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Response to the comment by M. J. Kohn on "Tooth enamel mineralization in ungulates: Implications for recovering a primary isotopic time-series," by B. H. Passey and T. E. Cerling (2002)

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We appreciate Kohn's interest in our work and his willingness to provide insight into this challenging subject. Our model is predictive in nature and as such is unwieldy in terms of its actual use for estimating primary input signals from measured isotope signals. Accordingly, Kohn's comment is very welcome in that it outlines a straightforward way in which this can be done. Kohn's approach will be useful in cases where it can be assumed that the input signal (isotopic composition of the body) is repeating and well balanced (see below), that the tooth grows at constant rate, and that the wavelength of the input signal is known.

Nevertheless, we feel it is important to show that cases exist where repeating, but not sinusoidal, input isotope signals give rise to measured signals that appear sinusoidal. In these cases one might be tempted to assume that the input signal is sinusoidal, and thus deem Kohn's method applicable. Climates exist where temperature, rainfall, and other climatic parameters do not have sinusoidal yearly variation (e.g., tropical climates), and even in temperate climates these parameters may not be sinusoidal for a single year, even though the long-term record is sinusoidal. Thus, to the extent that climatic parameters influence isotopic variation in animals, we should not always expect the input signal to be sinusoidal. Further deviations from sinusoidal variation may arise from yearly nonsinusoidal patterns in animal behavior. The following two examples do not criticize Kohn's method, but rather serve to show where the method might be misapplied, and where conclusions based on the method would be erroneous.

In the first example, the structure of an input isotope signal is defined by an isotopic baseline that has a once per year excursion with 90 d length (Fig. 1a). As Kohn shows, the wavelength of any repeating signal will be preserved regardless of the degree of attenuation, and examination of Figure 1a shows this to be the case. The measured signal appears sinusoidal to the extent that one might use Kohn's approach to estimate the amplitude of the input signal. The length of maturation for this scenario is equal to the half-wavelength of the measured signal (180 d), so $lm/t_{\Delta} = 1$, and the expected degree of damping is ~50%. In this case Kohn's method underestimates the amplitude of the input signal by a factor of two and is blind to the true structure of the signal. The method fails partially because the repeating signal is poorly balanced in the sense that the average value of the signal is much closer to the minima than to the maxima (Fig. 1a). Kohn's method works for well balanced repeating signals such as sine waves, where the average value of the signal is intermediate between the minima and maxima.

In the second example, the input signal is the monthly average rainfall recorded at Voi, Kenya from 1904 to 1970 (East African Meteorology Department, 1975). This record is characterized by two periods of increased rainfall during March-April and November-December. Flushes of C_4 grass follow the onset of rainy seasons in this region, and such events are associated with dietary change in some species (Phillipson, 1975; Spinage, 1982; Eltringham, 1982; Prins, 1996). Assuming this record constitutes a reasonable input signal, we model the equivalent signal recorded in tooth enamel with lm = 120 d. The result is approximately sinusoidal (Fig. 1b), and application of Kohn's method yields $t_{\Delta} = 180$ d and $lm/t_{\Delta} = 0.66$, giving ~30% damping for a sinusoidal signal. As with the first example, this approach underestimates the input amplitude and gives erroneous conclusions about the structure of the signal.

The tooth enamel signals in the above examples have features that suggest that the input signal is not sinusoidal, and these might serve to warn the investigator that a sinusoidal input cannot be assumed. However, these features might be missed when sampling resolution is low, or when incomplete yearly cycles are recorded. Many published isotope profiles exist where, regardless of sampling resolution or completeness, it is difficult to distinguish between a sinusoidal or nonsinusoidal input (Fricke and O'Neil, 1996; Stuart-Williams and Schwarcz, 1997; Fricke et al., 1998; Kohn et al., 1998, 2002; Sharp and Cerling, 1998; Feranec and MacFadden, 2000; MacFadden, 2000; Balasse and Ambrose, 2002; Zazzo et al., 2002). A further level of uncertainty lies in the fact that it is yet to be determined whether the linear maturation, constant growth-rate model presented in Passey and Cerling (2002) is applicable to teeth with determinate growth. Owing to these uncertainties, workers should be cautious when using measured signals to make assumptions about input signals.

