

# Hunter-Gatherers, Mismatch and Mental Disorder

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## Abstract

For most of human evolutionary history our species lived as hunter-gatherers; hence, much of our cognition and behaviour is adapted to this way of life. Given the magnitude of the sociocultural, economic and lifestyle changes experienced by *Homo sapiens* over the last 10,000 years, in particular the last several hundred years, aspects of human psychology may be maladapted to modern ways of life. This process of maladaptation following changes in the physical or social environment is referred to as 'evolutionary mismatch' and has been hypothesised to contribute to the high prevalence of mental disorders in industrialised societies. However, very few studies have examined the prevalence of these pathologies among contemporary hunter-gatherer populations; thus, empirical support for such *diseases of modernity* hypotheses is lacking. In this chapter, we review the limited existing research and theorise about the key differences between hunter-gatherer and industrialised societies that are likely to have profound implications for mental health. Specifically, we contrast the strong social support networks, egalitarianism, explorative modes of learning, sensitive child-rearing practices and present orientation of hunter-gatherers with corresponding features of industrialised populations. We argue that mismatches in these domains are partially responsible for a vast array of mental illnesses, ranging from common mood disorders to behavioural pathologies and psychotic spectrum disorders. We hope that this chapter stimulates the generation and testing of mismatch hypotheses and, eventually, trials of interventions based on mismatch reduction. We end by offering suggestions for methodological approaches to this future research.

## Keywords

child development, diseases of civilization, egalitarianism, evolutionary mismatch, human life history, hunter-gatherers, mental health

## Key Points

- Differences between the physical and social environment in contemporary industrialised societies and those experienced by our hunter-gatherer ancestors can result in maladaptive cognition or behaviour. This process is referred to as 'evolutionary mismatch'.
- Modern environments may produce novel pathological phenotypes that did not occur among hunter-gatherers (phenotypic mismatch). Additionally, some phenotypes that were adaptive in a hunter-gatherer context have not changed but are maladaptive or pathological in modern environments (environmental mismatch).
- Research with contemporary hunter-gatherers is scarce but indicates that their prevalence rates of various mental disorders may be lower – and level of psychological well-being higher – than in industrialised populations.
- Compared to hunter-gatherers, industrialised societies are characterised by smaller social support networks, increased social and economic inequality, less sensitive child-rearing, high-pressured didactic education and the requirement for long-term planning. All of these differences likely increase our vulnerability to an array of mental disorders.

## 5.1 Introduction

### 5.1.1 Mismatch and Its Relevance to Disease

Evolutionary mismatch refers to a scenario where there is a discrepancy between the physical or social environmental conditions an organism currently faces and past conditions in which some trait of that organism originally evolved – its *environment of evolutionary adaptedness* (EEA) – resulting in physical, cognitive or behavioural maladaptation (Barkow et al., 1992; Bowlby, 1969; also see Chapters 1 and 2 of this volume). Mismatch occurs because natural selection is a blind process relying on random mutations, of which an infinitesimally small proportion provide any adaptive benefit, and those that do are then selected for over extended time frames before reaching fixation. Therefore, there is often an *adaptive lag* after environmental changes.

Whilst the ‘goals’ of natural selection certainly do not always align with optimisation of health or well-being (Nesse, 2019), they often do. Given the magnitude of the sociocultural, economic and lifestyle changes experienced by our species over the last 10,000 years, and especially the last several hundred years, there has been growing interest in the potential of mismatch to explain a range of pathologies. A classic example is the ubiquitous preference for foods high in sugar and fat (see Figure 1.1). These preferences evolved to motivate the acquisition of such foods in ancestral environments where they were scarce and provided invaluable nutritional benefits; conversely, in present-day industrialised societies they are abundant and readily available. High consumption driven by the mismatched taste preferences and low physical activity levels characteristic of modern lifestyles has significantly contributed to epidemics of obesity, diabetes and cardiovascular disease in WEIRD (Western Educated Industrialised Rich Democratic) populations (O’Keefe and Cordain, 2004). Taking a mismatch perspective may offer unique preventative solutions and remedies by encouraging the replication of relevant aspects of ancestral lifestyles, thereby attenuating the mismatch.

### 5.1.2 Hunter-Gatherers and Mismatch

Given the explanatory potential of mismatch thinking, there has been growing interest among

public health researchers in the use of extant hunter-gatherer populations as models of ancestral lifestyles (Pontzer et al., 2018). The premise of this approach is that a hunter-gatherer lifestyle is likely to resemble the EEA for many traits relevant to health; for more than 95% of human evolutionary history, prior to the Neolithic Revolution, we occupied this mode of subsistence (Kelly, 2013). Broadly speaking, hunter-gatherer societies are defined by a primary reliance on the foraging of wild foods via hunting, gathering or fishing and a lack of domestication of plants or animals except dogs (Kelly, 2013).

Typologies usually divide such populations into *immediate-* versus *delayed-return* hunter-gatherers or *simple* versus *complex* hunter-gatherers. In each typology, the former lack food storage mechanisms, live in small, highly mobile groups and are politically egalitarian, whereas the latter store food, live in larger, more sedentary groups and have recognised social and economic inequalities (Woodburn, 1982). Compared to simple hunter-gatherers, evidence for the presence of complex hunter-gatherers appears much more recently in the archaeological record and tends to be confined to coastal regions (Arnold et al., 2016; Marlowe, 2005). Therefore, many anthropologists agree that the former are more representative of our species’ evolutionary history (Marlowe, 2005; Shultzner et al., 2010). Correspondingly, herein, our discussion of foraging societies and their relevance to mismatch refers to simple hunter-gatherers unless otherwise stated.

Epidemiological work has demonstrated an extremely low prevalence or a complete absence of various non-communicable diseases among contemporary hunter-gatherers (Pontzer et al., 2018), and less than 10% of deaths are caused by chronic disease (Gurven and Kaplan, 2007). Numerous promising mismatch hypotheses of mental disorder have also been put forward, pertaining to depression (Chapter 8 of this volume), schizophrenia (Abed and Abbas, 2014; Chapter 10 of this volume), attention deficit hyperactivity disorder (ADHD; Chapter 15 of this volume), eating disorders (Chapter 11 of this volume) and post-partum depression (PPD; Hahn-Holbrook and Haselton, 2014). However, epidemiological studies among hunter-gatherers, which test empirically whether these disorders are in fact *diseases of modernity*, are extremely scarce. In

Section 5.3, we briefly review the limited existing hunter-gatherer research relevant to mental illness and psychological well-being.

