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LETTER TO THE EDITOR

Methodological differences cannot explain associations between health, anthropometrics, and excess resting metabolic rate

We appreciate Ocobock's interest in methodological rigor. We largely agree with her commentary, which suggests that departures from standard protocols might have contributed to the high resting metabolic rate (RMR) measured for Tsimane. Indeed, our paper acknowledges many of the key departures from gold-standard indirect calorimetry methods of RMR assessment and attempts to adjust for several of these (Gurven et al., 2016). Bringing standard clinical methods into remote field settings often involves certain compromises, especially in our case, where RMR measurement was just one component of a large-scale health and aging project (Gurven et al., 2017). RMR data collection was from 2012 to 2014, and where we to measure RMR again for focused follow up, we would consider new available technologies, improve our protocol to the extent possible, and compare against our published estimates.

Ocobock summarizes gold-standard RMR testing protocol and highlights where our methods could be improved. As we already addressed several of these in our study Limitations section, we first respond to three of Ocobock's suggestions for improving the validity of our RMR measures that are not already mentioned in our original paper. Ocobock mentions that participants should have rested at least 20 min before assessment, and that participants should have ideally refrained from exercise for at least 14 hr. Although we do not have specific measures of activity directly prior to measurement, a 20-min resting period was almost certainly the case for the majority of our participants; they were often patiently waiting to visit the physician or being interviewed by other project members and waiting their turn for RMR measurement. It is simply not possible (or ethical), however, to expect active horticulturalists to refrain from any type of physical exertion for 14 hr. Ocobock also recommends that we use a canopy hood instead of a mask in our indirect calorimetry system. We initially considered this option, but ultimately dismissed it, because our priority was to ensure participant comfort and calm, especially under humid, tropical conditions. Lastly, although it may have been preferable to have patients lie in a supine position, we ended up having patients remain seated for logistical reasons and for participant comfort.

In the paper, our best attempt to adjust for deviations from ideal study conditions resulted in our more "conservative" RMR estimate—that takes into account recent eating, time of day, season, and ambient weather conditions. This conservative RMR was substantially lower than our measured RMR, especially in men, and moved our estimates closer to the range of predicted RMR using standard equations (see Figure 2 in the original paper). Although the concept of "resting state" itself may be subject to debate, it is possible that our RMR measures combine "true" RMR with the "metabolic rate of a given moment" (Ocobock). Hence, our attempt to model the "excess" RMR above and beyond that predicted using the most conservative prediction equation was an instructive exercise. Any prediction equation derived with a specific sample under certain conditions carries its own assumptions and is often a poor fit for some individuals (Wang, Heshka, Zhang, Boozer, & Heymsfield, 2001). As we already state in the paper, and as Ocobock reminds us, methodological limitations preclude definitive conclusions regarding the causes or precise magnitude of elevated RMR measurements among the Tsimane.

Instead, the main points of our article were broader: higher-than-expected RMR is due in part, to infection (intestinal helminths and from elevated white blood cell count), back pain, lactation, and other condition-related variables, even after adjustment for the variables mentioned above. Whether these account for absolutely elevated RMR relative to other populations is secondary to their importance in explaining differences between Tsimane who all were measured using the same protocol.

That said, we report that age- and mass-adjusted total energy expenditure (TEE), measured using doubly labeled water, is indeed elevated among Tsimane, and that the proportion of TEE due to RMR is similar to that observed elsewhere. Our comparative analysis showed that the higher than expected TEE among Tsimane disappears when you take into account their elevated RMR. Regardless of whether the elevation in Tsimane RMR is over-estimated, the fact remains that infection and other condition variables robustly associate with RMR within our observed range and account for a sizable portion of RMR. This is demonstrated with a much larger sample size than typical of most energetics studies and cannot be explained by the methodological concerns Ocobock raises. Moreover, these findings are consistent with other methods for estimating the costs of infection and immune response (e.g. Straub et al. 2010).

Another major point of our article was to evaluate age-related differences in RMR in adulthood. We found that the cross-sectional decline in RMR with age is similar to that reported in other populations, and that RMR makes up a larger proportion of TEE at older ages. We also find that

anthropometric and other health variables can account for over two-thirds of the age-related decline in RMR. Overall, our findings help motivate new, exciting directions for biological anthropology: How are total energy requirements changing with age and condition in different environments, and how does infection shift energy allocation in ways affecting behavior, reproduction, and maintenance?

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