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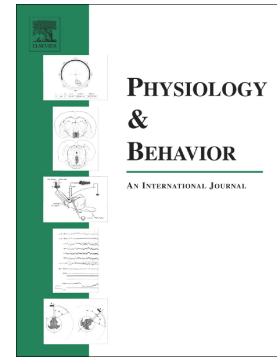
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Do humans still forage in an obesogenic environment? Mechanisms and implications for weight maintenance

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Abstract

Many people struggle to control their food intake and bodyweight. This is often interpreted as evidence that humans are generally predisposed to consume food when it is available, because adiposity offered insurance against the threat of starvation in our ancestral environment. In this paper we suggest that modern humans have actually inherited a far broader range of foraging skills that continue to influence our dietary behaviour. To evaluate this idea, we identify three challenges that would need to be addressed to achieve efficient foraging; (1) monitoring the 'procurement cost' of foods, (2) determining the energy content of foods, and (3) proactively adapting to perceived food insecurity. In each case, we review evidence drawn from controlled and observational studies of contemporary humans and conclude that psychological mechanisms that address these challenges are conserved. For contemporary humans who live in fast-paced obesogenic environments, this foraging 'toolkit' no longer serves the same function to which it was adapted, and in many cases, this leads to an increase in food intake. Understanding these forms of 'evolutionary mismatch' is important because it can provide a stronger theoretical basis for informed dietary interventions that leverage fundamental foraging goals rather than work against them.

Keywords: Food insecurity, hunter-gatherer, evolutionary mismatch, dietary restraint, energy balance, socioeconomic status

Highlights

- Humans are adapted as highly efficient foragers
- Modern humans have inherited a foraging ‘toolkit’ that still influences behaviour
- Foraging mechanisms often operate outside conscious awareness
- Mechanisms may no longer be adaptive and increase food intake
- Foraging strategies may undermine attempts to consciously restrict food intake

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1. Introduction

The recent increase in obesity reflects a transition to a dietary landscape in which food is abundant, especially energy dense [1, 2], and served in large portions [3]. However, the pursuit of industrial efficiency has also changed the way that humans obtain food. For around 90% of the ~1.8 million years that humans have existed, survival depended on the ability to forage - or to efficiently locate, acquire, and consume food. In this paper we consider specific psychological mechanisms that might have supported this capacity and, critically, whether they still influence the dietary behaviours of contemporary humans who struggle to resist temptation in an obesogenic environment.

2. Framing the question

On April 1st 2017, Dan Hannan, a conservative member of the European Parliament, told listeners of a BBC political panel programme, “I’m not sure there is an obesity epidemic.” “...it’s a consequence of choice it’s not a disease... it’s up to us as individuals...”, “...crazy that we should call upon the government because we are unable to say ‘no’ to our children or to ourselves...” This perspective is helpful, because it captures a widely held view - that overconsumption is largely a matter of personal preference. Numerous large-cohort studies suggest the converse – most people with obesity would like to lose weight and a large proportion are actively attempting to do so [4, 5]. However, conscious attempts to diet rarely lead to sustained and significant weight loss, even in clinical weight-loss interventions [6, 7]. In part, humans struggle because dietary restraint requires continuous cognitive effort [8], which is difficult to sustain alongside competing demands of a modern and sometimes fast-paced lifestyle (for a related discussion see [9]).

Restraining to lose weight is also historically unusual, in part, because it was probably difficult for an ancestral hunter-gatherer to consume enough food to become obese [10].

Indeed, and as is found in many other species, survival relied on highly efficient strategies. ‘Optimal foraging’ models assume that natural selection modifies feeding behaviours to achieve specific goals (*i.e.*, maximizing energy, minimizing starvation) while operating within specific constraints (*e.g.*, avoiding predation and minimizing violations of status hierarchy) [11]. Note that here we use the term ‘foraging’ to refer to this general capacity rather than a specific ability or activity, such as setting traps, or strategies to locate or hunt specific animals, fruits, and so on. Many species show a similar ability to make dietary choices that minimise ‘procurement cost’ [12] (or more precisely, impact on fitness), defined as the value of food as a function of costs associated with its acquisition. Human dietary behaviour is likely to have evolved in exactly the same way, which means that conscious food restriction (*i.e.*, dieting) might compete with highly engrained mechanisms that supported our historic capacity for efficient foraging and with biological and behavioural adaptations that protect against starvation [13].