Given the current dearth of epidemiological work, in Section 5.4 we discuss various aspects of hunter-gatherer existence – principally related to social organisation and child-rearing – that are notably different from WEIRD populations and likely have profound implications for mental health; we do not attend to lifestyle factors such as physical activity levels or diet since these have been discussed extensively elsewhere (e.g. Gurven and Lieberman, 2020). Importantly, there are two distinct routes by which such mismatches may contribute to psychiatric illness. Firstly, via the generation of novel pathological cognitive or behavioural patterns that would not manifest in a hunter-gatherer context, we suggest such cases are referred to as *phenotypic mismatch* (an environmental change has produced a novel maladaptive/pathological phenotype). Alternatively, it may be that the same ‘symptoms’ do occur among hunter-gatherers but in such contexts are considered neither pathological, because they do not impede an individual’s ability to function in society, nor maladaptive, because they are not associated with reduced reproductive success. We propose the term *environmental mismatch* to describe this second form of mismatch (the phenotype has not changed but is maladaptive/pathological in the new environment). For instance, some scholars have suggested that psychosis would have been less likely to occur in hunter-gatherer societies for reasons relating to social organisation (Abed and Abbas, 2014); using our classification scheme this would be a phenotypic mismatch hypothesis. Conversely, others have suggested that what we now call psychosis did occur in foraging societies, but rather than negatively impacting functionality, it was spiritually valued and a precursor to gaining prestigious shamanic status (Polimeni and Reiss, 2002); we consider this an environmental mismatch hypothesis. As said by one Inuit, ‘when the shaman is healing he is out of his mind, *but he is not crazy*’ (Murphy, 1976, p. 1022, emphasis in original).

We hope this chapter encourages anthropological research that can meaningfully contribute to the developing field of evolutionary psychiatry via the generation and testing of mismatch hypotheses. Additionally, we aim to equip

clinicians with a basic understanding of the lifestyle that much of our cognition and behaviour is adapted to, which may reframe how one thinks about the aetiology of mental disorder. In fact, it has been suggested that providing patients with evolutionary explanations for mental disturbances can have a therapeutic effect in and of itself (Nesse, 2019).

## 5.2 The Validity of Our Approach

Here, we briefly respond to potential objections to our approach, which have two key themes: the validity of using contemporary hunter-gatherers as a model for prehistoric societies and the relevance of mismatch within the domains of cognition and behaviour.

### 5.2.1 Are Hunter-Gatherers Useful Models of Prehistoric Human Societies?

Arguments that extant hunter-gatherers are not representative of ancestral societies are often focused around the impact of modern outside influences. This perspective was stressed in the *Kalahari Debate* by the *revisionists* who argued that the !Kung San Bushmen of southern Africa are no longer operating in an independent foraging economy but represent an underclass in an increasingly integrated market economy (Wilmsen et al., 1990). Indeed, most studied forager populations have a non-trivial level of interaction with the outside world. That said, an imperfect model is not a useless one, and many features of contemporary hunter-gatherer life discussed below likely approximate those of our ancestors (Gray, 2013; Shultziner et al., 2010).

Others have argued that contemporary hunter-gatherers are marginal remnants of ancestral societies that have been displaced and forced into low-productivity regions (Lee and DeVore, 1968). However, what constitutes productive land for foragers and non-foragers is not the same, and regardless, the lands inhabited by warm-climate foragers have higher net primary productivity than those occupied by non-foragers (Porter and Marlowe, 2007).

Some scholars have criticised the concept of a ‘hunter-gatherer way of life’ altogether, highlighting the substantial inter-population variation that exists (Bailey and Milner, 2002). There is certainly

variability across numerous domains, especially when comparing simple and complex hunter-gatherers. Nevertheless, there are many shared features among simple hunter-gatherers that distinguish them from societies practising other forms of subsistence. A lack of food storage, egalitarianism and high mobility are uniform features of simple hunter-gatherers (Woodburn, 1982). Given that the distribution of food, social hierarchy and foraging mobility are considered by many ethologists as the most important selective pressures acting on primate behaviour (Wrangham, 1980), the shared features listed above are certainly sufficient to qualify the (simple) hunter-gatherer way of life as a meaningful construct.

## 5.2.2 Is Human Psychology Subject to Evolutionary Mismatch?

There is also disagreement between scholars of the evolutionary social sciences regarding the occurrence and extent of mismatch in the domains of cognition and behaviour. Evolutionary psychologists argue in favour, asserting that inflexible genetic mechanisms underpin psychological processes; these mechanisms are thus subject to the aforementioned adaptive lags, resulting in a mismatch between modernity and our *Stone Age minds* (Barkow et al., 1992). Conversely, human behavioural ecologists take an adaptationist stance and make the *behavioural and phenotypic gambits* (Nettle et al., 2013). That is to say, they emphasise the plasticity of behaviour, assuming it can respond flexibly to environmental changes unconstrained by any underlying neurological mechanisms or genetic architecture. Finally, cultural evolutionists emphasise the importance of social learning as the foundation of behaviour (Henrich and McElreath, 2003). This perspective assumes that behavioural mismatch, as defined here, is less important since learned behaviour can change multiple times even within one lifetime, permitting far more rapid adaptation than genetic selection. In reality, these are not truly mutually exclusive approaches, but rather differences in emphasis. Distinct cognitive and behavioural processes unequivocally differ in the extent to which they are genetically, epigenetically or culturally determined. Therefore, to rule out the utility of any one approach or to assume that mismatch is a categorically redundant concept would certainly

diminish the explanatory power of the evolutionary perspective.

Evolutionary psychologists have also been criticised for generating *just-so stories* (i.e. reverse engineering explanations for a given psychological feature based on unsubstantiated assumptions about its EEA and, in turn, the nature of mismatch) (Richardson, 2007). It is true that some of the literature presents a picture of hunter-gatherer life that seems to be a caricature of 'tribal' peoples and has no anthropological or archaeological evidence base. However, by premising our discussion on our own experience of fieldwork with hunter-gatherers as well as the wider ethnographic literature, this chapter does not suffer from this flaw. In fact, we hope it serves to correct any inaccurate perceptions of foraging societies that readers may have acquired elsewhere.

