Response to Comments on "An Association Between the Kinship and Fertility of Human Couples"

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Analyses of 137,844 Icelandic couples born between 1800 and 1965 reveal a monotonic drop in fertility with increasing marital radius (distance between the birthplaces of spouses). Marital radius was moderately correlated with kinship between spouses. This correlation was strongest during the peak of urbanization (1875 to 1925) but very weak after 1950. These results raise doubts about the use of marital radius as a proxy for kinship in contemporary human populations.

Helgason et al. (1) reported a significant positive association between the kinship, fertility, and reproductive success of 160,811 human couples in Iceland born between 1800 and 1965. Kinship was estimated directly using genealogies up to a depth of 10 generations back from each couple; fertility was defined as the number of children born to each couple, and reproductive success was measured as the number of grandchildren (and the number of children who reproduced). We retain this terminology in the present text. Overall, a monotonic positive relationship was observed between kinship and fertility (with a maximum for couples related at the level of second cousins or closer), while the relationship between kinship and reproductive success followed an n-shaped curve (with a maximum for couples related between the level of third and fourth cousins). Although Icelanders experienced a radical socioeconomic transformation between 1800 and 1965, from a poor rural agricultural population to a rich urban industrialized population (2), the same general relationship between kinship, fertility, and reproductive success was observed throughout.

Based on an examination of figure S2 from our initial study (1), Labouriau and Amorim (3) rightly point out that the relationship between kinship and fertility for subintervals 1900 to 1924, 1925 to 1949, and 1950 to 1965 is not perfectly monotonic, where couples related at the level of second cousins or closer have slightly less fertility than those related at the level of second to third cousins (although this difference is only statistically significant for the subinterval 1950 to 1965; $P = 0.017$). However, their inter-

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pretation that this is indicative of inbreeding depression on human fertility is overly simplistic. Thus, in figure S2 (1), there is no evidence of an inbreeding depression for the earlier subintervals of 1800 to 1824, 1825 to 1849, and 1875 to 1899. Instead, there is a perfectly monotonic relationship between kinship and fertility, with significantly greater fertility of couples related at the level of second cousins or closer than those related at the level of second to third cousins for subinterval 1800 to 1824 ($P = 0.028$). Notably, the relative decrease in the fertility of the most closely related couples over time was accompanied by a drastic reduction in the overall percentage of such couples, from 5.81% in 1800 to 1824 to 0.016% in 1950 to 1965. Unlike unions between more distantly related couples, spouses related at the level of second cousins or closer are usually well aware of their genealogical relationship, as are others in their social environment. As such unions are subject to greater stigma in the largely urban and highly educated population of contemporary Iceland than in the rural preindustrial society of the 19th century, it seems more likely that the change in the relative fertility of the most related couples from 1800 to 1965 is attributable to social rather than biological factors.

After a reanalysis of their previous study (4), Labouriau and Amorim (3) further argue that their updated finding of an n-shaped curve describing the association between marital radius (the geographical distance between the birthplaces of spouses) and fertility among couples formed by all 42,165 Danish women born in 1954 is compatible with the results of our study. Further analyses of our data show that this conclusion is mistaken. First, their conclusion rests on an assumption that marital radius and the kinship coefficient are comparable measures of genealogical relationship. To evaluate this assumption, we obtained information about the birthplaces of both spouses for 137,844 couples in the 22 counties of Iceland. Defining marital radius as the

geographical distance between the centroids of counties, we calculated the Spearman rank correlation (ρ) between marital radius and kinship, standardizing both variables within 5-year intervals using the approach described in (1) to eliminate the confounding effect of temporal change. An overall correlation of $\rho = -0.298$ ($N = 137,433$, $P < 1^{-6}$) indicates that marital radius is informative about the genealogical relationship between couples, but only moderately so. Nevertheless, as would be predicted from our original results, a monotonic drop in fertility with increasing marital radius is observed (Fig. 1A). Contrary to the results presented by Labouriau and Amorim (3) for the Danish cohort, couples from the same county (with a marital radius of 0) have the greatest fertility in Iceland.

If it were assumed that marital radius is a relatively strong correlate of kinship in the Danish cohort, the discrepancy between our results and those of Labouriau and Amorim (3) could reflect a real and major difference between the two populations in the relationship between kinship and fertility. However, there is reason to suspect that marital radius is not a strong correlate of kinship for the Danish couples analyzed by Labouriau and Amorim. In Iceland, the negative correlation between marital radius and kinship shows substantial change over time (Fig. 1B). A key factor underlying these temporal differences is the large-scale migration associated with the development of urban areas in Iceland, which commenced around 1870 to 1890 (i.e., involving couples born after 1830) and reached its climax between 1920 and 1950 (couples born from 1880 to 1930) (5). For couples born from 1800 to 1825, who met their spouses in a rural preindustrial society, $\rho = -0.116$. However, as the rate and distance of migration into urban areas increased, so did the correlation between marital radius and kinship, which reached maximum strength for couples born between 1875 and 1925 ($\rho = -0.46$). As the rate of urbanization diminished, the negative correlation weakened to its value of -0.128 for the most recent cohort of couples (1950 to 1965), most of whom were born and met their spouses in the same urban areas. Figure 1C shows a breakdown of the relationship between fertility and marital radius in Iceland by subinterval. A comparison with figure S2 in (1), showing the same temporal breakdown for the relationship between kinship and fertility, demonstrates that when the correlation between marital radius and kinship is weak, the pattern of association of these variables to fertility can be quite different.