Behavioural ecologists sometimes draw a useful distinction between proximate and ultimate explanations for behaviour [14, 15]. Ultimate explanations consider *why* a behaviour might benefit fitness, whereas proximate explanations refer to mechanisms (*how*) that enable this benefit to be realised. For example, the proximate reason why infants cry is because they feel distressed, whereas an ultimate explanation is that crying evolved because it increases fitness by offering protection from abandonment. Similarly, an ultimate explanation for eating is that it prevents starvation and reproductive failure, and proximate supporting mechanisms include the anticipated pleasure of consuming delicious food. Normally, proximate and ultimate ‘needs’ coincide (proximate needs serve ultimate objectives). However, when an environment changes rapidly, as is the case with the transition from relatively food insecure ancestral environments to obesogenic and fast-paced industrialized environments, then proximal and ultimate needs can become decoupled [16, 17]. Several influential explanations for obesity

are based on such ‘evolutionary mismatches’ [18, 19]. In particular, it is often argued that a basic dietary strategy of humans was to consume food (especially energy-rich food) when it was available, because this offered protection from future starvation. In this context, mismatch occurs because modern foods are now highly palatable and readily available, and because famine (in many cases) is highly unlikely. Our contention is that the foraging strategy of humans (as well as hominids) was probably much more complex than simply eating opportunistically and that, as in other species, it adapted over a very long period to optimise responses to a diverse range of concerns (*e.g.*, energy expenditure and predation) in order to achieve behavioural efficiency and to optimise energy balance (for a related point see [20]). This system would have required flexibility and an ability to navigate different types of costs and benefits, rather than relying on a single heuristic - to consume food whenever it is available. Therefore, when addressing broader questions about how ‘modern humans’ interact with their food environment (and associated sources of mismatch that might promote obesity), it is essential to determine whether proximate mechanisms that facilitated ancestral foraging are actually conserved and expressed. This is a challenging problem, not least because many of our responses to food occur outside conscious awareness (perhaps because they emerged before the development of human language).

To explore the idea that an ancestral foraging ‘tool kit’ still exists we adopt a two-stage strategy. First, we outline specific ‘dietary problems’ that human foragers are likely to have encountered. Then in the section that follows we explore proximate mechanisms that might be adapted to address these problems and consider whether they still impact the behaviour of modern humans, focusing on the control of food intake and how this might be compromised by the fast pace of a modern dietary lifestyles.

3. Three challenges for a hunter-gatherer

Given the relatively higher risk of food insecurity in our ancestral environments, humans would have had to manage an overarching priority of minimizing risk of starvation, which may conflict with modern attempts at dietary restriction. Proximally, this priority may be reflected by an implicit goal to satisfy an optimal calorie budget, which would have leveraged a diverse toolkit of adapted behavioural and psychological processes. Here we outline three broad and persistent challenges that foragers would have confronted across diverse environments (to be clear, these are not meant to be exhaustive).

Monitoring procurement cost

Hunter gatherers tend to spend long periods searching for food [10], which can be counted as a cost, both in energy expenditure and in the time that might be spent performing other important activities, such as caring for infants. Various sources suggest that early hominids were also heavily predated [21], stimulating a further pressure to limit periods during which this risk is present. Therefore, less time should be allocated to foraging when recent foraging has been successful or when the associated costs are high. Solving this problem is complex, but as a minimum requirement, mechanisms would be needed that monitor both recent encounters with food (including amount/quality) and accompanying perceived costs in energy expenditure.

Determining the energy value of foods

Assuming equal availability, a food that has an energy density of 2.0 kcal/g will require 50% less time in foraging than a food that is 1.0 kcal/g. Therefore, there is good reason to expect a strong selection pressure for humans (and other animals) to acquire the ability to identify the energy that can be liberated from different foods. Note that we have expressed this problem

as an ultimate need. The associated proximate mechanism might reflect a differentiation of value based on relative palatability, enjoyment, desirability, and so on.