## 5.3 Existing Research

Psychiatric epidemiological research with hunter-gatherer populations is limited to a handful of studies. There are equally few non-medical studies examining subjective well-being and happiness (see Section 5.3.2). In this section, we provide a detailed review of these studies, interpret them within a mismatch framework and summarise the methods employed that may be of use to researchers planning to conduct similar work in the future.

### 5.3.1 Mental Illness in Contemporary Hunter-Gatherers

A study of PPD among the Hadza of Tanzania represents the most direct application of a clinical screening tool from Western psychiatry to a hunter-gatherer population (Herlosky et al., 2020). Herlosky and colleagues administered the Edinburgh Postnatal Depression Scale (EPDS) – which has been validated cross-culturally and used in rural settings (January and Chimbari, 2018; Small et al., 2007) – to 23 Hadza women with infants less than a year old. A total of 52% of the Hadza women scored above 12, which is commonly used as the threshold for probable depression. These rates are very high in comparison with industrialised populations: PPD prevalence rates average approximately 19% in low- and

middle-income countries (Woody et al., 2017). Complementary data indicated among the Hadza that the EPDS score was not associated with any measures of social support, including presence of a husband, which have been identified as major risk factors in WEIRD populations (Boyce, 2003). This may reflect the fact that in hunter-gatherer societies everyone has adequate access to social support derived from community living (see Section 5.4.1).

Several responses alluded to anxieties relating to offspring health, which is understandable given the Hadza experience an infant mortality rate of approximately 21% (Blurton-Jones et al., 1992) and that rates among hunter-gatherers tend to range between 20% and 35% (Hewlett, 1991). These findings highlight that even when mismatches do not increase the prevalence of a given mental disorder, they may affect the relevant risk factors. In the case of PPD, among WEIRD populations a lack of social support may have become a novel risk factor, whereas the high infant mortality rates experienced by ancestral populations are no longer primary drivers of maternal anxiety. Alternatively, PPD, whilst distressing, may have evolved as an adaptation to focus maternal behaviour on mitigating the high infant mortality risk faced by our ancestors. Despite the low risk in contemporary industrialised settings, the condition persists due to adaptive lag (i.e. it is an environmental mismatch).

Another study examined the distribution of dopamine receptor gene D4 (*DRD4*) variants among South Amerindian populations with a recent history of either agricultural or foraging subsistence (Tovo-Rodrigues et al., 2010). The 7R variant has been associated with novelty-seeking, impulsivity and hyperactivity (Tovo-Rodrigues et al., 2010). Accordingly, in a meta-analytic review of candidate genes associated with childhood ADHD, this polymorphism had the largest association of all genes examined (Gizer et al., 2009). Interestingly, in the study of South Amerindian populations, the frequency of the 7R allele at this locus averaged 0.58 across the populations with a recent history of hunting and gathering compared to 0.48 across recent farmers (Tovo-Rodrigues et al., 2010). Moreover, genetic analyses indicate that the 7R allele has undergone strong positive selection since its origin approximately 40,000 years ago, which also coincides with a period of major human expansion (Ding et al., 2002).

One interpretation of these findings is that personality and behavioural traits such as novelty-seeking and hyperactivity, which are now considered symptoms of ADHD, provided fitness-related benefits in a hunter-gatherer context. They may have encouraged nomadic foragers to explore new environments and, in turn, facilitated more effective resource exploitation. However, following the Neolithic Revolution, as sedentism and resource intensification became the norm, such traits were no longer adaptive. Hyperactivity and a reduced ability to pay attention to the same thing for extended periods are particularly mismatched to modern classroom environments. Therefore, ADHD fits neatly into the category of environmental mismatch; we continue this discussion in Section 5.4.2.1.

The final two epidemiological studies examined the prevalence and correlates of major depressive disorder (MDD) among the Tsimane of lowland Bolivia. The Tsimane are usually categorised as forager-horticulturalists rather than hunter-gatherers, since approximately two-thirds of their diet is derived from non-intensive farming and only a third is from foraging (Stieglitz et al., 2015b). Nevertheless, given their high physical activity levels, small community residences and relatively egalitarian political organisation, these studies still offer insight into mismatch.

Stieglitz and colleagues tested the host-defence hypothesis of depression, which proposes that depression is a 'sickness behaviour' and part of a coordinated response to infection (Stieglitz et al., 2015b). Depressive symptoms such as hypersomnia, social withdrawal, fatigue and anhedonia facilitate recovery from infection or tissue injury by promoting the reallocation of energy to immune function (Raison and Miller, 2012). Stieglitz and colleagues (2015b) examined associations between depressive symptoms and immune biomarkers and responses among the Tsimane ( $n = 249$ ). A structured interview examining the emotional, cognitive and somatic symptoms of depression was constructed by adapting items from Beck's Depression Inventory, Hamilton's Depression Rating Scale and the Center for Epidemiologic Studies Depression Scale. A total of 10% of the sample were classified as depressed, of which 90%, 86% and 84% experienced emotional, somatic and cognitive symptoms, respectively.

A 10% point-prevalence of depression is relatively low in comparison to most South American

countries (mean = 20.6%) (Lim et al., 2018). Nevertheless, this non-trivial prevalence highlights that the high physical activity levels, community living and egalitarianism characteristic of foraging life are not sufficient to eliminate depression. This is to be expected if one driver of depression is in fact infection, as proposed by the host-defence hypothesis and supported by this study's subsequent analysis. Baseline concentrations of tumour necrosis factor alpha (TNF- $\alpha$ ), interleukin-1 beta (IL-1 $\beta$ ), interleukin-6 (IL-6) and C-reactive protein (CRP) were the immune biomarkers measured. Additionally, the pro-inflammatory cytokine responses of the first three of these to *ex vivo* antigen stimulation were examined. Across each domain of depressive symptoms – emotional, somatic and cognitive – associations with immune activation at baseline were found; and consistent with the hypothesis, the somatic symptoms showed the strongest relationship with antigen stimulation.

Another study examined other predictors of Tsimane depression scores using the same scale (Stieglitz et al., 2015a). Stieglitz and colleagues' productive value hypothesis posits that depression may occur when an individual's ability to produce fitness-enhancing resources for self and kin is reduced. This may explain why feeling burdensome in old age and unemployment in general are major predictors of depression in WEIRD societies (Liang et al., 2001; McGee, 2015). Similarly, among the Tsimane, lower functional ability – measured using modified exercises from the MacArthur Studies of Successful Aging – and reduced involvement in subsistence were associated with high depression scores. However, there was no association between higher scores and older age.

