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Introduction  Researchers inevolutionary medicine set out to uncover the ways in which human susceptibilityto disease has been shaped by evolution (Vining and Nunn, 2016). The emergingdiscipline is revolutionising our understanding of the cause of illness and hasrecently become recognised within the domain of public health. The coreprinciples derive from life history theory, which analyses energy allocationbetween the major competing functions of growth, maintenance and reproduction, eachaffecting various health outcomes. By incorporating an evolutionary perspective, alternative conclusions of the outcomes of health and disease can be drawn, andsubsequently used to make public health interventions more effective (Wells etal., 2017). Tounderstand how life history theory has shaped human evolution and thus useevolutionary theory to approach the issues posed by global public health, it isnecessary for both fields of research to understand the concepts of bothadaptation and constraint (Wells et al.

, 2017). In simple terms, adaptation isthe evolutionary process enabling organisms to adjust to the environment andenhance evolutionary fitness (Stearns, 1986). In order to adapt, organisms mustovercome the various constraints posed by their surroundings which limit theproduction of advantageous phenotypes (Garland, 2014). This essay will arguethat whilst both concepts are necessary to understand in EMPH, adaptation ismore useful for improving the effectiveness of global health interventions. Theargument will be justified by examples routed in human anatomy including humangrowth variation, the “ small but healthy” hypothesis and the PredicativeAdaptive Response hypothesis.

Background The aim ofpublic health is to prolong life, prevent disease and promote health throughthe organized efforts of society in human populations (Winslow, 1920). Manyinterventions have been designed to benefit health and traditionally efforts werefocussed on pathogen related risk factors. The prevention of diseasetransmission focussed on improving nutrition and living conditions to induceresilience, and more recently lifestyle changes to reduce the risk in the riseof non-communicable diseases have been encouraged (WHO, 2011).

Evolutionarymedicine on the other hand, aims to delve further into understanding the causesof illness to uncover why humans have become susceptible to disease. Thecurrent state of medicine is mainly pre-evolutionary, with explanationsremaining descriptive and mechanistic and only scratching the surface inproviding explanations for the variation in disease susceptibility inindividuals and societies (Wells et al., 2017). The integration of evolutionarybiology and medicine forms the foundation of the discipline, which recognisesthat medical research can significantly benefit from a priori understanding ofthe concept of adaptation by natural selection and how it affects healthoutcomes. Evolutionary medicine uses an adaptionist perspective to explain whysome individuals become ill in different environments, which are subject todifferent constraints.

(Muehlenbein, 2010).  So far, public health has greatly benefitted from including an integrated perspectiveof evolutionary theory. An evolutionary perspective offers new understandinginto the resulting health consequences of changing environments and behaviourpatterns. This will inform the behavioural and physiological components ofinterventions that will likely improve effectiveness, for example it may beapplied to improve non-communicable disease interventions. It has been arguedthat without an understanding of adaptation, public health schemes may notachieve the aims that have been set out.

This is because adaptation by nature selectionhas been engineered to maximise the genetic fitness (reproductive success) ofan organism under harsh environmental conditions which may cause the hindranceof health and render organisms more susceptible to disease (Wells et al., 2017).  This is can be overcome using anevolutionary approach to highlight how human physiology and behaviour haschanged in response to the stresses of changing environments. Evolutionarytheory can be applied to explore the effects of biological, societal andphysical stresses and stimuli during the life-course (Kuh & Ben-Shlomo, 2004; Krieger & Smith, 2004, Marmot, 2005) which studies have alreadysupported in a range of species including humans (Stearns et al., 2000; Winterhalder, 2000; Nettle, 2013).

Evolutionary Constraints and Genetic Fitness  Anunderstanding of how environmental constraints shape trait heritability andevolution is necessary in evolutionary medicine to shed light on geneticvariability to shape health outcomes and susceptibility to disease (Wells etal., 2017). For many years, tension has existed between researchers within theevolutionary field who highlight the significance of adaptation by naturalselection and those who emphasize the role played by developmental andphylogenetic constraints on the development of an organism (Fitch, 2012). Darwinand Wallace’s theory of natural selection supplied the field of evolutionarybiology with new understandings of how the constraints of historicalenvironments shape biological variability (Darwin, 1859). This infers that anunderstanding of adaptation is more vital to researchers in EMPH thanunderstanding simply observable constraints. The theory suggests that traits arevaried and that this variability is heritable by chance; the greater the numberof offspring produced by an organism, the greater the frequency of their traitsin subsequent generations.