Adapting to food insecurity

Humans with a very low BMI benefit from a reduced cost in energy expenditure. However, having a low BMI also increases the chances of starvation when food becomes insecure [22]. In response, many species maintain higher-than-minimum fat reserves and also increase their food intake in anticipation of actual food shortages [23, 24]. It is likely that humans also acquired the same capacity to respond to the stochasticity of food encounters. However, humans are also unusual because food is shared within groups of hunter-gatherers [25, 26], and probably during the Pleistocene [27]. Coexisting in close social networks offers protection from food insecurity because group members can forage for others who may be unable or unwilling to do so. However, it also promotes a need to monitor the social distribution of food and to conform to food taboos, which may be determined by status. Therefore, solutions to the problem of food insecurity are likely to incorporate monitoring of social group cohesion and status hierarchies.

4. Behavioural observations in modern humans

Having outlined three problems for hunter gatherers we now review evidence for potential proximate mechanisms that are adapted to address these challenges, and explore ways in which they might influence the behaviour and ultimately the weight management of modern humans. Each challenge is considered in turn.

Monitoring procurement cost

Estimating procurement cost requires continuous monitoring of both the amount of food ('food amount') recently acquired and the 'procurement effort' associated with its acquisition (cost = food amount/procurement effort, where effort is broadly defined as a combination of

risk, energy expenditure, time, and so on). Note that we use the term ‘acquisition’ recognising that this might incorporate both securing, processing, and eating food, which do not always occur around the same time. In relation to monitoring food amount, one solution might be to simply track subjective changes in appetite after consuming a meal (greater reductions in hunger = greater food energy). In this regard, memory processes are known to play an important role. For example, when food is delivered via an intra-gastric infusion (sensory cues are bypassed) the effect on hunger is greatly attenuated [28, 29]. This demonstrates that memory of the visual and orosensory features of food influence appetite long after a meal has terminated. Consistent with this interpretation, patients with severe anterograde amnesia experience little satiety and are observed consuming multiple meals in quick succession [30, 31].

In a broader conceptualisation of this process, Higgs has demonstrated that this ‘memory for recent eating’ is extremely reliable, that it can be manipulated [32], and that it is supported by a well-defined underlying neurobiology (for a review see [33]). It also operates outside conscious awareness (*i.e.*, without the need to form an explicit representation of a recent meal) [34]. Previously, some have speculated that this process works in combination with other physiological mechanisms merely to avoid the aversive effects of overconsumption or to provide additional inhibition of food intake in the interval between meals [34, 35]. Our suggestion is that it plays a more fundamental role because it is ideally suited to monitoring foraging outcomes (food amount) based on a record of recent encounters with food.

Consistent with this idea, ‘episodic memory’ is found to have a profound impact on foraging in other species [36] and, as with amnesic patients, rats with selective neuro-toxic hippocampal lesions show disrupted eating patterns [37] and increased food intake [38].

Several studies show that poor hippocampal function is also associated both with obesity and with deficits in spatial learning performance in animals [39]. One suggestion is that synaptic

plasticity is attenuated by the consumption of a diet rich in fats and sugars, which reduces brain-derived neurotrophic factor (BDNF) [40]. Typically, this process is framed as an impairment but it might also reflect a change in reliance on a monitoring process that becomes redundant when the environment provides an extreme surfeit of calories. Critically, reduced spatial memory performance has also been observed in obese humans [41] and also after acute exposure to an especially energy-rich diet [42], which indicates that a range of experiences are encoded, including those associated both with eating and remembering the location of foods. The second component of procurement cost relates to the monitoring of procurement effort (separate from other costs associated with finding water, procreation, and so on). Here interesting parallels are found with the same cognitive processes that might monitor food amount. For example, memory function and BDNF are also reduced in individuals who are less active and improvements are observed following an exercise intervention [43]. In relation to memory for recent eating (food amount), there is also strong evidence that cognitive distractors, which may disrupt monitoring and memory for eating, impact food intake and appetite (for a review see [35]). For example, participants who eat while distracted by a computer game experience greater hunger at the end of a fixed meal [44] and, importantly, distraction also increases the amount of food consumed at a subsequent meal [45, 46]. Similarly, there is strong evidence that cognitive distraction increases levels of physical activity [47-49] and again, one suggestion is that this is caused by a limited attentional capacity [50, 51], which impacts episodic-memory encoding.

