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REPLY TO GROSSMAN:

The role of natural selection for the increase of Caesarean section rates

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Recently, we presented the "cliff-edge model" (1) to explain why natural selection has not reduced the high rates of fetopelvic disproportion (FPD) in childbirth. This evolutionary model predicts that birth-relevant anatomical dimensions have changed in response to the regular use of Caesarean sections (C-sections). Grossman's (2) interesting comment on our report allows us to clarify several issues.

As noted by Grossmann (2), we present a theoretical model, not empirical data, for this recent evolutionary change. Medical treatment has systematically changed survival rates and thus, by definition, the selective regime faced by modern humans. Hence, an evolutionary change of anatomical properties is not surprising. In our quantitative model (1), only moderate directional selection for a large fetus, a narrow birth canal, or both accounts for the high disproportion rates. Accordingly, fetal size—including head size—relative to size of the birth canal would have changed only slightly within two generations (we predicted an increase of 0.04-0.08 SDs). Because of the tight fit of the fetus through the birth canal and the nonlinearity in the tail of the phenotype distribution, these small changes still have led to a considerable increase of the initial disproportion rate. However, additional countervailing factors may conceal this evolutionary effect: For example, reduced gestational age in the United States has even led to a decrease in average birth weight (3).

Importantly, our model is only about FPD rates, not C-section rates, which are much higher because of numerous medical, social, and legal reasons, partly enumerated by Grossman (1, 2). The predicted increase

of the initial FPD rate by 10–20% is only one among many reasons for the multiplication of the C-section rate. We do not claim that the massively increased C-section rate can be explained by our model alone. Note also that only the C-sections carried out in cases of actual FPD account for the evolutionary change. Strong variation of C-section rates across countries, ethnicities, social groups, hospitals, and age groups challenge the empirical assessment of our prediction.

In addition to skeletal FPD, multiple other anatomical and physiological factors influence childbirth, including obesity. However, the evolutionary dynamics of the skeletal dimensions can be modeled independently as long as they are sufficiently uncorrelated with these other factors, which seems a plausible assumption (1). Certainly, increased FPD and C-section rates are partly caused by changed nutrition and lifestyle. In our paper, we acknowledged that some of the estimated "selective forces" are attributable to nutritional changes throughout the last decades (1).

Every formal model is based on idealization; in fact, the exploration of key factors is the very purpose of modeling. We represent the disproportion of fetal and maternal dimensions by a single scalar quantity, D, whereas a comprehensive parameterization of pelvic shape requires a multivariate representation (4, 5). The qualitative behavior of the evolutionary dynamics could still be shown by our model (1); numerical estimates of selection gradients and evolutionary changes, however, are meant to represent orders-of-magnitude only. Hopefully, future theoretical and empirical work will refine our predictions.

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- 2 Grossman R (2017) Are human heads getting larger? Proc Natl Acad Sci USA 114:E1304.
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- 5 Fischer B, Mitteroecker P (2017) Allometry and sexual dimorphism in the human pelvis. Anat Rec, in press.

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