group behaviour are rare, with the exception of  
30 Santos et al. (2015) who explore resource sharing strategies when groups encounter prolific  
31 resources in the form of whale carcasses. As such the model contributes to this emerging  
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## 45 **Conclusions** 46 47 48 49 50

51 We demonstrate here that external ecological factors may have been more significant in the  
52 process of increasing human social tolerance and population connectivity and in turn the  
53 emergence of “modern human behaviour” than has previously been suggested.  
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57 As we have shown, archaic communities are particularly sensitive to the effects which  
58 ecological changes have on the relative advantages and disadvantages of intergroup social  
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behaviour. They display some *capacity* to share resources between groups and depend on a *variety of* different resources. The capacity to be tolerant and interact with unfamiliar individuals would be under particular selection pressures in the period 300,000 years onwards because of the relationship between archaic human resource requirements and ecological changes. Firstly, plant foods and animal resources needed not only for food but also to make tools or medicines are affected by ecological changes, and moreover groups may depend on access to other essential resources, such as lithic raw materials found outside of their own home ranges. Secondly, ecological factors which influence availability of resources and resource access including both overall harshness of environment and increasing variability and unpredictably would have influenced selection pressures on intergroup attitudes and behaviours.

Our model demonstrates that *severe resource pressures* as well as *ecological variability*, occurring in environments where population densities are sufficient to allow intergroup interaction, place particular selective pressures on intergroup social tolerance. As a result particular conditions in Africa after 300,000 years ago may have pushed humans past a turning point in adaptive changes. Once physiological changes passed beyond a certain threshold point intergroup collaboration may have become the stable state, leading to increasing dependence on varied resources and high levels of social connection, and in turn laying the basis for social and cultural transformations.

The effect of ecological changes on intergroup dispositions provide us with an important alternative explanation for changes in social behaviour in recent human evolution. Whilst there has been some understanding of the significance of intergroup collaboration in resilience to ecological changes, this model adds an understanding of how and why intergroup collaboration may have emerged. This approach moves beyond concepts of the progressive development of cognitively “modern” cognition towards a more complex relationship between mind, body and social relationships and moreover provides a means of linking theoretical approaches to ecology and anatomical changes with approaches to social-cognitive changes. Further, by focusing on how ecological context can influence physiological and behavioural changes we hope to move towards an understanding of social transformations as part of different evolutionary branches and possibilities rather than a ladder of progression.

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## Supplementary information

Commented [PS1]: addresses s7, s8, s9, s10

**Model details**

**Hunting** See supplementary figure S1 for a graphical outline of the protocol. Steps are executed in series. First, an individual is selected at random from the whole population. If that individual is of age 10 or above they move a random distance drawn from a uniform [0,1] in a random direction. If the move would take them more than 7 grid units from their home they immediately return home, (from where they can start a new hunting foray next time they are selected). At the end of the move they hunt. Hunting success is set by the animal density of the current landscape square (more success in higher animal density populations (pop) with a simple linear probability of  $\text{pop}/100$ ). With a successful hunt the local animal population level is reduced by 1 and the group's food stock increases. This process is repeated 30 x current population size times, selecting a random individual each time. This means that each individual does not take a fixed number of move steps but will make a number of steps that is Poisson distributed with a mean of 30.

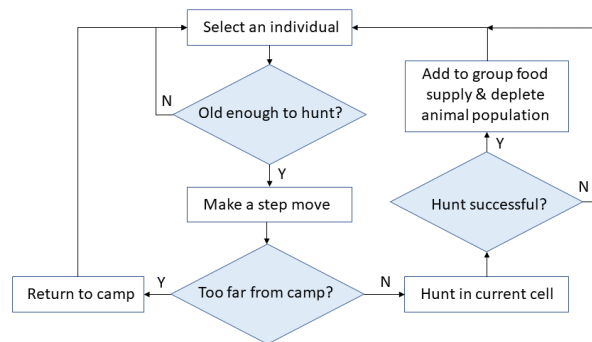


Figure S1 - workflow for hunting protocol.

**Intergroup interactions** Pairs of groups are selected at random and the Euclidean distance between group foci calculated. There is a declining probability of interaction with distance such that groups 25 grid units apart will meet 75% of the time while those more than 50 grid units apart never interact. This leads to about 5% of groups having interactions in a season. When 'tolerant' groups meet they may transfer resources. If one group has a deficit of resources (i.e. not enough for subsistence for all members of the group) and the other has a surplus (i.e. more than enough for both subsistence and one birth) then 10 units of resources are passed from one group to the other.

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**Starvation and relocation** When the pool of resources that a group gains during hunting is insufficient for maintenance starvation may occur. Each individual in a group has a probability of:  $(\text{group size} - \text{food available}) / \text{group size}$  of death due to starvation. For example, if there was enough food for half of the group all members would have a 0.5 mortality probability applied in this phase. If any starvation occurs, the group will look for a new location and move their base camp. A random location within 14 grid units of the current group focus is selected. The group will shift focus and all individuals will move there if the local food level (animal population in the alternative location cell) is higher than that in the current location.

**Group fission and relocation** Groups reaching a size of 50 will split into two. Each individual in the parent group is assigned at random, with even probability, to one of the two daughter groups. At the fission event one of the two daughter groups, determined at random, retains the parent groups focus ('camp' location). The other group focus, and all individuals in this daughter group, moves to a random location within 14 grid unit points of the previous focus. To ensure a good starting location is selected, the new focus must be located in a landscape cell with a higher animal population level than that in the original location - to represent some scouting of the location before moving.