A further strong prediction is that distraction during exercise will influence food seeking later in the day. This is because distraction will impact the monitoring of procurement effort which contributes to procurement cost. To our knowledge this idea remains to be tested.

However, reminders of physical activity, which historically may be linked to energy expended to procure food, do appear to stimulate compensatory changes in energy intake. For

example, manipulating information about energy expended during exercise influences the amount of food that is consumed at a subsequent ad libitum meal [52]. Participants also serve themselves and consume more calories after simply thinking about [53] or anticipating a bout of exercise [54, 55], and they consume more calories after a bout of exercise that is framed as mandatory [56] or “fat burning” [57] rather than autonomous or enjoyable, indicating that specific forms of physical activity (particularly outside of leisure) are monitored and readily stimulate food intake.

Finally, most people no longer spend long periods looking for food. Yet many commit long hours working for money. This raises questions about how different forms of employment might be ‘counted’ towards procurement cost and if so, to what extent? Similarly, do the economic costs of paying for food overlap with the effort exerted to procure food? Arguably, modern humans multitask more than ever. Eating frequently occurs ‘on the go’ and often in combination with other activities such as work or screen-based activities. In controlled studies we see evidence that modern humans still monitor the essential metrics associated with procurement cost. However, targeted studies are needed to understand their chronic influence on the energy balance of humans who no longer forage ‘directly’ for food.

Determining the value of foods

Related to procurement cost, a second problem for a hunter gatherer would be to judge relative differences in energy that can be obtained from foods. As noted above, this does not require an explicit appreciation of ‘calories’ but rather an ability to differentially prefer foods on this basis. Humans are born with an innate preference for sweet tastes [58] which may prime the consumption of energy rich foods, including breast milk. Sweetness might also be important because it signals a change in dietary composition. Ripened fruit contains a greater

proportion of easily digested starch and so foraging efficiency is enhanced when sources are discriminated on this basis [59].

Water content explains around 85% of variance in the energy density of foods [60] and because foods that contain more water require less mastication [61], the ease with which a food can be chewed and swallowed might provide another valuable cue. Numerous studies show that slowing eating rate reduces meal size [62]. However, the effect of natural variation in eating rate on preference remains unclear. Modern processing techniques have facilitated the development of energy rich foods that can be eaten very quickly, and faster than the more fibrous diet to which we are adapted. In turn, this may compromise an otherwise useful heuristic, especially when calories are consumed in liquid form [63].

In addition to these sensory influences, humans also learn about nutritive value over time. In non-human omnivores the evidence is very clear and the basic biological processes are well understood. Reliably, rats will learn to prefer a novel energy-rich food based on an association that forms between its sensory characteristics and its positive postingestive consequences [64]. In humans this process has also been observed, and learning probably occurs unconsciously [65]. However, many studies have failed to replicate earlier findings [66] and a number of explanations have been considered [67]. One idea is that learning is compromised by the sheer number of different brands and varieties of foods that are often available, especially when foods are sourced from outside the home. For example, one study reports a four-fold difference in the energy content of pepperoni pizzas ($N = 71$) that are available in an urban area of the UK, and participants who had previously eaten a particularly wide variety showed greater food intake after consuming pizza [68]. It may also be relevant that human foragers are very unusual because unlike other primates they routinely share food [69]. Coexistence in close social networks means that information about liked and disliked foods can also be transmitted culturally, based on a collective wisdom that is gleaned from

flavour-nutrient learning over generations [70]. Consistent with this idea, peer modelling has been observed under controlled conditions [71] and can have a powerful effect on preferences in humans [72]. Interestingly, the potency of this process appears to be moderated by the level of social connection with the observer. For example, social facilitation from parents is especially important [73] as is the effect of congruence in age and gender across the observer and the observed [74]. These findings are important because they provide a basis for concerns about how children interact with media and advertising, and the increased and historically unusual opportunities for implicit social learning that they provide [75, 76]. Similarly, changes in food availability combined with recent and rapid changes to family and social structure may dilute the opportunity for cultural learning, thereby further degrading performance in energy discrimination.