Because the process of urbanization occurred in Denmark at roughly the same time as in Iceland, it follows that a relatively weak negative correlation between marital radius and kinship would be expected for the Danish couples examined by Labouriau and Amorim (3), whose females were all born in 1954. If our prediction is correct, then little can be inferred about the relationship between kinship and fertility from

Fig. 1. The relationship between fertility and marital radius and between marital radius and kinship among Icelandic couples. (**A**) shows the mean and 95% confidence intervals of the standardized number of children per couple as a function of seven intervals of marital radius. (**B**) shows the Spearman rank correlation between standardized values of kinship and marital radius for seven successive cohorts of couples born between 1800 and 1965. (**C**) shows the mean and 95% confidence intervals of the standardized number of children per couple as a function of seven intervals of marital radius for each of the seven different cohorts of couples.
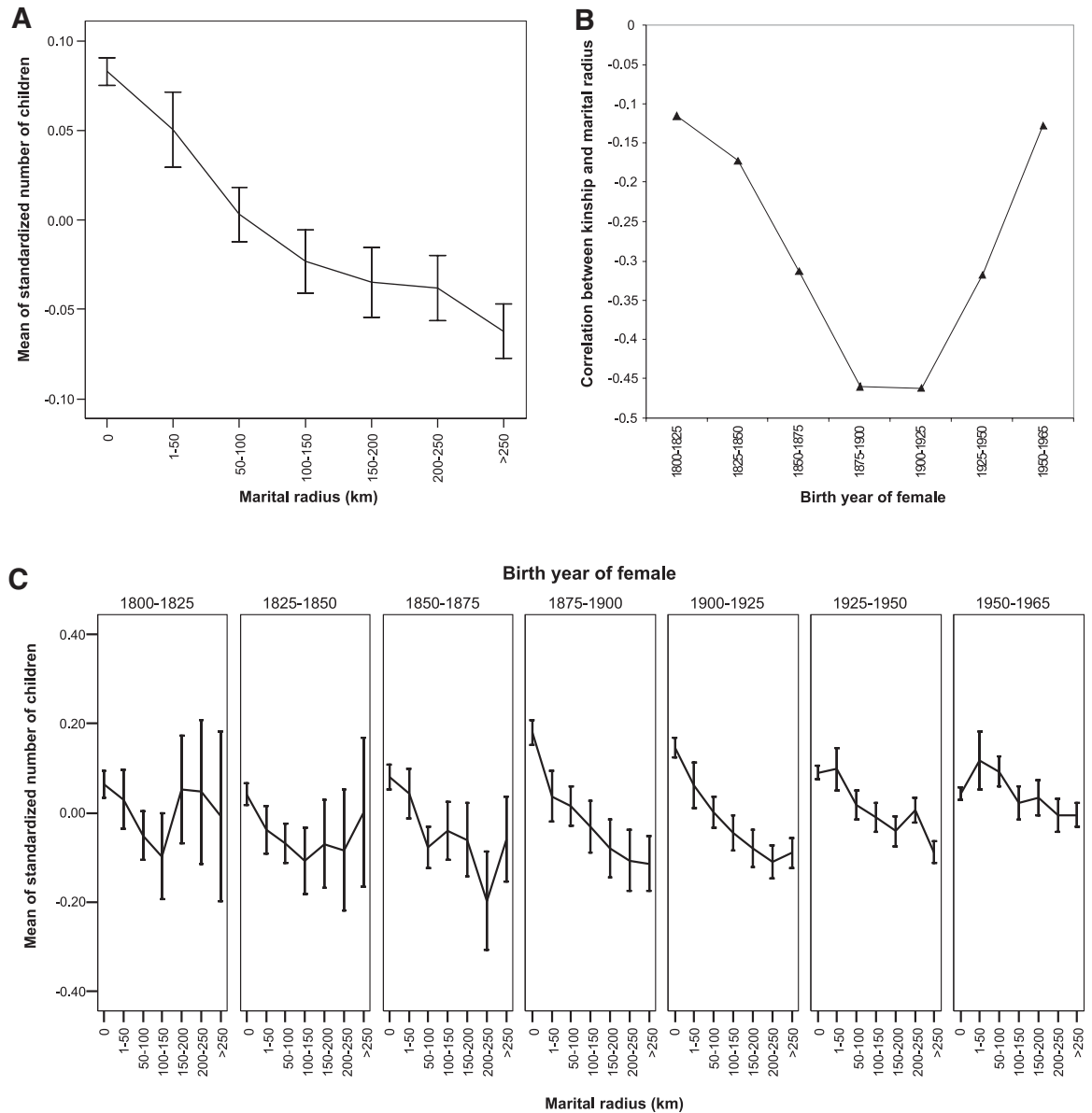
the relationship between marital radius and fertility for these Danish couples.

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