**Animal population growth** Each landscape grid cell supports an independent population of animals which is similar to Janssen and Hill (2014; 2016). Animal populations follow logistic growth with an  $r$  of 0.1 and  $K$  of 100 using this equation:  $\text{pop}_{t+1} = \text{pop}_t + (\text{pop}_t * r * (1 - \text{pop}_t/K))$ .

If any animal population falls below 1 it is reset to 1 to prevent local extinction. Unlike Janssen and Hill (2014) there is no movement of animals between grid cells. Animal populations are not restricted to integers.

### Sensitivity analysis

**Group size** We collected data on the size of groups at the end of simulations (time 1000). The mean group size is ~23 individuals (which fits with records of modern foraging populations, see Kelly 2013), the distribution of group sizes is shown in figure S2. Few groups are small and close to dissolution (size 4) and few groups are large and close to fission (size 50).

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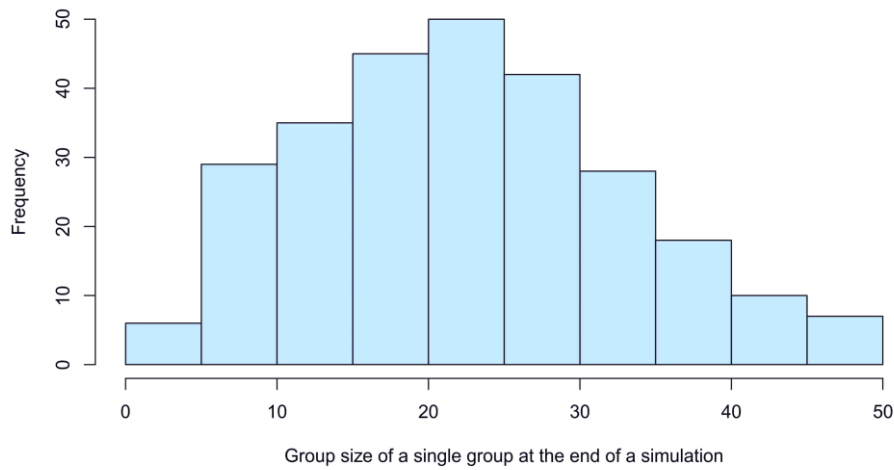
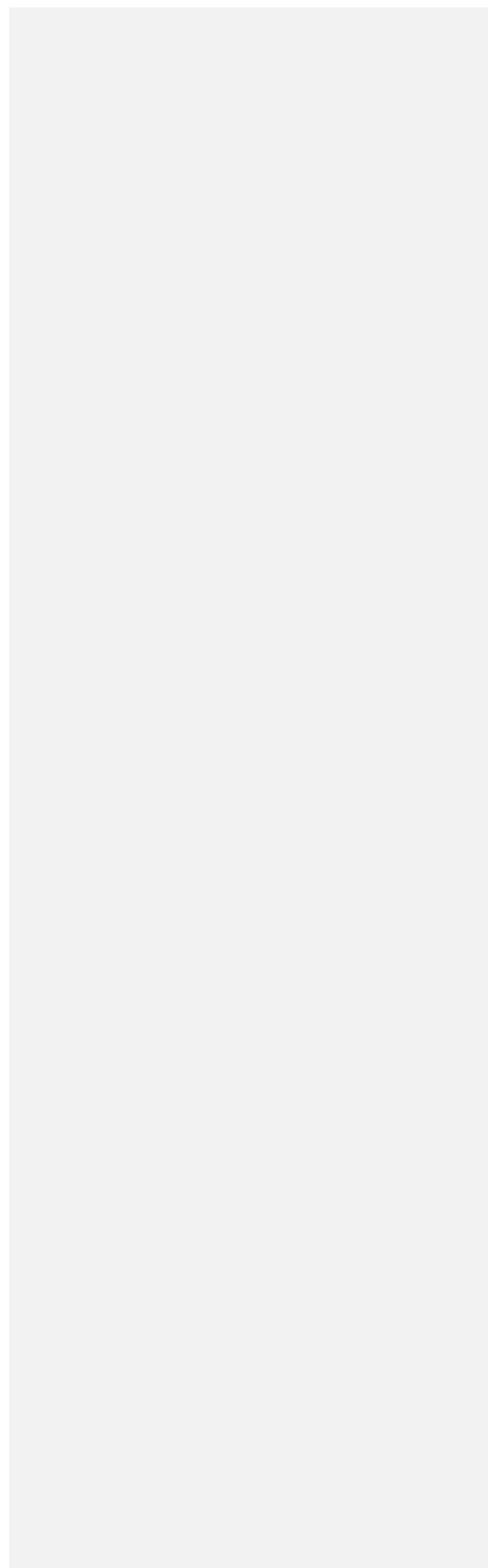


Figure S2 - distribution of group sizes at the end of simulations.