Some have also argued that modern humans are poorly adapted to consume especially energy-rich foods. Although climate and geographical location influenced human dietary patterns, pre-agricultural humans would have been limited to very low energy-dense wild plants and animals, with minimal processing [17]. Cooking and simple non-thermal processing methods increase the energy density and digestibility of many foods [77]. Nevertheless, one estimate suggests that foods consumed in non-industrialized environments have an average energy density of roughly 1.1 kcal/g (based on recent diets in Gambia) [78]. By contrast, fries from fast-food restaurants typically yield 3.2 kcal/g. (Honey, a naturally occurring energy-rich food, is an exception, but its consumption would have been limited by availability, and its procurement carries risk, especially in the absence of fire to generate smoke). Consistent with this idea, young children show an almost perfect linear relationship between preference for different fruits and vegetables and their respective energy density [79]. However, in a recent study in adults, performance was shown to be greatly degraded when 'modern' energy-dense foods were assessed [1]. (For a discussion around the

underlying physiological limits of human energy sensing see [1]). This observation chimes with Cordain's concept of 'evolutionary discordance' [17] and with related evidence that the intensity of basic tastes can provide a reasonably good readout of the macronutrient composition of foods, but typically only in those that are unprocessed [80].

Based on the above, we see plenty of evidence that the ability to identify and form a preference for energy rich foods remains intact in modern humans. However, there is also good reason to suspect that some of the associated processes are now compromised, and especially in the context of historically unusual energy-rich foods and the sheer variety that feature in many obesogenic environments. The wider effect this has on chronic consumption patterns is controversial and remains to be resolved.

Adapting to food insecurity

Current UK guidelines suggest that women should consume 2000 kcal (8400 kJ) per day. However, on this basis a lean 65 kg person already has more than 55 day's supply stored in fat tissue. This simple calculation demonstrates that humans draw on a large reservoir of body energy that offers considerable protection against starvation [81]. Other species lay down fat deposits for the same reason but they also adapt this strategy in response to changes in the environment. For example, captive birds increase their food intake when offered access to food at unpredictable times of day [82, 83] and resource predictability (not absolute resource) promotes fat reserves in overwintering birds [84]. Importantly, various sources indicate that the same 'insurance eating' also occurs in humans. For example, in controlled and observational studies irregular meal patterns are associated with both increased food intake [85] and weight gain [86]. Similarly, food intake increases when a period of fasting is anticipated [87], and in the Minnesota Starvation Experiment, after returning to their original weight, participants continued to binge on food [88].

One predictor of food availability is social rank. Large herbivores with lower status are observed expending relatively more energy in foraging when food availability is reduced [89] and low-ranking mice spend relatively more time on an exercise wheel [90]. Similarly, in humans, low socioeconomic status (SES) is associated with higher bodyweight, especially in women (for recent systematic reviews see [91, 92]). However, the underlying relationship is weak and, paradoxically, it tends to be observed in more affluent countries. The prevailing view is that this reflects poor dietary choices and reduced access to lower energy-dense foods among those of low SES [93]. However, relationships between access to unhealthy foods and obesity are also often weak [94] and large-scale interventions that reduce financial burden are found to increase rather than decrease in body mass [95]. Instead, across wealthy countries (typically those less liberal), *relative* income inequality or subjective socioeconomic status is a better predictor of body mass than per capita gross domestic product [96] and mediates the observed relationship between objective SES (*e.g.*, education and income) and body mass [97], suggesting a role for subjective rather than actual social gradients. Indeed this relationship has been observed across a wide range of health outcomes, including body-fat distribution, and even after controlling for objective measures of SES [98, 99]. (For a general review see [100]). Together, these observations suggest that to really understand connections between SES and obesity we should focus our attention on the psychological mechanisms that determine perceived social status (the key mediating variable) and how these processes are triggered by forms of absolute inequality. Historically, social and economic resources may have served as a means to secure access to food, producing a psychological overlap or inter-changeability of security for socioeconomic resources and calories [101-103].

