REPLY TO UNDERDOWN AND OPPENHEIMER:

Roles of selection, plasticity, and genetics in the integration of human pelvis shape and head size

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In our paper (1) we report on a previously unknown association between human pelvis shape, head size, and stature that appears to ameliorate—but in no way resolve—the obstetric dilemma. In an interesting response to this article, Underdown and Oppenheimer (2) emphasize that "one must explicitly consider whether the suggested relationship is an evolutionary-selective phenomenon or an analytic artifact produced by combining multiple anatomically related variables (each of which potentially underwent differential patterns of selection) or plasticity in the individual."

Independent selection of pelvis shape, stature, and head size would produce covariation of average population phenotypes across evolutionary time, but not of individual phenotypes within a population, as we have observed. The emergence of covariance patterns within a population does require a scenario of correlational selection or a change in the developmental structuring of variation (3). Correlational selection is present because cephalo-pelvic disproportion depends on the size of the neonatal head relative to the dimensions of the female birth canal. Persistently disfavoring unfit trait combinations leads to a nonrandom association (linkage disequilibrium) of alleles that affect head size and pelvis shape. It can also lead to the evolution of pleiotropic gene effects (joint effects on multiple traits). In principle, pleiotropy might already have emerged before the obstetric dilemma arose, in response to other developmental or selective constraints, but this is difficult to test.

To explain the observed association between pelvis shape and head size by plasticity, one trait would have to influence the development of the other, or a common environmental factor would have to influence both. The first scenario seems unlikely, because the brain ceases to grow at about 6 y of age, whereas the sex-specific shape of the pelvis mainly emerges during puberty. It is also unclear how a common environmental factor can account for the specific pattern of covariation that we observed. One possible mechanism could be extensive variation in nutritional status. Malnutrition leads to reduced stature and brain size along with lowered estrogen levels, which in turn affect pelvic growth. Note, however, that we present the association between head size and pelvis shape independent of stature; common environmental or epigenetic effects that correlate with body size are thus removed, or at least substantially reduced within our analysis.

Underdown and Oppenheimer (2) further speculate that the slight decrease of both brain size and stature at about 35–20,000 B.P. "only makes obstetric sense if smaller populations allow easier delivery." We disagree on this point, because the obstetric literature clearly demonstrates that shorter women experience higher risk of birth complications than taller women (4, 5). However, we find that shorter women tend to have a pelvis with a rounder inlet: a shape that is, within the constraints of short stature, well-suited for childbirth (1). If this association was present already in earlier humans, it might have contributed to the later reduction of stature. An early persistence of this association would be supported by a broad consistency of the association within and across modern populations.

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2 Underdown S, Oppenheimer SJ (2016) Do patterns of covariation between human pelvis shape, stature, and head size alleviate the obstetric dilemma? *Proc Natl Acad Sci USA* 113:E258.
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5 Parsons MT, Winegar A, Siefert L, Spellacy WN (1989) Pregnancy outcomes in short women. *J Reprod Med* 34(5):357–361.

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