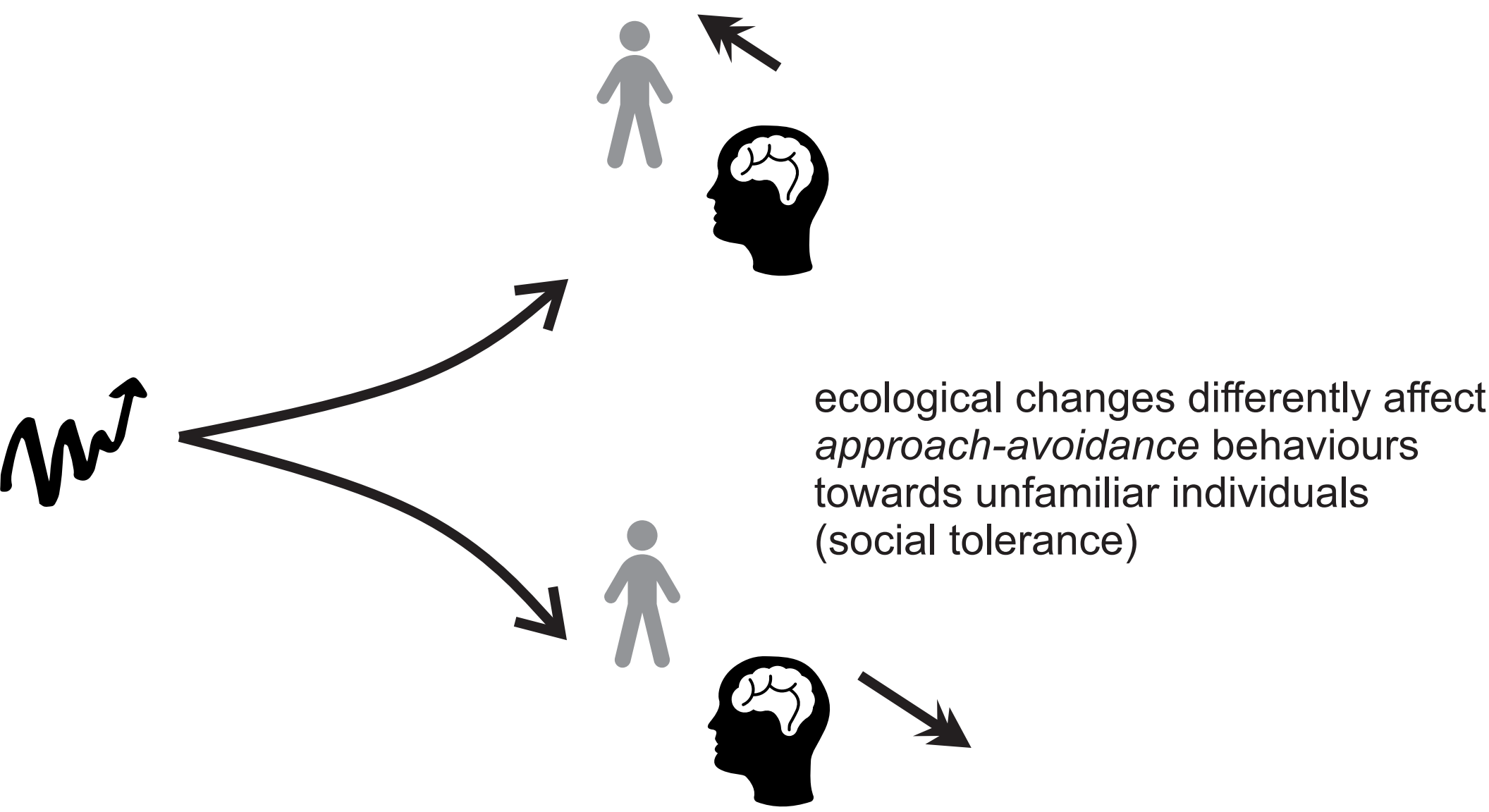


ASSUMPTIONS

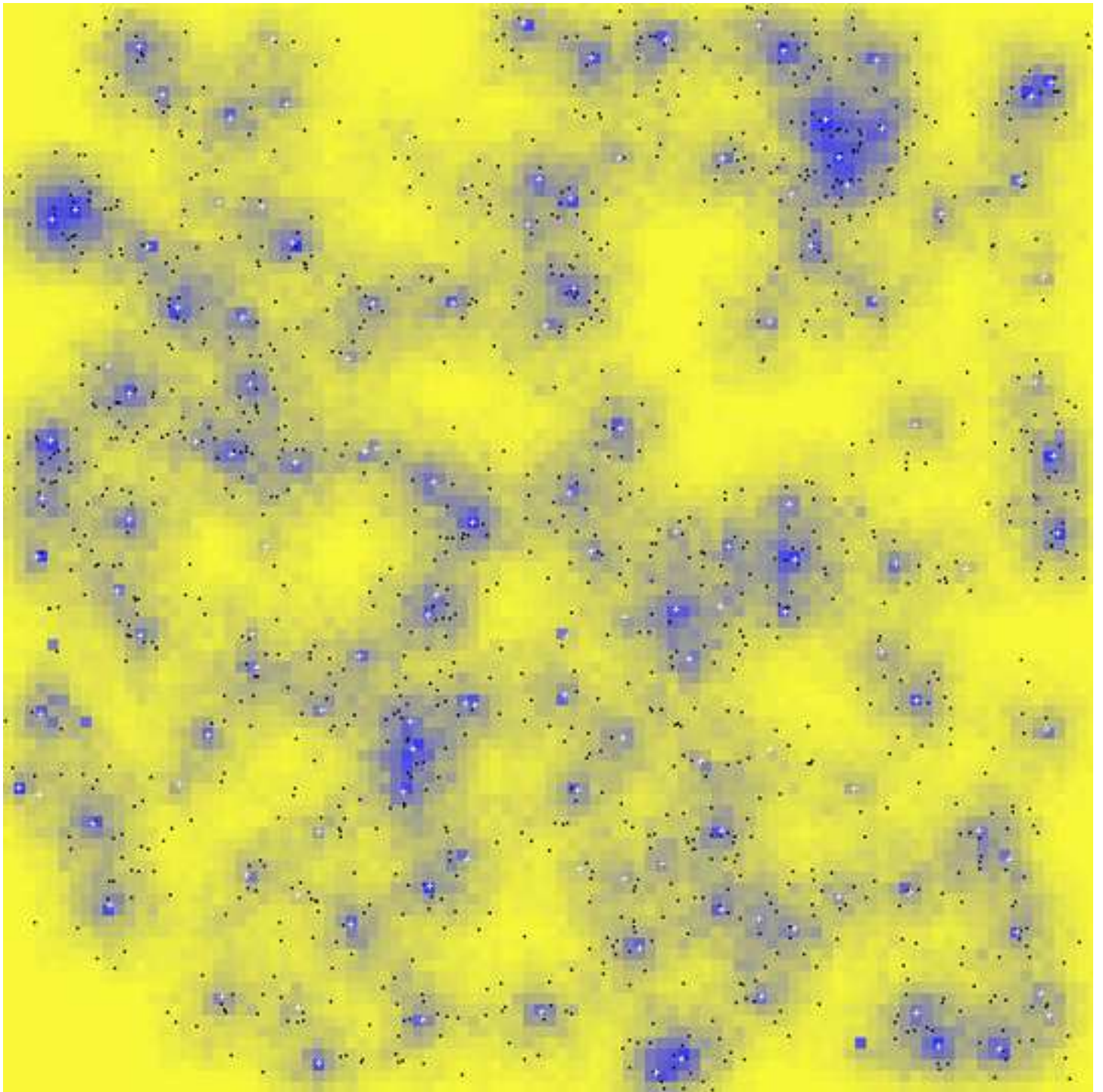
evolution of **biological-anatomical** characteristics through influence of changing ecology