This may reflect a generalised difference between foraging and WEIRD societies, which is driven by others' perceptions and self-perceptions of elder members of the community and their value. In WEIRD contexts, the pace of technological change is now so fast that in many industries an individual's skill base becomes redundant quickly, and older members of society do not participate in the workforce at all. Conversely, in foraging societies, the contribution of the elderly is irreplaceable due to the extensive ecological knowledge accumulated over the life course. For instance, Hadza women's foraging productivity increases continuously and into old age because

identifying where to find carbohydrate-rich tubers is an experience-dependent skill (Kaplan et al., 2000). This vital contribution of elderly women has been proposed as a leading driver of human longevity and our extended post-reproductive lifespan, since it allowed elderly hunter-gatherer women to substantially enhance the survival prospects of younger generations (Hawkes, 2003). Similarly, in many hunting and gathering societies elders contribute traditional medical knowledge. We conducted a study with the BaYaka hunter-gatherers residing in the rainforests of northern Congo and found participants in the oldest age category (45+) had the greatest knowledge of medicinal plants (Salali et al., 2016). Therefore, old-age depression may be a form of phenotypic mismatch caused by the productive redundancy among the elderly in WEIRD societies.

The findings of these studies make clear that mental disorders, as we conceptualise and define them clinically, do occur among hunter-gatherers, highlighting that the romantic notions of ancestral utopias pervading popular culture should be discarded. This does not negate the explanatory value of mismatch, and the exiting studies discussed have already offered some intriguing insights. The prevalence of MDD, especially among the elderly, may have been lower in foraging societies and principally driven by infection rather than the common risk factors in industrialised contexts such as social isolation, low physical activity levels and unemployment. In contrast, the prevalence of PPD may have actually been higher among hunter-gatherers due to considerable infant mortality but is now redundant in WEIRD societies and only persists due to adaptive lag. Similarly, genes contributing to ADHD may have encouraged adaptive exploration and novelty-seeking among ancestral foragers, but such behaviours are dysfunctional in the context of modern education systems. Based on this work, public health scholars may test novel interventions for improving psychiatric outcomes in industrialised societies; we consider potential avenues in Section 5.5.

### 5.3.2 Happiness and Subjective Well-Being among Hunter-Gatherers

Two recent studies have examined happiness in hunter-gatherers, both of which suggest foragers have relatively high subjective psychological well-being. The first examined scores on items from

the Subjective Happiness Scale that address generalised happiness on a seven-point Likert scale (Frackowiak et al., 2020). The Hadza ( $n = 145$ ) scored 1.28 points higher than the Polish respondents ( $n = 156$ ). Moreover, the Hadza score of 5.83 is significantly higher than scores from all 12 industrialised societies where the same scale has been previously applied. There was also a significant decline in happiness among older Polish participants, whereas age had no effect among the Hadza, offering further support to the relationship between mood and old age discussed in Section 5.3.1.

Another study examined subjective reports of general well-being (Reyes-Garcia et al., 2021). The following single question was asked: ‘Taking everything into consideration would you say your life is . . .’ Responses were on a Likert scale from 1 (very bad) to 5 (very good). Participants were from three populations: the Baka, Penan and Tsimane. The Baka and Penan are hunter-gatherers residing in the forests of Cameroon and Brunei, respectively. Good (3) was the modal response in all three populations. The authors also note that participants tended to provide justifications, usually related to health, for low scores, but were less likely to provide reasons for high scores. They interpret this as moderate happiness being the baseline state in these societies such that respondents only felt compelled to justify sadness, not happiness.

The studies reviewed in this section suggest that moderately positive life satisfaction may be the baseline state among foragers, and their self-reported happiness is higher than those living in industrialised societies. Moreover, the prevalence of maladaptive mental pathologies appears to be lower among hunter-gatherers. In the next section, we outline key differences between foraging and WEIRD lifestyles that may be responsible for these trends and provide preliminary hypotheses to direct future research.

## 5.4 Differences between Hunter-Gatherer Life and Modernity with Implications for Mental Health

### 5.4.1 Social Organisation

#### 5.4.1.1 Social Structure and Community Living

Simple hunter-gatherers live in multi-household camps, with an average camp size of 37.5

individuals (Marlowe, 2005) (see Figure 5.1). The composition of each household tends to resemble a nuclear family, though it is not uncommon for some extended family members such as a grandparent to co-reside in the same household; most households have five to six residents (Dyble et al., 2016). A common misconception is that camps are composed only of closely related individuals. In fact, the genetic relatedness between adult camp mates is low; from the perspective of the average adult resident, only 7% of co-resident adults are close kin (siblings or parents) and only 25% are distant kin ( $r \geq 0.03125$ , equivalent to third cousins) (Hill et al., 2011).

To understand the tight relationships between mental health and sociality, it is necessary to consider the *ultimate* drivers of the social organisation outlined above. In comparison with other primates, our species has traditionally occupied a high-risk foraging niche. Chimpanzee diets are composed of approximately 95% predictable and easy-to-collect foods such as leaves and fruits; in contrast, hunter-gatherers rely on unpredictable resources, which require both high skill and good luck to obtain (Kaplan et al., 2000). For instance, in some foraging societies, successful acquisition of meat occurs on fewer than 20% of hunting trips (Biesele and Barclay, 2001). However, when it does occur, it produces large nutrient-dense food packages, which provide more meat than the hunter’s household can consume before it rots. This diet drives hunter-gatherer group living because on days when one hunter is successful they can share meat with those lacking food at a low cost; this donation will then be reciprocated and provide a large benefit when the same hunter is unsuccessful (Dyble et al., 2016). For instance, without food sharing, isolated Ache households would have less than 1,000 kcal/person on approximately 30% of days, but with food sharing, this figure drops to 3% of days (Kaplan et al., 1990); and within BaYaka camps, individuals with larger social networks have a higher body mass index and greater fertility (Chaudhary et al., 2016).