At this point one might wonder if and when meaningful input signals can be recovered from measured tooth enamel signals, given that superficially similar measured signals are sometimes produced by extremely different input signals. Clearly, there will always be a loss of information when a continuous signal is made discrete and subjected to measurement error, so a perfect estimate of the input signal will never be possible. We mention here that we are now in the final stages of developing inversion methods that are capable of retrieving meaningful

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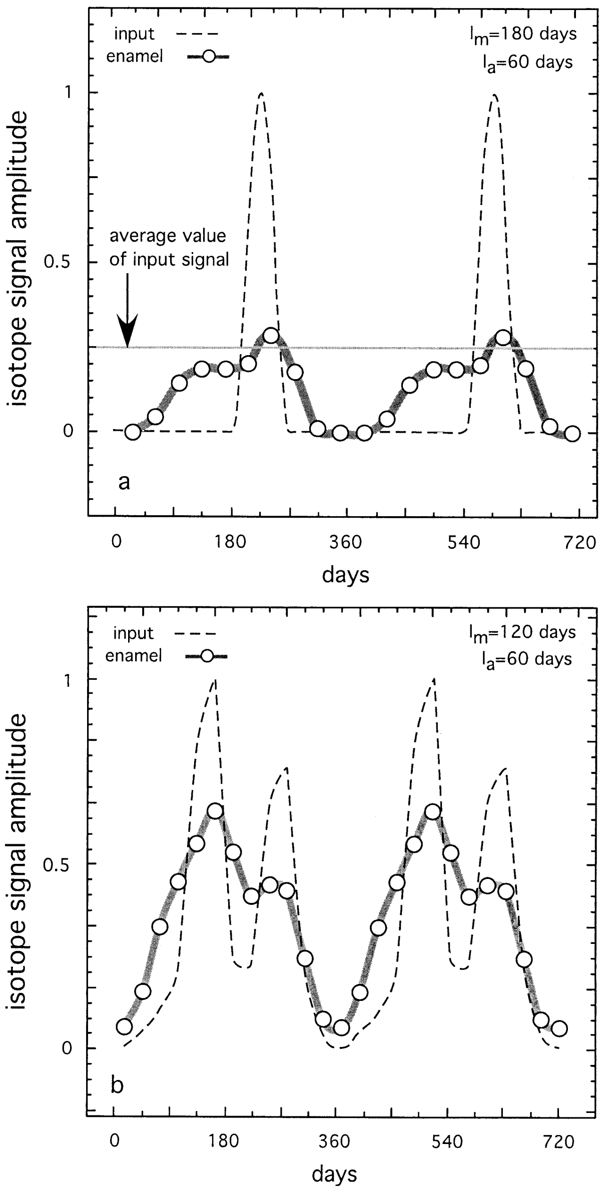

Fig. 1. Examples of nonsinusoidal input signals (dashed lines) that give rise to quasi-sinusoidal tooth enamel signals (gray lines with circles). Tooth enamel signals were modeled from the input signals using eqns. 1, 2, and 3 in Passey and Cerling (2002) with initial mineral fraction (f_{init}) = 0.25. (a) Input signal is synthetic with annual 90 d excursion from baseline. (b) Input signal is average monthly rainfall amount at Voi, Kenya, 1904–1970 (East African Meteorological Department, 1975), normalized on a scale of 0 to 1.

input signals from complex measured signals such as the cases outlined above. We have had success applying these methods to a variety of isotope patterns and we expect these methods to give reliable results for many problems.

We also mention a concern with Kohn's estimate of 2–3 mm for length of maturation (l_m) for small Bovidae. This estimate was made using graphical data in Suga (1982), and our concern arises because l_m = 2–3 mm seems short compared to maturation intervals for similarly sized cow, pig, and goat teeth. In these teeth the maturation length is usually a larger fraction of the overall crown height (e.g., Robinson et al., 1978, 1987; Suga et al., 1979; Passey and Cerling, 2002). Unfortunately, Suga (1982) does not provide a length scale, and it is uncertain whether the magnification factors cited in the figure captions refer to analytical magnification, or postpress magnification. It is also uncertain whether saturation of X-ray absorption in the occlusal portions of figures 1d, 2c, and 3c in Suga (1982) signifies fully mature enamel, or simply absorption saturation for that mineral density. If the latter were true, the apparent length of maturation would be artificially short. A final concern that may or may not be applicable to data in Suga (1982) is that the spatial zone over which enamel matures does not have a fixed length for teeth with determinate growth (not ever-growing, such as all Bovidae molars), and must vanish to zero length during the final stages of maturation. Thus the length of maturation measured on fairly mature teeth can only be considered as a minimum estimate of the maturation time. Future investigators should regard the 2–3 mm estimate for l_m of small bovids in the context of these uncertainties.

Perhaps the most certain conclusion that can be drawn from this discussion and recent developments in this field is that the full potential of isotope profiling of teeth will not be realized until further background work is done. Maturation parameters and attenuation models need to be quantified for a variety of teeth and species, additional methods need to be developed to estimate input signals from measured signals, and yearly patterns of isotopic variation in modern animals need to be characterized for more environments.

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