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## RESEARCH ARTICLE



WILEY

# Some orangutans acquire enamel defects at regular intervals, but not according to seasonal cycles

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## Abstract

**Objectives:** Developmental defects of tooth enamel are associated with systemic physiological stress and have been linked to seasonal environmental factors such as rainfall, temperature, and fruit availability. Here, we evaluate whether linear enamel hypoplasia and accentuated perikymata occur with any cyclicity on lower canines and then whether cycles differ between Bornean and Sumatran orangutans.

**Materials and Methods:** Epoxy casts of lower canines from *Pongo abelii* ( $n = 14$ ) and *P. pygmaeus* ( $n = 33$ ) were evaluated for perikymata and dental enamel defects. Individual developmental sequences (IDSs) were generated for each canine, tracking the position of each defect in the context of continuous perikymata (time). Autocorrelation, a form of time-series statistical analysis was run for each canine to identify whether any cyclicity of defect expression was discernable.

**Results:** Autocorrelation revealed cycles of defect expression within canines, but no common cycle periodicities were identified between individuals of the same species or across species. *P. pygmaeus* averaged more linear enamel hypoplasia per year than *P. abelii*, but no other comparisons (number of defects, number of perikymata between defects, and autocorrelation analysis) revealed differences between the species.

**Discussion:** Although no common patterns of defect expression were identified within or between *P. abelii* and *P. pygmaeus*, the potential for autocorrelation analysis is promising for primatological and paleoanthropological studies of seasonal phenomena.

## KEYWORDS

enamel defects, linear enamel hypoplasia, rLEH, seasonality, stress

## 1 | INTRODUCTION

Ecological factors such as precipitation, rain, and fruiting patterns significantly influence the health and wellness of wild primates (Skinner, 2021; Skinner & Skinner, 2017). In this study, we examine whether orangutan canines exhibit cyclically occurring markers of physiological stress and, if so, whether any difference in pattern is identifiable between Bornean and Sumatran orangutans.

Defects in the density, thickness, or structure of enamel are relatively common during dental development (Hillson & Bond, 1997). Here, we focus on localized, horizontal defects that occur when an individual experiences a systemic, physiological stress that causes an abnormal slowing or cessation of enamel production (Dobney, 1991; Giro, 1947; Goodman & Rose, 1990; Guatelli-Steinberg et al., 2012; Hillson & Bond, 1997; Kreshover, 1960; Newman & Poole, 1974). “Physiological stress” is a non-specific and ambiguous term often used in anthropological studies (Temple & Goodman, 2014). In the case of

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developmental defects of enamel, physiological stress events may refer to insults such as illnesses, infections, cold discomfort, maternal separation, and psychological stress, among others (Dirks et al., 2010; 2002; Goodman & Rose, 1990; Guatelli-Steinberg, 2001; Guatelli-Steinberg & Benderlioglu, 2006; Guatelli-Steinberg et al., 2012; Lemmers et al., 2021; Skinner, 2021; Skinner et al., 2019).

Enamel defects of the type we focus on in this paper may appear as a single, enlarged accentuated perikyma on the enamel surface or as a linear enamel hypoplasia (LEH), which is a wide band (furrow) of depressed enamel involving many afflicted perikymata (Simon Hillson, 2014; Hillson & Bond, 1997). Incrementally formed structures of enamel (perikymata and striae of Retzius) can be used to identify an individual's developmental age associated with enamel defects, as well as the amount of time between the formation of defects (Dirks et al., 2010; Macho et al., 1996; Skinner, 2014; Skinner & Hopwood, 2004).

It has been suggested that the seemingly regular timing and frequency of dental defects in nonhuman primates may represent cycles of increased physiological susceptibility related to local environmental factors (Chollet & Teaford, 2010; Hannibal & Guatelli-Steinberg, 2005; Skinner et al., 2014; Skinner & Hopwood, 2004; Skinner & Pruetz, 2012). Studies have attempted to link developmental defects with environmental and ecological phenomena that occur with a seasonal regularity (e.g., monthly, semi-annual, annual, or supra-annual cycles) such as rainy, dry, and cold seasons as well as seasonal food resource depletion (Chollet & Teaford, 2010; Dirks et al., 2002; 2010; Macho et al., 1996; Skinner, 1986, 2014, 2021; Skinner et al., 1995; Skinner & Hopwood, 2004; Smith & Boesch, 2015). Previous studies of *Pongo* have indicated that *Pongo pygmaeus* and *P. abelii* may exhibit different cycle periodicities due to environmental differences between Borneo and Sumatra (Skinner, 2014; Skinner & Hopwood, 2004; Skinner & Skinner, 2017). In both Borneo and Sumatra, orangutans subsist primarily on ripe fruits, followed distantly by leaves and bark (Kanamori et al., 2010; Knott, 1998; Wich et al., 2006). Soft-pulp fruits are strongly preferred to hard fruits with hard skins (Kanamori et al., 2010). While Borneo and Sumatra are characterized as having both seasonal environments, the timing, duration, and magnitude of seasonal phenological changes varies year to year. Both islands are subject to mast fruiting events that happen on an irregular, supra-annual schedule which has been known to significantly alter dietary patterns and physiological responses to subsequent months of low fruit availability in Bornean orangutans, but not Sumatran orangutans (Knott, 1998; van Schaik & van Noordwijk, 1985; Wich et al., 2006). Sumatra has two dry seasons per year, one of which corresponds to an annual peak in fruit availability, but the timing and size of the peak in fruit availability can be quite variable (van Schaik, 1986; van Schaik & van Noordwijk, 1985).