Thus, for our ancestors, social networks were a matter of life and death, group living was the norm and social isolation was rare, carrying fatal risks. In turn, psychological mechanisms promoting the maintenance of social relationships have been heavily favoured by natural selection. Social



**Figure 5.1** A BaYaka camp situated in the rainforest of northern Congo (credit: Nikhil Chaudhary)



exclusion shares the neural underpinnings of physical pain, altering activity in the dorsal anterior cingulate cortex and the anterior insula (Eisenberger, 2012). In combination with changes in affect, such as loneliness, these proximate mechanisms have evolved as a kind of behavioural homeostasis, producing an aversive and corrective response to isolation. Such is the magnitude of our evolved psychological dependence on social interaction that, even when surrounded by individuals who have committed the most heinous crimes, solitary confinement for more than 15 days is considered psychological torture by the United Nations (2015).

In contrast to foragers, social isolation is common among members of WEIRD societies. They rarely live in close proximity to any natal kin and often have no relationships with extended kin and their friendships are not characterised by the same commitment or frequency of interaction as in foragers. We suspect that the driver of this decline in high-quality social support networks relates to changes in subsistence interdependence. Hunter-gatherers have obligate group living due to their risky foraging niche and requirement for daily food sharing and cooperation. At the other end of the spectrum, those participating in market economies usually have reliable and predictable access to income and nutrition and engage in specialised individual-based labour tasks, shrinking their residential and high-quality networks to the nuclear family.

This enormous increase in social isolation has likely resulted in overexpression of the aforementioned aversive psychological responses. Loneliness is associated with increased stress, anxiety and hypervigilance, partially mediated via heightened cortisol levels (Hawkey and Cacioppo, 2010; Steptoe et al., 2004). Due to the rarity and substantial danger associated with isolation for our ancestors, such considerable responses were acute, appropriate and served an important function. However, given the high frequency and low danger of isolation in industrialised societies, they can now be considered pathological and a form of environmental mismatch. Moreover, chronic loneliness – affecting 15–30% of those living in economically developed populations (Hawkey and Cacioppo, 2010) – results in overstimulation of these psychological responses to isolation, representing a form of phenotypic mismatch. Correspondingly, social

isolation is associated with a vast number of psychiatric problems, including increased risk of personality disorders, psychosis, MDD, PPD, Alzheimer's disease and suicide (Hawkey and Cacioppo, 2010; Leigh-Hunt et al., 2017).

Beyond the size and quality of social networks, their structure among hunter-gatherers is more conducive to mental well-being relative to WEIRD societies. Being part of a community – a social network, often with some shared goal or interest, in which one's social partners are themselves social partners with one another – provides a sense of belonging, purpose and mental well-being (Tajfel and Turner, 2019). Spiritual communities in particular create a strong sense of group identity via ritual practices that bond participants. It is no coincidence that across the world, from football fans to devout members of the Abrahamic religions, group-based rituals share the same highly conserved ingredients: synchronous chanting and movement. These synchronous activities have been shown to lower cortisol and increase oxytocin levels, to stimulate the release of beta-endorphins and to increase trust, entitativity and cooperation among group members (Beck et al., 2000; Fischer et al., 2013; Pearce et al., 2015; also see Chapter 13 of this volume). Such rituals were likely selected via cultural evolution since they enhanced the functioning and resilience of ancestral groups, which were so heavily dependent on cooperation and group cohesion.

Our experience of living with the BaYaka highlighted the fundamental importance of ritual in building community. The BaYaka practice *massana*. These are rituals comprised polyphonic singing, dancing and synchronous swaying and clapping (see Figure 5.2), which *all* camp members – from infants to the elderly – are present for. They have a spiritual focus, and each *massana* is associated with a particular *mokondi* – spirit of the forest – and aims to achieve some mutual goal such as bringing fortune in an upcoming hunt or ensuring the successful passing of a recently deceased individual. *Massana* can go on for days and sometimes stimulate trance-like states among participants. In contrast, ritual engagement in WEIRD populations has declined rapidly. For instance, in the UK, less than 1% of the population attends church on a weekly basis, of which a third are over the age of 70 (Church of England Research and Statistics 2019).



**Figure 5.2** BaYaka women dancing together during *Ngoku massana* (credit: Nikhil Chaudhary)

The void of spiritual-based communities appears to have drastic consequences for mental well-being. A study of completed suicides in New York found that the odds of dying by suicide were six times higher for individuals not engaged in any form of religious congregation (Duberstein et al., 2004). Such insights offer unintuitive remedies to the phenotypic mismatch resulting from an absence of ritual practice. Further work is required, but one study examined the outcomes of a charity programme in which individuals with chronic mental illness or issues with substance abuse participated in weekly choir groups (i.e. synchronous singing) (Dingle et al., 2004). Participant responses were overwhelmingly positive and included reports of feeling more positive, release from anxiety and worry, increased self-esteem and aiding in reducing the consumption of alcohol and methadone.

#### 5.4.1.2 Egalitarianism

Another key impact of the hunter-gatherer foraging niche on social organisation is the absence of dominance hierarchies. Even the households with the best hunters rely heavily on food sharing to secure stable access to nutrition. This universal interdependence within foraging societies means that dominant behaviour is not a viable behavioural strategy. As such, hunter-gatherers are characterised by the *egalitarian syndrome*: consensus-based decision-making, no formal social ranks, an emphasis on autonomy, rejection of self-aggrandising behaviour and very weak notions of personal property (Woodburn, 1982). This ethos is enforced via *reverse hierarchy*, whereby any individual attempts at authoritarian behaviour are rebutted by a coalition of all other camp members via *levelling mechanisms* such as ridicule, ostracism and, in some cases, violence (Boehm et al., 1993). This value on social equality manifests in intriguing ways; for instance, if a hunter returns to camp with meat, they will speak in a self-deprecating manner about their kill or abilities. If they do not, others will do this for them: ‘When a young man kills much meat, he comes to think of himself as a big man, and he thinks of the rest of us as his inferiors. We can’t accept this. We refuse one who boasts, for someday his pride will make him kill somebody. So we always speak of his meat as worthless. In this way we cool his heart and make him gentle’ (Lee, 1969: 4).