Consistent with this idea, some researchers have discussed the relationship between perceived SES and elevated hunger [104], and others have manipulated SES directly. For example, inducing an acute subjective state of insecurity about the adequacy of one's SES, or

perceived inequality of resources compared to others, is found to bring about an increase in self-selected portion sizes, preference for energy-dense foods, and actual energy intake [103, 105]. Importantly, demonstrating how these broader sociological factors (*e.g.*, inequality), may “get under the skin” through psychological processes (perceptions of inadequate SES) to influence physiological mechanisms, recent findings have revealed that experimentally-induced states of low subjective SES can produce increase circulation of the appetite stimulating hormone ghrelin in response to a palatable high-energy food [106].

Together, the evidence that perceived social status impacts food intake is rather compelling. Because humans are adapted to ‘vigilant sharing’ [107], social bonds are an important source of security – if one member becomes unable to forage for a period (*e.g.*, through injury) then others are available to assume this responsibility. Therefore, it is likely that humans would have also acquired an ability to track social status and to increase food intake in response to a concern about social ostracism [108]. Arguably, the advent of social media and broadcasting methods has increased awareness of social gradients and opportunities for damaging social comparisons [109]. Insurance eating may be further promoted by a decline in cohabiting extended family networks or the tendency for meals to now be consumed alone. Consistent with this idea, sharing of family meals is associated with a healthier weight status [110] and people with anxiety about their social attachments are more likely to overeat and are found to have a higher BMI [111].

More broadly, the literature abounds with evidence that stress can induce ‘comfort’ or ‘emotional eating’ [112, 113]. However, this level of interpretation only considers the proximate mechanism. In our ancestral environment food insecurity may have been a predominant source of stress. One possibility is that one of stress’s ultimate functions was to promote insurance eating in response to a perceived threat to body energy stores (*e.g.*, resource-scarce or harsh environments). In other words, because palatable food reduces

activity in the HPA axis [114], it provides a motivational context for eating to be especially rewarding (via negative reinforcement), which in turn, offered protection from food insecurity by increasing fat stores. In the modern environment these proximate and ultimate goals are likely to be decoupled, such that stress-induced comfort eating is now promoted by threats to perceived status and by other modern life stresses, even in the absence of actual food insecurity.

The same parallels might also be drawn with the effects of mood on eating. Several studies show that mood induction procedures can influence food intake [115], and that depression is associated with obesity, and again, especially in females [116]. One creative and recent proposal is that mood serves a similar proximate role of moderating behaviour, but perhaps over longer periods. By analysing momentary fluctuations over time, the authors of one study conclude that mood may be dictated by a summation of recent experiences [117]. Expanding on this, a further suggestion is that mood provides a 'medium term' assessment of the collective momentum of experiences and whether outcomes have progressed better or worse than expected. Thus, mood can be regarded as an adapted proximate mechanism that serves several functions, one of which is to improve foraging efficiency by tracking successes over time rather than relying solely on single encounters [118]. Framed in this way, it is easy to see how changes in mood might help to promote efficient foraging by encouraging decisions to move to a new foraging location or to focus on alternative sources of flora or fauna.

5. Concluding discussion

In the introduction we highlighted the striking contrast between widespread attempts to diet with actual sustained weight loss. Our suggestion is that dietary restraint often fails because it competes with highly engrained psychological and physiological processes that were adapted over most of human (and hominid) history to promote efficient foraging. To explore whether

these proximate mechanisms are preserved, we identified a minimum set of requirements for successful foraging and then considered evidence for their ‘footprint’ exposed in empirical and observational studies in modern humans. In each case we observed preliminary evidence, which, in combination support our overall proposition. However, before expanding on this, we note again that the three foraging requirements are not exhaustive and recognise that the behaviours that fulfil them may manifest in different ways, depending on circumstance (*e.g.*, high versus low predation risk). Here, our primary objective was to garner initial evidence that might stimulate discussion around an important and often neglected research question.