A major challenge has been defining seasonal and/or cyclical patterns of defect expression. In the present study, the word "cycle" refers to a regular pattern of defect occurrence within an individual; a cycle's "periodicity" refers to cycle duration. Skinner and colleagues (Skinner, 2014, 2021; Skinner & Hopwood, 2004) have counted perikymata between sets of adjacent LEH, averaging the time between all defect pairs from multiple individuals. In doing so, they found clusters of six, 12, and 18 months between defects. These clusters, however, reflect means in the sample and do not necessarily reveal the

frequency with which *individuals* have experienced repetitive stress events with 6-, 12-, or 18-month periodicity.

The present study evaluates whether developmental defects of enamel occur on a cyclical schedule in orangutans from Sumatra or Borneo (*P. abelii* and *P. pygmaeus*, respectively), and, if so, whether a common periodicity for the individuals of either or both orangutan species. To address these questions, this study applies time series analysis to the chronological sequence of defects over individuals' lower canine crown formation times.

## 1.1 | Enamel defects in Bornean and Sumatran orangutans

Physiological responses to environmental conditions have been compared extensively between *P. pygmaeus* and *P. abelii* using dental developmental defects (Guatelli-Steinberg et al., 2012; Hannibal & Guatelli-Steinberg, 2005; Skinner, 2014; Skinner & Hopwood, 2004). Orangutans have some of the highest rates of dental defects compared to other primates and are therefore well-suited for studies seeking to understand the repetitive nature and regularity of developmental defects as they may relate to environmental conditions (Guatelli-Steinberg, 2001; Guatelli-Steinberg et al., 2012; Hannibal & Guatelli-Steinberg, 2005; Newell et al., 2006).

Skinner and Hopwood (2004) found significantly more perikymata between defects in *P. abelii* than *P. pygmaeus* (36.5 vs. 25.6 perikymata, respectively). Guatelli-Steinberg et al. (2012) found that *P. abelii* had significantly more defects per tooth than *P. pygmaeus* ( $7.5 \pm 2.8$  and  $4.5 \pm 2.0$ , respectively). This implies that, with a greater number of LEH per tooth, the average counts of perikymata between LEH should be fewer for *P. abelii* than *P. pygmaeus*, reflecting more stress episodes and shorter intervals between episodes. This study appears to conflict with that of Skinner and Hopwood (2004), who concluded that *P. abelii* had more perikymata between LEH, longer cycles (on the order of 12 months), and were, overall, less stressed than *P. pygmaeus*. Skinner (2014) continued this line of investigation by comparing the average amount of time (number of perikymata\* repeat interval) between adjacent LEH in Bornean and Sumatran orangutans to identify the periodicity of the defect expression cycles and to test the hypothesis that Borneo is an inferior habitat (i.e., is more stressful) compared to Sumatra for orangutans. Skinner took the natural log of the perikymata counts between adjacent LEH (inter-LEH perikymata counts) and identified three clusters with means close to 6-, 12-, and, rarely, 18-month intervals. He concluded that Borneo is an inferior environment because the inter-LEH perikymata counts trend towards a mean of 6 months whereas the Sumatran orangutans have inter-LEH perikymata counts that trend towards a mean of one year. Most recently, *P. abelii* was revealed to have significantly deeper defects (Skinner & Skinner, 2017), suggesting more frequent and more severe physiological perturbations in Sumatra.

The source of these inconsistent results may be that while Guatelli-Steinberg et al. (2012) compare the total number of defects per tooth, Skinner and Hopwood (2004) and Skinner (2014) consider each pair of LEH as independent data points (as well as number of perikymata between LEH). A tooth's crown formation time provides a "window of vulnerability" for developmental defects to be acquired (Guatelli-Steinberg, 2001, 2004; Guatelli-Steinberg et al., 2012; Guatelli-Steinberg & Skinner, 2000). Thus,

the more defects that occur over the course of a fixed formation time, the fewer perikymata can be counted between any pairs.