Interdependence and the absence of storage produce both economic and social equality within foraging communities. However, in post-Neolithic societies, once food storage mechanisms had developed, the risk and concomitant obligate cooperation encountered by foragers were eliminated. Kin groups differed in their ownership of land and livestock and accumulated heritable wealth, and the emerging dependence of the poor on the rich translated this economic inequality into social inequality. These remain rife in large-scale nation-states today: the income held by the richest 10% of a nation reaches 30.2% (USA) in the Western world and 51.8% (Namibia) elsewhere (Roser and Ortiz-Ospina, 2013). Social classes pervade the industrialised world, from those that are based purely on wealth to more culturally entrenched and inflexible institutions such as the Indian caste system. For the majority of society, having to accept an inferior economic and social status to the elite is a profound mismatch when contrasted with the egalitarianism of foraging communities.

Many public health scholars have highlighted the explanatory power of inequality for understanding variation in the prevalence of mental disorders across high-income countries, and there is a strong correlation ( $r = 0.73$ ) between these two variables (Pickett and Wilkinson, 2008). It seems that one’s relative social standing and wealth have much greater impacts on mental health than one’s absolute economic circumstances. This comparison-based system of affect determination is intuitive from an evolutionary perspective since competition is the fundamental driver of natural selection: material wealth only translates into a competitive advantage in survival or reproduction if one has relatively more than other members of society. For instance, whilst gross domestic product (GDP) per capita is approximately 40% higher in the USA than Germany, the Gini index of inequality is also 30% higher (World Bank, 2020). Correspondingly, more than a quarter of residents living in the USA had experienced a mental health condition in the past year, while this proportion is less than 10% in Germany (Pickett and Wilkinson, 2008).

Associations with inequality are particularly high for anxiety and impulse control disorders (Pickett and Wilkinson, 2008). This is intuitive from the evolutionary perspective: those at the bottom of the economic and social ladder are

likely to engage in risky and impulsive behaviours since they have much to gain and little to lose. They are also likely to experience stress in order to motivate such ‘corrective’ behaviours. Conversely, an evolved anxiety response is experienced by those at the top of the ladder, who must be hypervigilant towards others who threaten their position. Indeed, there is strong empirical evidence for the relationship between inequality, crime rates and violence across industrialised populations (Kelly, 2000). Stress responses to hierarchical positions are phylogenetically conserved, being suggestive of deep evolutionary roots. For instance, among male savannah baboons, an inverse relationship between hierarchical position and faecal glucocorticoid levels was found (Gesquiere et al., 2011). The exception to this trend was the alpha male, who had the highest glucocorticoid levels of all males in the group; his exceptionally high stress levels were likely induced by the constant threat and frequent attempts to usurp his position.

In contrast to non-human primate and post-Neolithic human societies, the absence of economic and social inequality among foragers, who do not accumulate wealth and are politically egalitarian, likely removes inequality as a potential driver of mental health problems. Accordingly, in a study of Hadza women, no relationship was found between ‘social status’ and chronic stress proxied by cortisol concentrations in hair (Fedurek et al., 2020). In fact, the authors highlighted their difficulty in identifying any proxies for social status due to the strong egalitarianism of the Hadza, and finally they used interviews to measure popularity and foraging reputation.

Some studies also point to a raised risk of psychotic disorders as inequality increases (Kirkbride et al., 2014). Paranoid schizophrenia and persecutory delusions may represent a phenotypic mismatch caused by overstimulation of a threat-detection response to resource competition and associated hostile local social environments, which were likely less prevalent in egalitarian ancestral communities. Similarly, a recent meta-analysis identified an association between inequality and depressive disorders (Ribeiro et al., 2017). One evolutionary hypothesis of depression is that it is an ancient adaptation to low status in dominance hierarchies. Symptoms such as social withdrawal, low self-

esteem, feelings of shame, anhedonia and fatigue may have functioned to promote submission and discourage aggression towards more dominant individuals; some analogous behaviours such as avoidance of eye contact and social interaction with dominants occur in low-status baboons (Price, 1967). Price describes this hierarchy-driven behavioural syndrome as a ‘vestigial and useless heirloom in man’ (1967: 246). Indeed, among hunter-gatherers, this depressive psychology would not have been stimulated since hierarchies were absent altogether, and thus subordinate behaviour was never required. However, following the re-emergence of social status and class over the last 10,000 years, depression induced by low status may have returned as a novel risk factor for our species.

## 5.4.2 Childhood

Infancy and early childhood represent critical periods in which individual psychology is calibrated to prevailing socioecological conditions (Bowlby, 1969), and therefore they evolved as the periods of greatest neural plasticity (see also Chapters 14 and 15). Whilst increased stress reactivity may be an adaptive response to harsh environments, chronic exposure to psychosocial stressors in early life results in dysregulation of the hypothalamic–pituitary–adrenal axis and substantially increases the risk of an extensive range of mental disorders (McEwen, 2003). The childhood experiences of WEIRD and hunter-gatherer children differ markedly. The following sections describe these differences and consider their implications for mental health.

### 5.4.2.1 Autonomy, Exploration, Social Learning and Play

According to embodied capital theory, the long period of human childhood evolved to allow the necessary time to develop the complex skills required for our species’ foraging niche (Kaplan et al., 2000). During childhood, foragers learn subsistence skills via exploration, practice and play.

Hunter-gatherer societies place heavy emphasis on individual autonomy (see Section 5.4.1.2), and this extends to children too. Parents rarely interfere with children’s activities even when they play with machetes or burning embers (see Figure 5.3; see also [www.youtube.com/watch?](http://www.youtube.com/watch?)



**Figure 5.3** A BaYaka infant and child practicing using machetes (credit: Nikhil Chaudhary)

[v=drJNIG0o0II](#) for footage from our field site). Our analysis of the ontogeny of BaYaka learning demonstrated that from infancy to early childhood learning occurs principally via imitation; after weaning, children are free to explore their surroundings and learning occurs in the context of playgroups and through practice (Salali et al., 2019).

The autonomous nature of childhood in hunter-gatherers contrasts with a WEIRD childhood, most of which is spent in formal education and supervised ‘helicopter parenting’. In our observations, teaching accounted for only 6% of BaYaka learning events (Salali et al., 2019), and unlike in Western education, hunter-gatherers do not often give direct instructions when teaching. Instead, they create a learning opportunity, like providing a tool, and monitor the children’s actions without interfering; children then adjust their behaviour according to the feedback they receive (Hewlett and Roulette, 2016; Salali et al., 2019). Therefore, teaching is more based on practice and feedback than in WEIRD cultures. For example, teaching via verbal explanation occurred only six times in the 10-hour videotapes of Aka (from the Central African Republic) caregiver–infant interactions (Hewlett and Roulette, 2016). Peer teaching is also common, and studies of Hadza and BaYaka children showed that child–child teaching represented 75% of observed teaching episodes (Lew-Levy et al., 2020).

