DID NATURAL SELECTION MAKE THE DUTCH TALLER? A CAUTIONARY NOTE ON THE IMPORTANCE OF QUANTIFICATION IN UNDERSTANDING EVOLUTION.

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Abstract

One of the main achievements of the modern synthesis is a rigorous mathematical theory for evolution by natural selection. Combining this theory with statistical models makes it possible to estimate the relevant parameters so as to quantify selection and evolution in nature. While quantification is a sign of a mature science, statistical models are

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/evo.12803.

unfortunately often interpreted independently of the motivating mathematical theory. Without a link to theory, numerical results do not represent proper quantifications because they lack the connections that designate their biological meaning. Here, we want to raise awareness and exemplify this problem by examining a recent study on natural selection in a contemporary human population. In their study, Stulp et al. (2015) concluded that natural selection may partly explain the increasing stature of the Dutch population. This conclusion was based on a qualitative assessment of the presence of selection on height. Here we provide a quantitative interpretation of these results using standard evolutionary theory to show that natural selection has had a minuscule effect.

Main text

While the use of advanced statistics and complex mathematical models flourishes in evolution and ecology, the field has shown a remarkable lack of attention to quantification and the meaning of measurements (Houle *et al.* 2011). One outcome of this is that results are often presented numerically, but not interpreted quantitatively in a theoretical context. This type of pseudoquantification is most familiar in the common confounding of statistical and biological significance (e.g., Yoccoz 1991), but also manifests itself in other ways. A typical example of such lack of quantification can be found in a recent study asking whether natural selection may help explain the remarkable 20 cm increase in human height that has taken place in the Netherlands over the last 150 years. Stulp *et al.* (2015) presented an exemplary statistical analysis of natural selection on human height in an impressive data set of 42,612 Dutch men and women. They found evidence for selection and showed, in particular, that taller men had more surviving offspring than shorter men. They suggested that this could have led to evolutionary changes that may help explain the increase in stature in the Dutch population. This suggestion was eagerly taken up by the popular media as a potential explanation for why the Dutch are currently the tallest people on earth (e.g. Zimmer 2015, Agence France-Presse 2015, Enserink 2015).

While the existence of natural selection in humans is not surprising (e.g. Byars *et al.* 2010, Courtiol *et al.* 2012), it has to be remembered that evolution is a quantitative process that has to be assessed in quantitative terms. Despite sophisticated statistical model fitting, Stulp *et al.* (2015) only assessed natural selection in a qualitative manner, and did not make use of standard mathematical theory to quantify the potential evolutionary response to selection (e.g. Lande & Arnold 1983). In its simplest form, the evolutionary response to selection can be predicted from the breeder's equation as the product of the trait heritability and the selection differential. The selection differential is the covariance between relative fitness (i.e. fitness divided by its mean) and the trait (e.g. Frank 2012).

We obtained the selection differential on the height of Dutch men from the supplementary material in Stulp *et al.* (2015), where Poisson regressions of the number of surviving offspring (the best measure of fitness available) on height are provided. A standard Poisson regression uses a log link function and therefore predicts the natural log of the response variable. Because log fitness is a good approximation of relative fitness, and height had been mean centred and variance standardized, the linear term of the regression can be used as a (variance-standardized) selection gradient that, when multiplied with the trait standard deviation, gives a selection differential (e.g. Hereford *et al.* 2004). In our calculation, the selection gradient was estimated from the regression of the number of surviving children on male (linear) height as given in Table S14 in Stulp *et al.* (2015). This term is controlled for several environmental factors, such as level of education, income and health, and is probably the least confounded estimate presented in the study. The selection gradient was estimated to be 0.014 per standard deviation per generation, which means that relative fitness is predicted to increase by 1.4% per standard deviation increase in height. Multiplying the selection gradient with a standard deviation of 6.83 cm for male height (Table S2 in Stulp *et al.* 2015), gives a selection differential of 0.96 mm per generation. Hence, the within-generation change in mean male height due to selection is predicted to be about 1 mm. If we next assume a constant heritability of 80% (an estimate cited in Stulp *et al.* 2015), and no selection on female height (i.e. ignoring the stabilizing selection on females detected in the study), the predicted evolutionary change in mean height would be 0.80×0.96 mm/2 = 0.38 mm per generation (the selection differential is divided by two because selection acts only on males). If we further assume that selection has been constant over time and acted for about six generations (i.e. within 150 years in this case), the predicted evolutionary increase in height is 2.28 mm, which is only 1.1% of the observed 20 cm increase. Even with a heritability of 100%, we would only predict a change of 2.88 mm, or 1.4% of the total increase. We can think of no obvious violations of the statistical assumptions in Stulp *et al*'s or our analysis that are likely to substantially increase this prediction. These calculations are less an attempt at precise prediction, than an illustration of the potential impact of the estimated selection under the most favourable circumstances.

In conclusion, the application of quantitative genetics theory to quantify the results shows that the natural selection estimated by Stulp *et al.* (2015) can only explain a tiny fraction of the observed increase in Dutch height. Although Stulp *et al.* (2015) do mention that the effect is small, the lack of quantification leaves room for the false impression that natural selection has been important, when in fact there is strong evidence against any substantial effect. More generally, the problem arises when statistical results are presented without being interpreted in a quantitative theoretical context. While numerical results are routinely presented in the form of p-values and estimates of coefficients in statistical models, this does not constitute proper quantification unless the statistical results are converted back to a quantitative model that can be used to answer the biological question of interest (Schneider 2009; Houle et al. 2011). Avoiding this type of statistical pseudoquantification requires paying close attention to the context of numbers, never divorcing them from their scales and units, and always asking the question: "What does the number mean?"

Acknowledgements

This communication sprung from the discussion seminar BEEhive at NTNU and we would like to thank all participants for stimulating buzzing. We also thank Jonathan Wright, Tim Burton, Bernt Rønning, Dennis Hasselquist, Maria Servedio, John Hunt and Erik Postma for constructive comments on an earlier version of the manuscript. Last but not least, we want to thank Gert Stulp for fruitful discussions. Maja Tarka was supported by the Research Council of Norway through its Centres of Excellence funding scheme, project number 223257. The authors have no conflict of interest to declare.

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