Over time, the phenotypes and genes of thosereproducing the most successfully will be continued throughout the lineage (Dennett, 1995). Geneticfitness therefore, is shaped by natural selection to improve genetic fitnesswhich demonstrates that an understanding of adaptation is vital to provideexplanations of genetic variability.  Researchersin evolutionary medicine can use this knowledge to treat disease in relation togenetic variability. For example, personalised, gene-based medicine can bedeveloped to treat the disease risks prompted by genetic variation betweendifferent ethnic groups (Ono et al., 2013).

Two major concernsexist within contemporary medicine that can be addressed using an understandingof environmental constraints shape evolution. Firstly, the evolution of anti-biotic resistant or drug resistantstrains of pathogens, which develop when bacteria become resistant to treatment(due to phenotypic adaptation, transfer and expression from resistant tosusceptible organisms or genetic mutation) (Arias & Murray, 2009; Händel et al., 2013). Secondly, the emergence of infectious diseases, for example those caused by Ebola virus, HIV and SARS (Jones et al., 2008). Using an understanding of constraint mayshed light on why treatment resistant pathogens and new infectious diseaseshave evolved, which in turn may be of vital importance for developing methodsto overcome them. Developmental Constraints and Human Growth Variation Developmentalconstraints are perhaps the most significant factor in the overall influence ofconstraint on the evolution of complex traits (Fitch et al., 2012).

They are often interpreted as limitations onphenotypic variability or constraints on the production of phenotypic variation(Maynard-Smith et al., 1985). The recurrent laryngeal nerve in humans, whichstretches seven lengths longer than necessary to connect the brain and thelarynx, is an example demonstrating the effects of developmental constraints onphenotype which can be used by researchers in EMPH to shed light on theevolution of human anatomy (Bergman, 2010).  Internationalpublic health organizations are expected to use an understanding of constraintto shape health outcomes and susceptibility to disease through the influence oftrade-offs (Wells et al., 2017).

Trade-offs are a concept in life historytheory which occur when one trait cannot increase in fitness without a decreasein fitness of another trait (Garland, 2014). They are a crucial concept forpublic health organisations and researchers in evolutionary medicine becausethey enforce recognition on the consequences of changing one trait. For example, a major issue presented within global public health is human growth variationwhich is constrained under poor environmental conditions.

Growth is limited viaenergetic constraints and acts as an indicator of how resources are allocated foroptimal reproductive value (McDade, 2003). Many bio-anthropological studies of humangrowth trajectories have focused on the effects of nutritional stress as theprimary influence of constraints on growth (Stulp & Barrett, 2016). Insmall-scales societies, a study by Walker et al. (2006) found that trade-offsbetween growth and maintenance occurred in response to poor environmentalconstraints, resulting in small adult stature, later ages of menarche and slowgrowth rates compared to richer quality environments. Small stature therefore, is an example where investment of energy favours maintenance over growth producingan adaptive trade-off (Stulp & Barrett, 2016). This reinforces the argumentthat whilst understanding constraint is necessary for researchers in EMPH, anunderstanding of adaptations which stem from constraints is more useful for interpretingthe cause of phenotypic variability. For example, global health interventionscan use an understanding of adaptive trade-offs to develop supplementary foodprograms in developing countries. By increasing energy available for growthfrom better nutrition, improvements in growth rates and reduced stunting havebeen made to improve health outcomes.

This example shows that by influencing trade-offsbetween growth and maintenance, researchers in EMPH can make significantimprovements in human health (Beaton & Ghassemi, 1982).  Evolutionary Adaptation and Plasticity The conceptof adaptation offers the most significant insight into human vulnerabilities todisease and is arguably the most important concept for researchers in EMPH tounderstand (Muehlenbein, 2010). An adaptation can be described as a change or alteration in aheritable trait which correlates to the improved reproductive success of anorganism. Adaptive traits, in the form of genetic or phenotypic alterations, will thus increase in frequency within the population through the reproductivesuccess of adapted organisms which are better suited to the changingenvironment (Stearns & Medzhitov, 2016). The way in which an organism adaptsis determined by the resources available and the constraints that haveaccumulated in its lineage, which have in turn been altered by the process ofadaptation (Griffiths & Grey, 1994).  Adaptation acomplex concept which is vital for researchers in EMPH to understand, so that interventionsconcerning global public health are as effective as possible in improvinghealth and preventing disease. The “ small but healthy” hypothesis put forwardby David Seckler, is an example of an adaptive response to poor environmentalconditions constraining growth (Seckler, 1982).