Learning via play is much more common than teaching in the early childhoods of hunter-gatherers. After weaning, children start spending more time in mixed-aged playgroups, and field observations suggest that work-themed play facilitates the acquisition of subsistence skills based on gendered division of labour, social norms via supervision of younger members of the playgroup and cultural values during other forms of play (Boyette, 2016; Salali et al., 2019). Thus, in contrast to the dichotomous relationship of lesson time and play time in WEIRD schools, learning and play in hunter-gatherers are two sides of the same coin. Moreover, hunter-gatherer play is not competitive and fosters the collaborative interaction that is essential for successful subsistence (Boyette, 2016).

According to the Good Childhood Report (The Children’s Society, 2020), declines in children’s overall happiness with life and school are partially explained by increased fear of failure. WEIRD education is dominated by continuous grading, high-stakes concentrated examination periods, class separation based on abilities, teacher-led learning and punishment. This system, which encourages competition and is highly pressured, must negatively impact children’s self-esteem and stimulate fear of failure. In contrast, hunter-gatherer learning does not include any of these ingredients, and learning via play is fun rather than pressured, ‘assessed’ incrementally and informally, peer to peer and, above all, inherently cooperative rather than competitive. It is therefore unsurprising that learning, which many argue has been the driving selective force for human brain expansion (Hermann et al., 2007), can generate phenotypic mismatch in children.

Given that an extended childhood likely evolved for developing and practicing subsistence skills (Kaplan et al., 2000), for most of our evolutionary history, a ‘successful’ childhood was characterised by high levels of physical activity and exploration. However, these learning styles are founded upon behaviours that are considered pathological in modern classroom environments and can result in ADHD diagnoses. Several of the Diagnostic and Statistical Manual of Mental Disorders, 5th Edition (DSM-5) diagnostic criteria explicitly refer to the disruptive effects of inattention in the context of schooling, and their associations with poor academic attainment are

well established (Loe and Feldman, 2007). If ADHD is an environmental mismatch, improved outcomes may be possible via altering modern pedagogy. Clinicians have highlighted that young people with an ADHD diagnosis report the beneficial effects of physical activity intervals between academic classes (Swanepoel et al., 2017). Moreover, a recent meta-analysis of physical activity interventions ranging from swimming to climbing identified positive effects on all examined domains of executive function – inhibition, shifting, working memory and attention – among those with an ADHD diagnosis (Welsch et al., 2021).

#### 5.4.2.2 Child-Rearing Practices

Although hunter-gatherer caregivers have a more *laissez-faire* approach to child-rearing, this does not mean that children are left alone. On the contrary, infants and young children are looked after by multiple caregivers, both parents and others (alloparents) (Apicella and Crittenden, 2015). Ethnographic observations have revealed common child-rearing features across several hunter-gatherer groups. These are on-demand breastfeeding, weaning between the ages of two and three, care from multiple individuals, close physical contact with caregivers and co-sleeping (Apicella and Crittenden, 2015).

Our focal sampling observations of BaYaka infants show that over the 12 daylight hours they are held for 4 hours, receive some form of direct care for 7 hours and are alone for less than half an hour, and crying is responded to promptly via singing, carrying and breastfeeding (Chaudhary, unpublished data, 2014). This indulgent and responsive caregiving likely aids in the development of secure attachment (Konner, 2016). ‘Attachment’ refers to the bond that develops between an infant and caregiver during the first years of life, and a secure attachment – where the infant seeks out the attachment figure in times of distress and feels comfortable to explore the environment in a caregiver’s presence – is considered crucial for healthy development (Ainsworth, 1978).

In WEIRD societies where nuclear families prevail, infants usually form attachments with one or two principal caregivers. In contrast, hunter-gatherer children have extensive caregiver networks. For example, among the Efe of the Democratic Republic of the Congo, infants are

in physical contact with an alloparent for 60% of the day, interact with 14 alloparents per day, are passed among caregivers 8 times per hour and are nursed by multiple women (Ivey, 2000; Tronick et al., 1987).

Mismatches in caregiving may affect the mental health of infants. Breastfeeding patterns in WEIRD societies are markedly different from those in hunter-gatherer societies. In the UK, only 23% of mothers continue breastfeeding until nine months (NHS Digital, 2012), whereas this is guaranteed among hunter-gatherers. Importantly, endocrine processes stimulated by breastfeeding relieve anxiety symptoms (Hahn-Holbrook and Haselton, 2014). Colic is less common among hunter-gatherers (Lummaa et al., 1998), indicative of lower psychosocial stress. It is hypothesised that given the constant physical proximity between hunter-gatherer and primate infants and their caregivers, infant crying literally functions as a ‘cry for help’ upon separation from caregivers. The substantially lower time in physical contact, especially skin-to-skin contact and co-sleeping, and higher frequency of being left alone among WEIRD infants represent pronounced mismatches that we believe are responsible for considerable infant distress.

The large alloparenting networks among foragers also permit constant physical proximity and continuous responsiveness to infants even when parents are occupied with other activities. Moreover, having multiple attachment figures buffers the negative impacts of having an insecure mother–infant relationship (van Ijzendoorn et al., 1992). Given the associations between unavailable or insensitive attachment figures in early life and a vast array of mental illnesses – depression, anxiety, post-traumatic stress disorder, obsessive-compulsive disorder, eating disorders, schizophrenia and suicidal tendencies (Mikulincer and Shaver, 2012) – we cannot overstate our expectation that hunter-gatherer childcare reduces psychiatric risk, or rather WEIRD childcare increases this risk. We strongly encourage further research into the long-term effects of alloparenting and highly sensitive caregiving on hunter-gatherer mental health. We expect that the benefits also extend to caregivers. For instance, breastfeeding and skin-to-skin contact are associated with lower incidence rates of maternal PPD (Hahn-Holbrook and Haselton, 2014; Mörelius et al., 2015). Moreover, alloparental support reduces the

pressure and burden placed on parents; in our analysis of childcare in Agta and BaYaka foragers, only approximately 30% of infant and young children's close-proximity interactions were with their parents (Chaudhary, unpublished data, 2014).