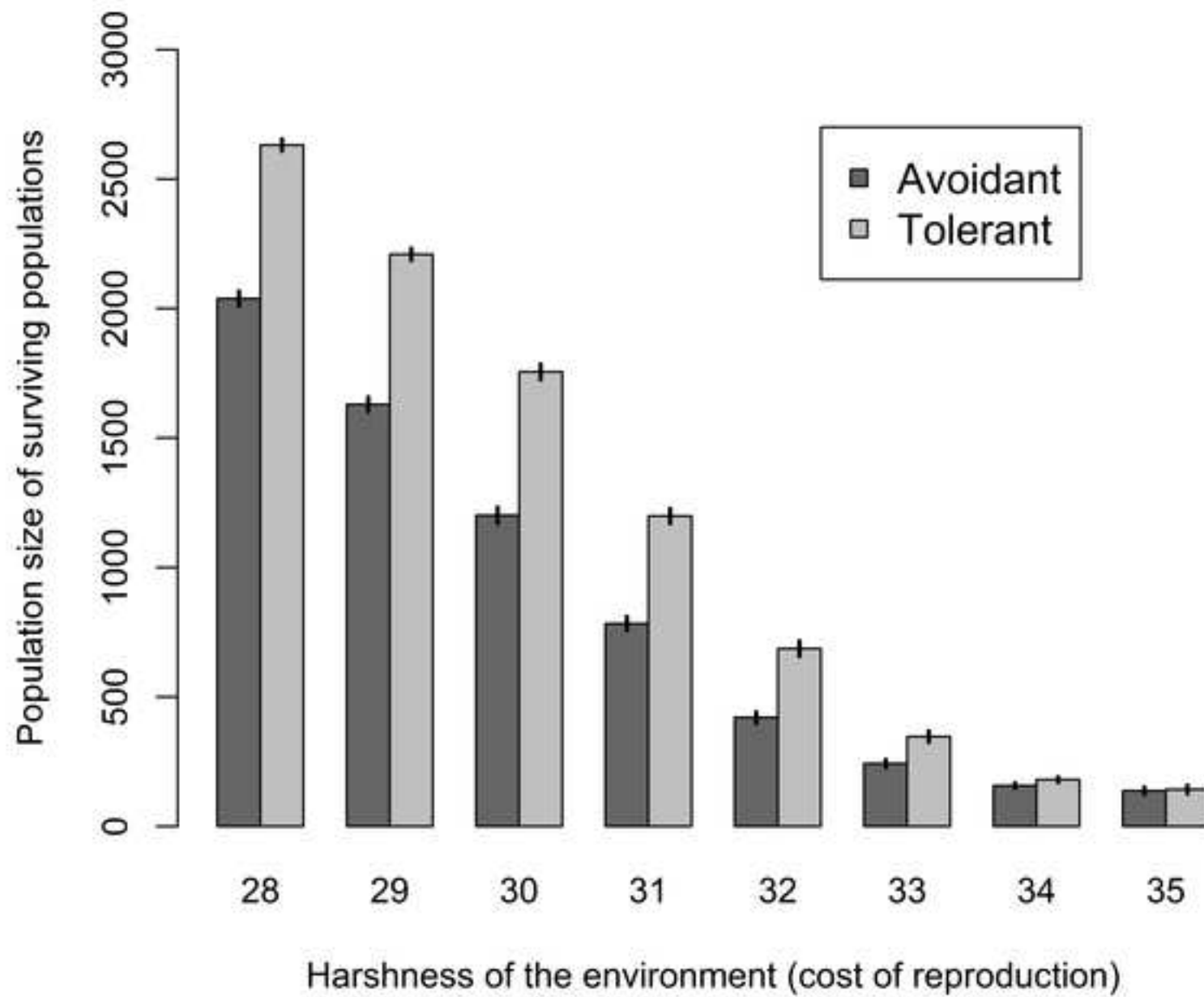
evolution of **social-cognitive** characteristics through internal processes