The hypothesis stated thatindividuals short in stature, having faced malnutrition in childhood, are infact healthy and well-adapted to the constraints of the environment surroundingthem. This raises issues that challenge researchers in evolutionary medicineand public health concerned with the characteristics and nature of humanadaptations. The “ small but healthy” hypothesis argues the following: the bodyreduces its rate of growth as an adaptation to low nutrient intake, in doingso, the body retains a physiological equilibrium. This adaptation, Secklerargues has no consequences for health other than short stature and since “ smallbut healthy” individuals are more likely to face nutritional constraints, populationssurviving impoverished intakes should no longer be considered malnourished, even though classified as such by international standards such as WHO (Messer, 1986). International health interventions that focus on nutrition shouldtherefore direct attention to individuals who are not “ small but healthy” yet stillfaced with serious nutritional constraints leading to physical debilities, hestates (Seckler, 1982). If correct, this hypothesis suggests that public healthinterventions could focus on a smaller and more manageable proportion of theglobal population and reduce food aid and program budgets without harmful effects.

Adaptation therefore, lead the millions of individuals facing nutritionalconstraints to be better suited to a lower nutrient intake (Pelto & Pelto, 1989). The hypothesis had potentially profound implications for public healthand evolutionary medicine taking action to combat nutritional constraints if itis supported. The argument however, has been heavily criticised. Whilst inlife-history terms it remains relatively simple: being small under harshnutritional conditions is beneficial because energy can favour maintenance overgrowth, there is substantial evidence against it (eg Pelto & Pelto, 1989; Rohmatullayaly et al., 2017). Seckler’sargument suggests that researchers in EMPH should direct very little attentionto individuals that are in fact in need of vital health interventions.  This example demonstrates how an understandingof adaptation is vital so that the appropriate measures are taken byresearchers in EMPH to improve global health and prevent disease.  Taking anevolutionary perspective inclusive of developmental plasticity can also be usedto  improve the effectiveness of health interventions (Rickard, 2016).

Plasticity involves responses to the environment by an organism frompotentially a single genotype (Wells et al., 2017). Responses occur eithermomentarily or range across generations and are aimed at enhancing behaviour, development or physiology to maximise fitness (Stearns & Medzhitov, 2016). Developmentalplasticity can evolve by natural selection in such a way that organisms whichhave developed advantageous responses to improve their chances of survival willproduce a greater number off offspring with a higher evolutionary fitness(Rickard, 2016). The importance of plasticity in EMPH is evident in theadaptations of organisms, which have evolved in response to environmentalconstraints. The Predicative Adaptive Response (PAR) hypothesis argues thatcues received during development influence the future development of aphenotype in accordance to the conditions in the form of an adaptive response (Batesonet al.

, 2014). This can be useful for researchers in EMPH to predict how anindividual will develop based on early life conditions and interventions can bedeveloped earlier in order to overcome future health outcomes. For example, ifa foetus experiences undernutrition it will adapt by altering itsinsulin-glucose metabolism so that so that when faced with undernutrition inadulthood, it is capable to survive.

In this case, the PAR hypothesis is auseful concept within adaptation because it holds important implications concerninghealth and disease patterns which may prove useful for the development offuture public health interventions (Rickard, 2016).  Conclusion Understandingthe concepts that have shaped evolution are vital in the fields of evolutionarymedicine and public health. The concepts of adaptation and constraint providealternative conclusions to interpretations of patters of health and disease. The concept of adaptation offers significant insight into human vulnerabilitiesto both infectious and non-infectious disease (Muehlenbein, 2010).

The conceptof constraint provides explanations on the bias and channelling of variationthat may explain and facilitate adaptation, thus providing the very frameworkupon which natural selection acts (Fitch, 2012). This essay argues thatadaptation is a more vital concept to understand than constraint because itoffers the most significant insight into human vulnerabilities to disease andhas the most important influence on the effectiveness of health interventions. The concept of constraint remains vitally important in evolutionary medicineand public health to shape health outcomes and susceptibility to disease andaddress the evolution of treatment resistant pathogens and emergent infectiousdiseases. Finally, the concepts that shape evolution can be used in EMPH tolook towards the future of overcoming adverse health and potentially newemergent diseases, and to shed light on the future implications of how humansand organisms have evolved to what they are today.