### 5.4.3 Time Perspective and Future Orientation

*Immediate-return* (simple) hunter-gatherers acquire resources on a daily basis, consume them immediately and do not have food storage systems (Woodburn, 1982). Thus, long-term planning is largely redundant for foragers. For instance, we played a *future-discounting* game in which we asked the BaYaka and a neighbouring farmer population whether they would like one food item now or five tomorrow (Salali and Migliano, 2015). Approximately 80% of the BaYaka chose the one item today option compared with 40% of the farmers, who are presumably more accustomed to future planning seasons in advance. We expect that future orientation is largely determined by the timescales of resource acquisition and storage. WEIRD societies are at the extreme end of this spectrum: we frequently predict the impacts that our current choices will have on our lives decades later. Career trajectories are planned to optimise resource accumulation over a period of approximately 50 years, and considerable wealth is saved over similar timescales. Highly valued personal goals also tend to be realised over extended periods.

Emotions function as a behavioural motivation system; accordingly, our mood is heavily impacted by progress towards current goals rather than one's overall life situation (Nesse, 2004). When progress halts or reverses despite continued effort, low mood may be an adaptive driver of termination of this effort. However, in WEIRD societies, it can be very difficult to abort goals that have been planned for and worked on over extended periods. Continually attempting to achieve goals over extended periods without seeing any progress has been hypothesised as a major driver of depression in industrialised societies (Nesse, 2004). Similarly, anxiety is an emotional response that occurs in the anticipation of a future threat. Thus, the pronounced preoccupation with the future in WEIRD populations likely increases vulnerability to high levels of anxiety.

These differences between WEIRD and foraging societies in the timescales of resource acquisition and personal goals and, in turn, in time perspective represent a phenotypic mismatch, potentially contributing to mood disorders (Salali et al., 2021). In the West there has been growing interest in mindfulness practice, which encourages focusing on present experience rather than the future, which likely explains its well-established anxiety-reducing effects (Khorey et al., 2013). Increased mindfulness is also strongly associated with decreased intolerance of uncertainty, one of the largest predictors of anxiety (Salali et al., 2021). Priming experiments also suggest that time perspective may be highly flexible (Shevorykin et al., 2019); hence, therapies aiming to recalibrate it may be viable psychological treatments.

## 5.5 Future Directions and Conclusion

Here, we have outlined key mismatches in the domains of social organisation, child-rearing and timescales of goals and speculated about their impacts on mental health. Research testing these hypotheses is extremely scarce. We propose two key future directions for research: (1) epidemiological work testing whether the prevalence and severity of mental disorders are lower among hunter-gatherers; and (2) in such cases, identifying and quantifying the specific mismatches that may underpin this increased prevalence of mental disorders in WEIRD populations and trialling interventions that reduce these mismatches.

Epidemiological studies must consider cultural differences and the fact that most hunter-gatherers are illiterate with limited numeracy. Most psychological evaluations are done using established screening tools that often involve Likert scales or other forms of rating. From our own experience, asking the BaYaka to rate anything or about the frequency of a particular event is often met with confusion since these thinking styles are unfamiliar and unused in their culture. As such, tools from Western psychiatry must be adapted to ensure cultural appropriateness and comprehension. Balancing emic (culture-specific) with etic (universal) approaches is key; on the one hand, we aim to obtain comparable cross-cultural epidemiological data, while on the other, the expression and manifestation of emotions and mental illness (*idioms of distress*) vary across

cultures (Littlewood, 1990). For instance, in India, depressed and anxious patients frequently present with pain in the extremities and other bodily symptoms, but this is uncommon in the West (Desai and Chaturvedi, 2017). Similarly, methods of identifying symptoms must be culturally calibrated. For example, social withdrawal is an important diagnostic criterion for many mental disorders; however, hunter-gatherers co-reside with many camp mates and live in open dwellings; thus, operationalising 'social withdrawal' is difficult. One solution we have considered is examining whether any camp members are not participating in *massana* rituals, which are usually camp-wide activities; this is a more culturally appropriate measure (emic) of a universal diagnostic criterion (etic). Moreover, given the complexity and subjectivity of emotion, it is difficult enough for individuals to effectively communicate inner mental states even when speaking the same language. Therefore, substantial time must be committed to harnessing a nuanced understanding of emotion-related vocabulary.

Identifying which mismatches are responsible for the higher prevalence rates of mental disorders among WEIRD populations must be hypothesis-driven. One technique would be detailed characterisation of the differences between WEIRD and hunter-gatherer populations and then implementing interventions to minimise any mismatch. For instance, the study of depression among the Tsimane found no association with old age, a relationship that is common in WEIRD contexts, which the authors speculated is caused by the elderly's productive redundancy (Stieglitz et al., 2015a). Future research could trial the impact of resident participation in productive activities such as gardening and cooking on mental well-being within elderly care homes, or foster a platform whereby the elderly can share their accumulated

life experience and 'wisdom' with younger generations. Other promising avenues include examining how alternative education systems that foster exploration, peer learning and non-didactic teaching affect the educational attainment and distress of children with ADHD, as well as the prevalence of common mental health problems among students more generally. Data examining the long-term effects of replicating hunter-gatherer sensitive caregiving (i.e. breastfeeding on demand, co-sleeping, high responsiveness to crying and continuous proximity) would be invaluable. Additionally, studies examining the psychological well-being of individuals living in communes or 'intentional communities' will offer insight into the possibility of reducing mismatches in social organisation and support networks in modern society. Finally, engagement in synchrony-based community 'rituals' may be a particularly effective intervention for those experiencing chronic loneliness.

We hope that the descriptions of hunter-gatherer life and the speculations regarding their effects on mental health provided here will aid scholars in formulating and testing similar mismatch hypotheses. Like other fields of medicine, psychiatry has suffered somewhat from an emphasis on biochemical mechanisms and from neglect of upstream aetiology. Whilst the relationships between life circumstances and psychiatric health do receive some attention, expanding this approach to consider mismatches between industrialised and hunter-gatherer life will improve our understanding of *why* such relationships exist and will complement the heavy focus on the mechanistic *how*. Given the speed at which extant hunter-gatherer societies are becoming integrated into market economies, the window of opportunity to conduct this research is rapidly closing, and so this should be considered an urgent priority.

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