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Commentary proposal on Nettle et al: Towards a behavioural ecology of obesity --Manuscript Draft--

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Commentary on **Food insecurity as a driver of obesity in humans: The insurance hypothesis** by Daniel Nettle, Clare Andrews, and Melissa Bateson.

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Title: Towards a behavioural ecology of obesity

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Abstract

Addressing the obesity epidemic depends on a holistic understanding of the reasons that people become and maintain excessive fat. Theories about the causes of obesity usually focus proximately or evoke evolutionary mismatches, with minimal clinical value. There is potential for substantial progress by adapting strategic body-mass regulation models from evolutionary ecology to human obesity by assessing the role of information.

Main Text

Progress in understanding fat storage has followed from research on the adaptive use of energy reserves by non-humans (Wells, 2009). We fundamentally agree with Nettle et al (NAB henceforth) that applying evolutionary thinking to human fattening dynamics will provide insights for understanding the incidence of obesity and other metabolic diseases. Nevertheless, we feel that the IH as formulated by NAB misses key nuances that limit its explanatory power unnecessarily, and may underpin its failures to capture details of their data analysis. Here, we suggest how progress can be made from building on these foundations.

Missing from the IH is an explicit treatment of information (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005): why is it that people living in wealthy countries with social security - making it very unlikely that they will starve to death – store fat reserves as though starving to death is a distinct possibility? In the notation of their model, it is crucial to distinguish actual p, the probability that food is found, from perceived p, and understand how they can come to differ. For instance, NAB point out that disadvantaged people are more likely to be obese, but fail to consider why their perceived p should be differentially biased. Mismatch hypotheses for humans have recently come under fire. Rather than discard them completely, we suggest a refined IH, which would have to explicitly incorporate information dynamics driven by evolutionary mismatches. As the authors point out, if restriction of food during dieting is taken to influence perceived p then target fat reserves should

increase after dieting, which as we have shown (Higginson & McNamara, 2015) is a contrast effect (McNamara, Fawcett, & Houston, 2013).

In NAB's model food insecurity is taken to be 1-*p*. Thus, under their model the maximum availability of food is inversely proportional to food insecurity. A refined IH would allow for both food insecurity and current food abundance such as in our models (Higginson & McNamara, 2015; McNamara, Higginson, & Houston, 2015). The simplest way to do this is to vary both *p* and maximum meal size *N*. Low *p* and high *N* would be food insecure, whilst high *p* and low *N* would be food secure, whilst having the same mean availability.

Human fattening patterns often involve "ratchetting" whereby any given stored fat level and/or body mass is associated with a metabolic profile that "defends" the steady state body condition (fat or lean) from short term perturbations via compensatory metabolic processes (e.g. Leibel, Rosenbaum, & Hirsch, 1995), even when differentially fat individuals share the same nutritional environments. Such dynamics are not captured in any IH model we are aware of and will require the incorporation of factors that have not yet been considered. Models show that gathering information about the environment may be neglected when energy insurance is necessary (Dall & Johnstone, 2002), which could provide a mechanism for divergence of actual p and perceived p. Because the central nervous system is costly, natural selection will have exploited the fact that physiological states (such as fat stores) contain information about environmental conditions (Higginson, Fawcett, Houston, & McNamara, 2016). Chronic obesity may result from an informational ratchet effect if current state is taken to provide information that in the current environment it is appropriate to store a large amount of fat.

Such information dynamics could underlie the differences we see among populations, not least the lack of effect amongst children, who may not yet have stable estimates of prevailing levels of food insecurity. On the other hand perceived p may not be limited to what is experienced within a particular individual's lifetime. There is the possibility that children respond to experiences of the mother during her life or during pregnancy (epigenetic effects). We expect selection on what mother passes on and on how offspring respond (McNamara, Dall, Hammerstein, & Leimar, 2016; Wells, 2007). Because different individuals (mothers and offspring) have different experiences they would have different target body reserve levels. Models of offspring provisioning under the risk of starvation (Dall & Boyd, 2002) could be developed for humans. Divergence of metabolic rates may lead to persistent differences among individuals (Mathot & Dall, 2013).

Evolutionary ecology theory predicts that individuals with poor prospects should take more risks and discount the future, so there may be similarities in the cause of obesity and the causes of unsustainable debt (Shah, Mullainathan, & Shafir, 2012), in that low income people prioritise the present. NAB posit one hypothesis for why the IH is only supported for women in high income countries. The behavioural ecology literature on hierarchies (e.g. amongst birds) points to one explanation: in patriarchal societies women can be perceived to be in some sense 'subordinate' (Acker, 1989); they are more likely to suffer in difficult circumstances and so should store more fat.

Strategic body mass regulation theory makes few assumptions about how the adaptive body mass dynamics predicted in any given scenario are controlled proximately. Most models assume that any decision-making system (hormones, cognition, etc.) is highly flexible such that it can be optimised (Fawcett, Hamblin, & Giraldeau, 2012). But it is likely that animals including humans actually have simple mechanisms that have evolved to perform sufficiently well in most conditions that have been experienced over evolutionary time (McNamara & Houston, 2009). Having a highly specific and flexible rule may be costly, and this cost will be traded off against the cost of inaccuracy of decision-making: humans may have evolved inexpensive 'rules' that perform well in most environments, but lead to over-eating in rich environments (Higginson, Fawcett, & Houston, 2015).

In summary, we need to develop human-specific evolutionary models of body mass regulation that take information use and physiological "rules" into account. We need to work with clinicians, psychologists, and physiologists, among others, which will help to incorporate the human-relevant details in order to build better theory. This could elucidate what aspects of the environment drives over-eating and weight gain and provide an evolutionarily informed solution to the obesity epidemic.

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