In addition to understanding failed volitional control, this analysis also speaks to a broader set of questions about how modern humans now interact with their dietary environment. Many regard overconsumption as a consequence of exposure to an abundance of inexpensive, calorific, and highly palatable foods, coupled with a metabolism and physiology that is adapted to store calories whenever they are available [19]. Our proposition is that modern humans have actually inherited a far broader and more dynamic range of foraging skills that incorporate a capacity to monitor encounters with foods of varying quality, to assess associated costs, and to respond proactively to perceived signals of food insecurity. When living in an environment to which we are adapted, these ‘tools’ would be invaluable. For modern humans, they may be unnecessary, yet they continue to influence our behaviour, and in many cases, they do so outside conscious control, and at the peril of excessive energy intake.

Taking this further, another oversimplification may be the widely held view that sectors of the food industry are ‘culpable’ for the ubiquitous provision of energy-rich foods. In addition to recent and profound dietary changes, the modern food environment is also highly unusual because it can now be modified. Although there is some evidence that early pre-agricultural humans changed their environment by manipulating the landscape (using fire to clear land)

[119], the range and availability of foods was largely outside human control. Commercial enterprise now enables the environment to be changed dynamically to meet consumer demand, leading to a proliferation of products and eating opportunities at any time of day. This is critical, because it means that foraging processes might actually generate market forces that shape the development and distribution of foods. Low procurement cost is one potential example (we are drawn to foods that require little or no effort to obtain or prepare), but other more subtle cues might also nudge the food industry as well. The so called ‘portion size effect’ is one such example – invariably, and without knowing, humans eat more food when larger portions are available, and do so even when the portion presented is larger than can be consumed in a single meal [120]. Indeed, this effect is observed even in very young children [121], suggesting an inherited preparedness for this trait that may be reinforced further by socialization (*e.g.*, pressure to plate-clean by parents). In our ancestral environment it may have also been adaptive to be drawn to and to increase intake of foods that are found in abundance. Today this expectation or consumer demand actually feeds back to shape the food environment, such that large portion sizes are reinforced by their popularity, leading them to be routinely offered to gain market share. In other words, the food industry (and ultimately, the modern food environment) does not adapt in isolation, and many of the offerings that are regarded as ‘unhealthy’ (*e.g.*, snacks ‘on the go’) may exist precisely because humans have become directors of their own environment, making purchasing decisions based on strategies that historically benefited foraging.

Finally, and as we note throughout, rapid changes to food systems are likely to generate an evolutionary mismatch between proximate and ultimate needs. However, there is no reason to assume that all sources of mismatch will increase food intake, some might promote a reduction and others may have little influence. Indeed, identifying occasions when a reduction is observed might inform targeted interventions. In this regard, it might be helpful

to disentangle various sources of mismatch by distinguishing two broad categories of mismatch. Certain proximate mechanisms might be clustered according to their ‘failure to engage,’ or the disruption of a historically adaptive behaviour by alien features of a modern environment. Evidence indicating that humans are poorly adapted to discriminate energy-rich foods that feature prominently in the modern dietary environment and that distraction (*e.g.*, screen-based activities) impacts ingestive memory processes, are two such examples. Respectively, these are cases where proximate mechanisms are compromised by a change in diet and constrained by limited attentional capacity. Another form of mismatch might be otherwise referred to as ‘inappropriate engagement,’ or the misapplication of a behaviour in an unnecessary context or in response to an irrelevant signal. One example might be the effect of perceived SES on insurance eating. In our ancestral environment this would have offered protection from starvation. Today the same response is observed, but in individuals who, by objective standards, are either relatively food secure or in response to stressors that are unrelated to actual food insecurity.

In this article we have proposed that behavioural processes that supported foraging in ancestral environments now compete with dietary restriction and weight management in contemporary, fast-paced, societies. Although this initial proposal requires further support and investigation, it does offer a launching point for an important (and often lacking) dialogue between researchers of human dietary behaviour from diverse disciplines (psychology, anthropology, behavioural ecology, and cognitive neuroscience). Additionally, even though modern humans may be constraint by ‘instincts’ to forage, we are not suggesting that they are devoid of all dietary free will - merely that intentions to control food intake work alongside other pre-potent processes and goals. Overly deterministic accounts of eating behaviour can be counterproductive because they reduce perceived dietary autonomy and may even promote increased food intake [122]. Our contention is that interpreting

contemporary dietary behaviour in this way might actually inform the development of novel interventions that leverage foraging mechanisms rather than work against them.

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