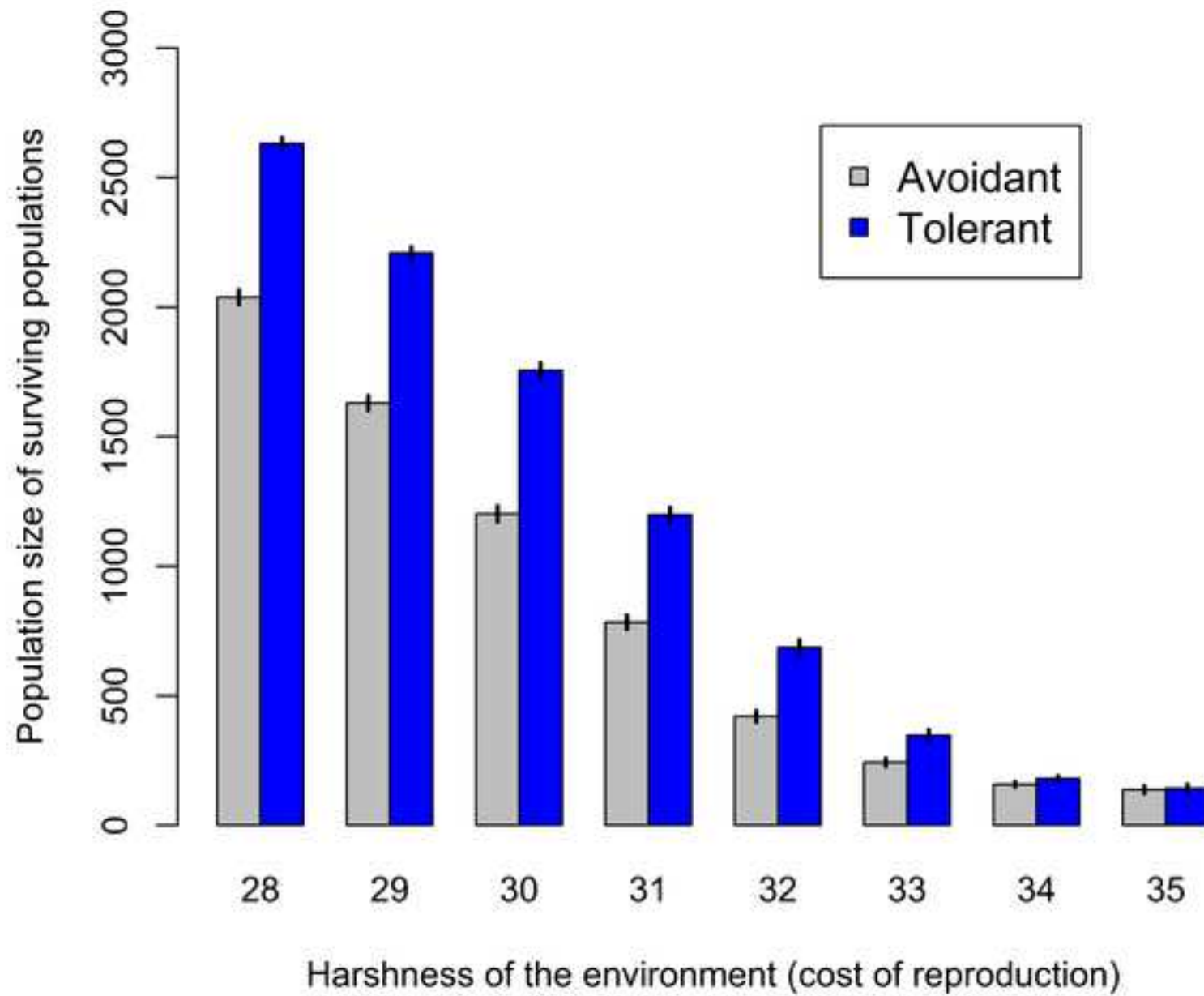
limited indirect influence between (eg via population density)

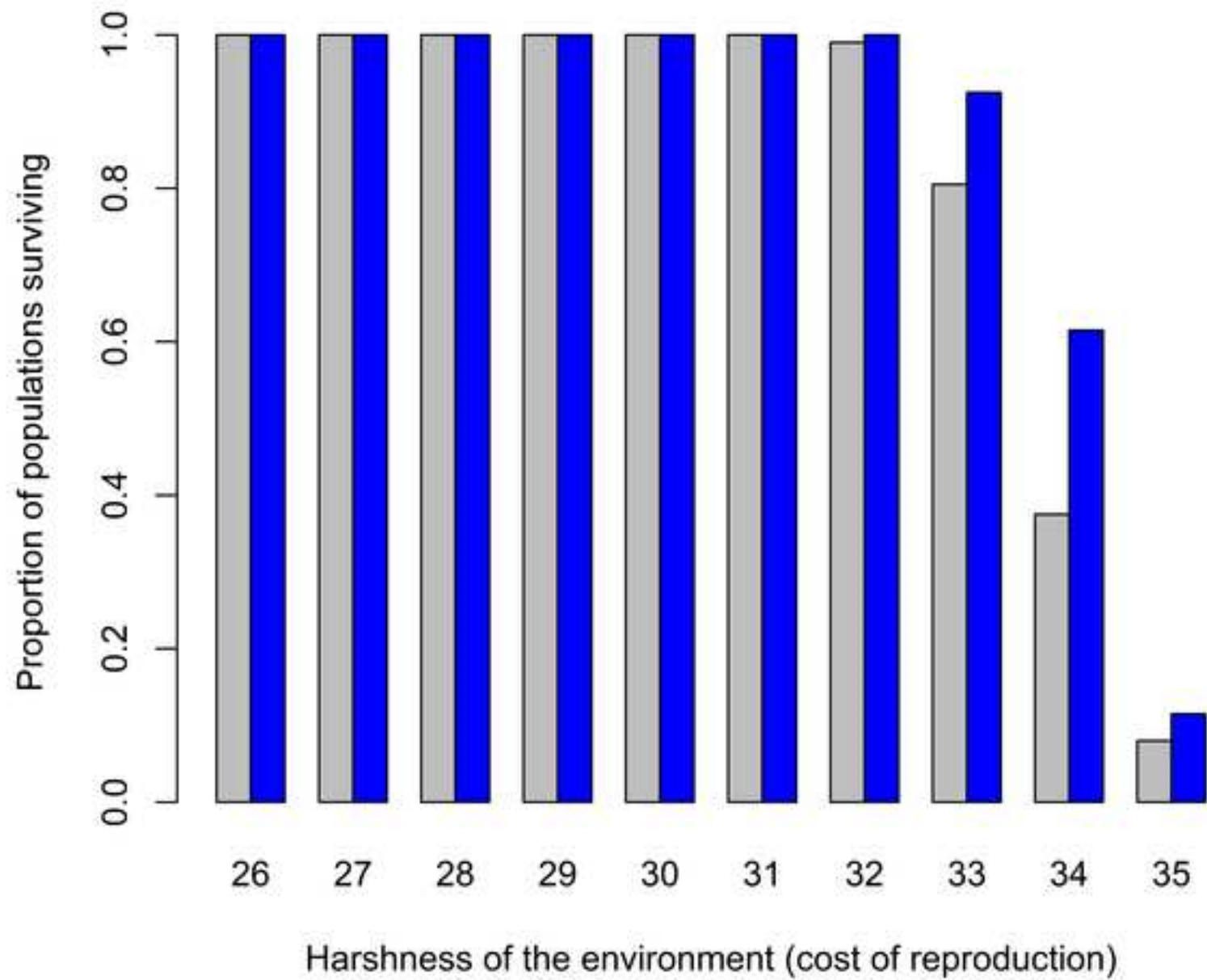


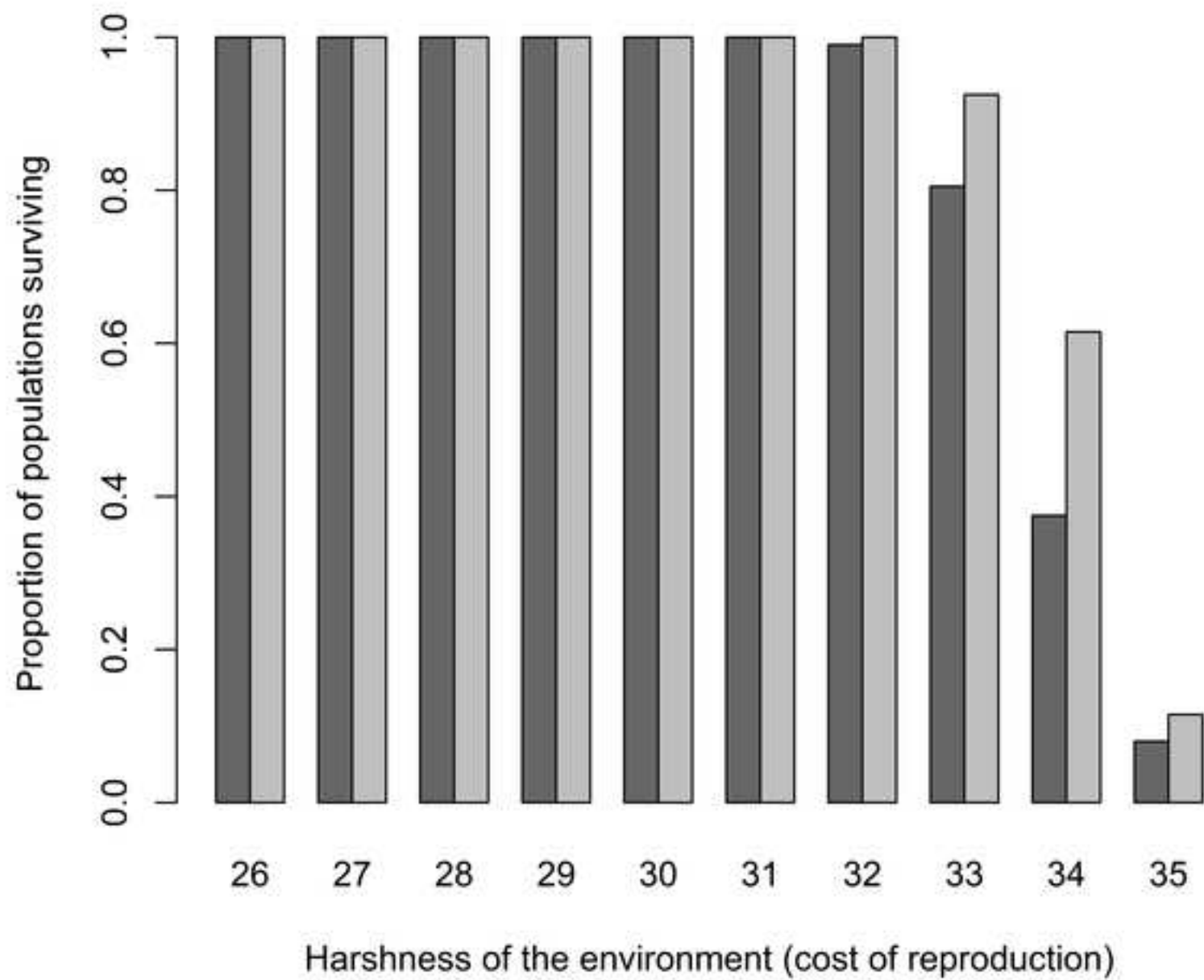


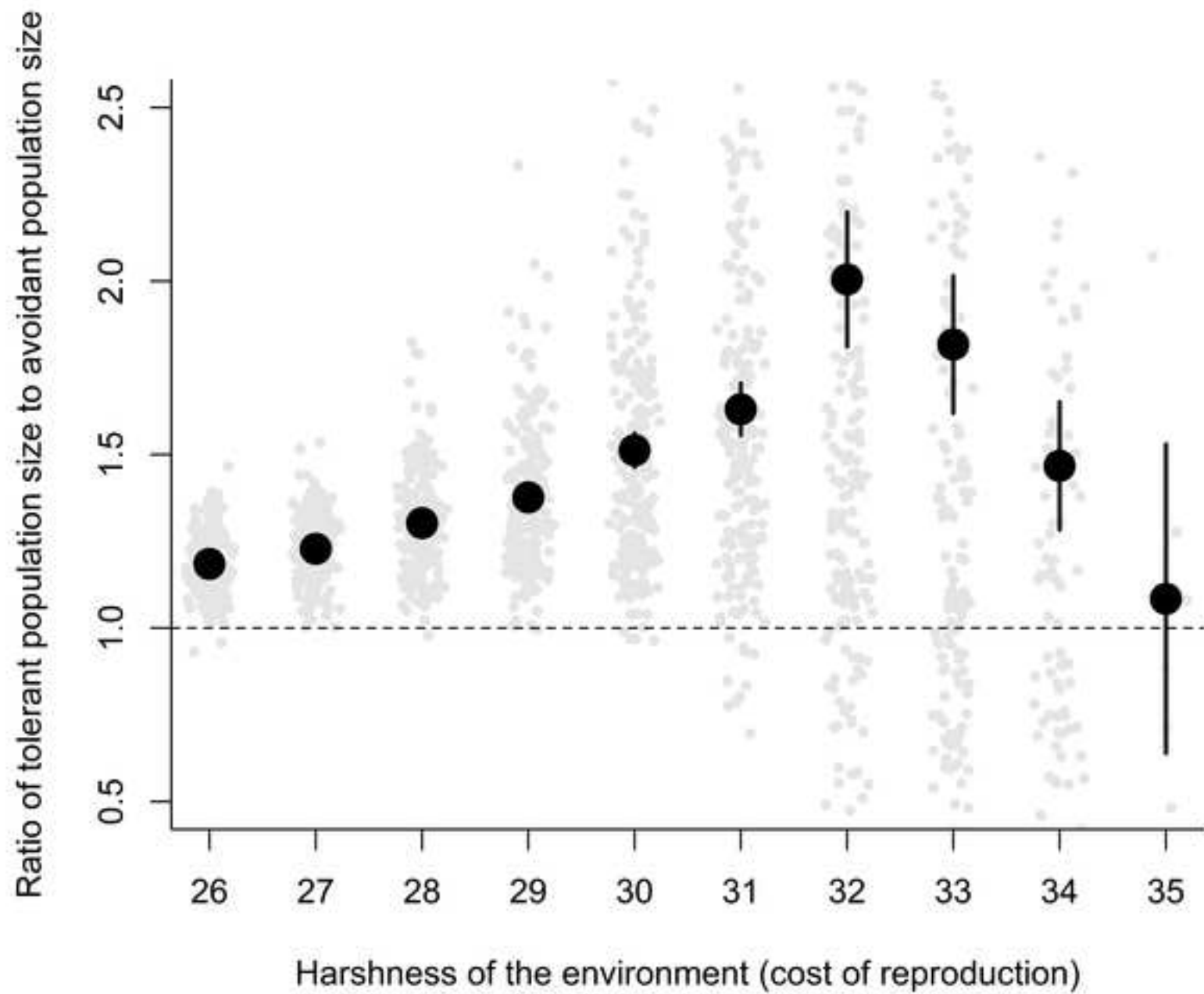


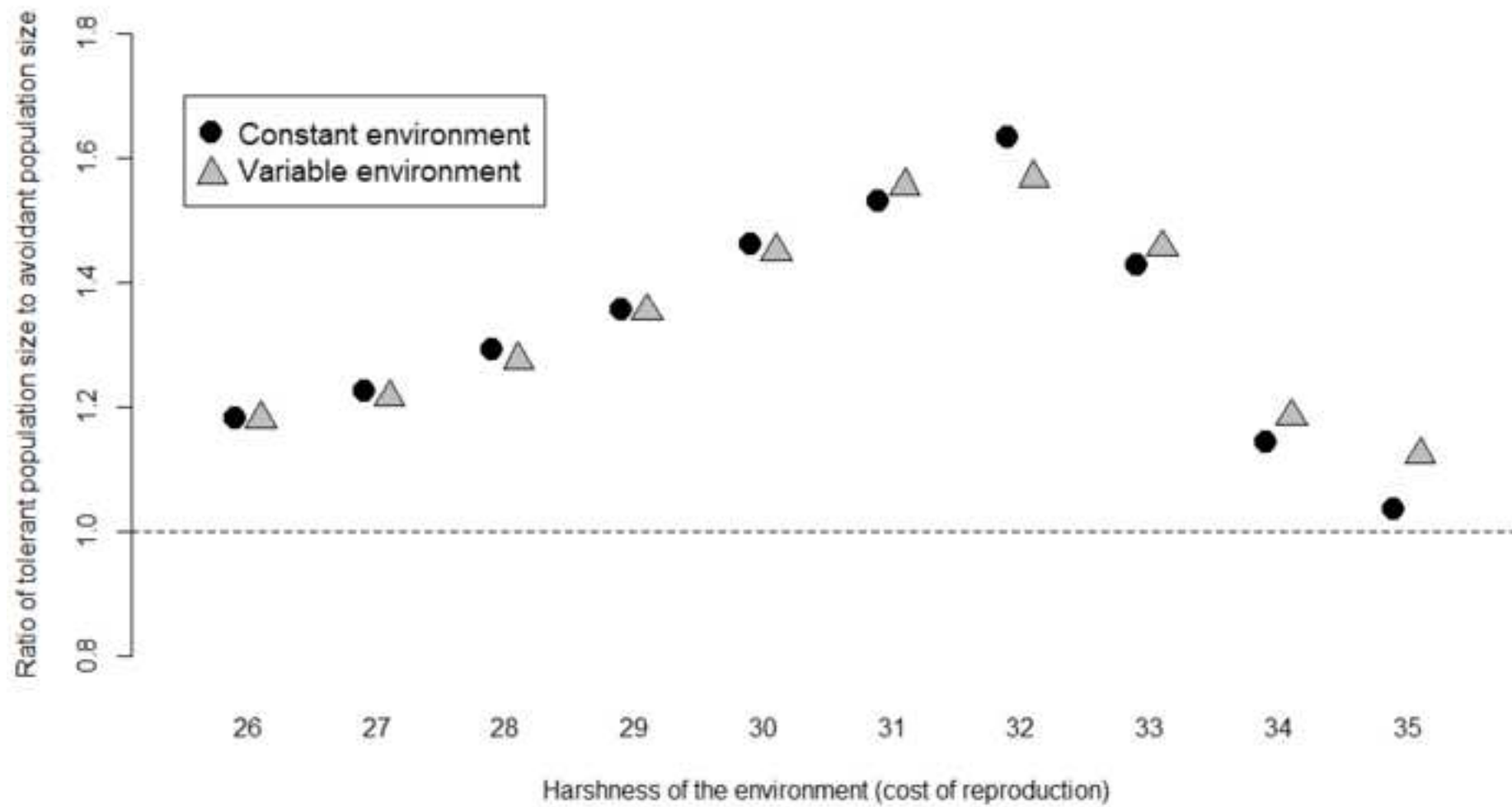


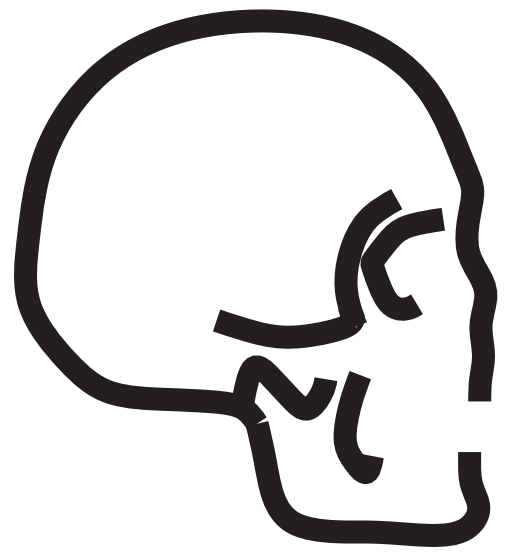












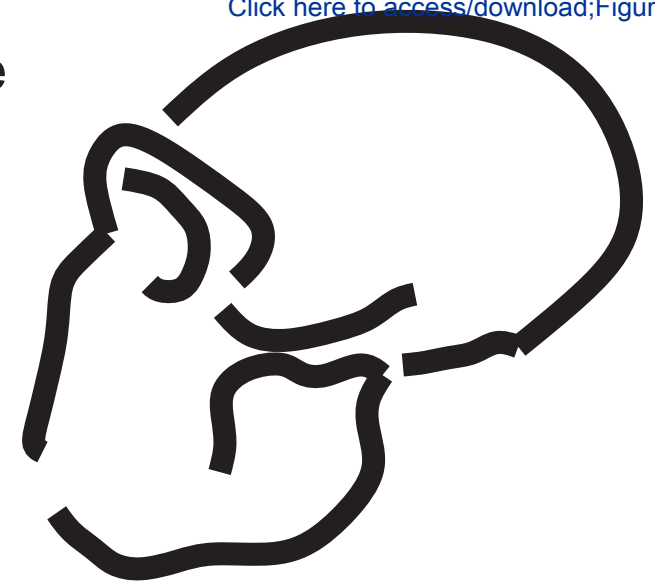
braincase  
shape and size

browridge

nasal bone  
projection

tooth size

jaw projection  
and prognathism



*'modern' human (ACMH)*

*archaic human*



braincase  
shape and size

muzzle  
projection

tooth size

thickness of jaw



*domestic dog*

*wolf*