If seasonal environment factors are driving the physiological stress episodes that result in dental developmental defects, it is important to consider the events as a function of and in the context of time. Since perikymata record regular intervals of dental developmental time and are visible on the surface of the tooth, they are used here as a proxy for time. Each perikyma represents a certain number of days of development. For *Pongo*, each canine records several years of an individual's development and the episodes of physiological stress experienced by that individual (Schwartz et al., 2001). Each canine should therefore represent a single set of data that records the total development time, location of each defect, and the amount of time between defects (via the number of perikymata). Thus, this project attempts to investigate the question of environment and developmental stress further by detecting cycles of stress within an individual's developmental time sequence.

## 2 | MATERIALS AND METHODS

### 2.1 | Sample

The *P. abelii* and *P. pygmaeus* samples come from Harvard's Museum of Comparative Zoology, the American Museum of Natural History, and the Smithsonian National Museum of Natural History (Table 1).

**TABLE 1** Sample by sex and species

Species	Specimen number	Sex	Museum	Locality
<i>P. abelii</i>	37518, 37519	F	MCZ	Neys collection (Sumatra)
	143596, 143600	F	Smithsonian	Aru Bay, Indonesia, Asia
	270807	F	Smithsonian	Locality unknown
<i>P. abelii</i>	37516, 37517, 50960	M	MCZ	Neys collection (Sumatra)
	143587, 143588, 143591, 143593, 143594	M	Smithsonian	Aru Bay, Indonesia, Asia
	578647	M	Smithsonian	Locality unknown
<i>P. pygmaeus</i>	80088	F	AMNH	Locality unknown
	18010, 200900	F	AMNH	Borneo
	35549, 239847	F	AMNH	Zoo
	37363, 37364, 37365, 50958	F	MCZ	Kinabatangan River, Borneo
	11111, 153833	F	Smithsonian	Indonesia
	142169, 142170	F	Smithsonian	Sungai Sama, Indonesia
	145303, 145306, 145309, 145321	F	Smithsonian	Sempang River, Indonesia
	153808, 153822	F	Smithsonian	Kendawangan River, Indonesia
	153828	F	Smithsonian	Mambuluh River, Indonesia
197664	F	Smithsonian	Sungai Menganne, Indonesia	
<i>P. pygmaeus</i>	28252	M	AMNH	Borneo
	140426	M	AMNH	Sandakan, Borneo
	5061, 5211, 5296, 5296x, 37358	M	MCZ	Kinabatangan River, Borneo
	142200	M	Smithsonian	Sakaam River, Indonesia
	145301	M	Smithsonian	Sempang River, Bayu, Indonesia
	153823	M	Smithsonian	Kendawangan River, Lanchut, Indonesia
	546840, 153834B	M	Smithsonian	Indonesia

Zoo specimens were used for perikymata counts, but their developmental defects were not analyzed. Although the wild specimens stem from a variety of collections, nine *P. pygmaeus* individuals were all caught and killed within a 3-month period in 1937 along the Kinabatangan River at Camp Abai in Borneo (Carpenter, 1939). These individuals can serve as a conservative sub-sample and may have been more likely than the rest of the sample to have experienced similar environmental conditions.

No difference in perikymata distributions were noticed between zoo and wild-caught specimens. Lower canines were chosen because they have a growth period of several years, allowing multiple LEH to appear on a single tooth, and, in great apes, have been documented to record 99% of all the LEH evidenced in the rest of an individual's dentition (Guatelli-Steinberg & Skinner, 2000; Skinner, 1986). A tooth was only used for analysis if more than 70% of its original crown height was present.

### 2.2 | Casts

Lower canines (Table 1) were cleaned with acetone prior to taking dental impressions of the labial surfaces using Coltene's President Jet Regular Body dental impression material and casts of the impressions were made using Struer's Epofix dyed red to enhance microscope viewing (Dean & Reid, 2001; Guatelli-Steinberg et al., 2007; Guatelli-Steinberg & Reid, 2010; Reid & Dean, 2000, 2006). When both an individual's left and right canines were present, both teeth were cast

so defects could be compared between the antimeres, although only the side with the more visible incremental structures was used for analysis. Sex was assigned according to the museum's designation.

## 2.3 | Crown height reconstruction

Crown height is the vertical distance from cemento-enamel junction (CEJ) to the tip of the crown and follows the midline of the tooth (Plavcan, 1993). For teeth that were partially worn, original crown heights were digitally reconstructed following the method described by Saunders et al. (2007) and further confirmed by Guatelli-Steinberg et al. (2009).

## 2.4 | Identifying enamel defects

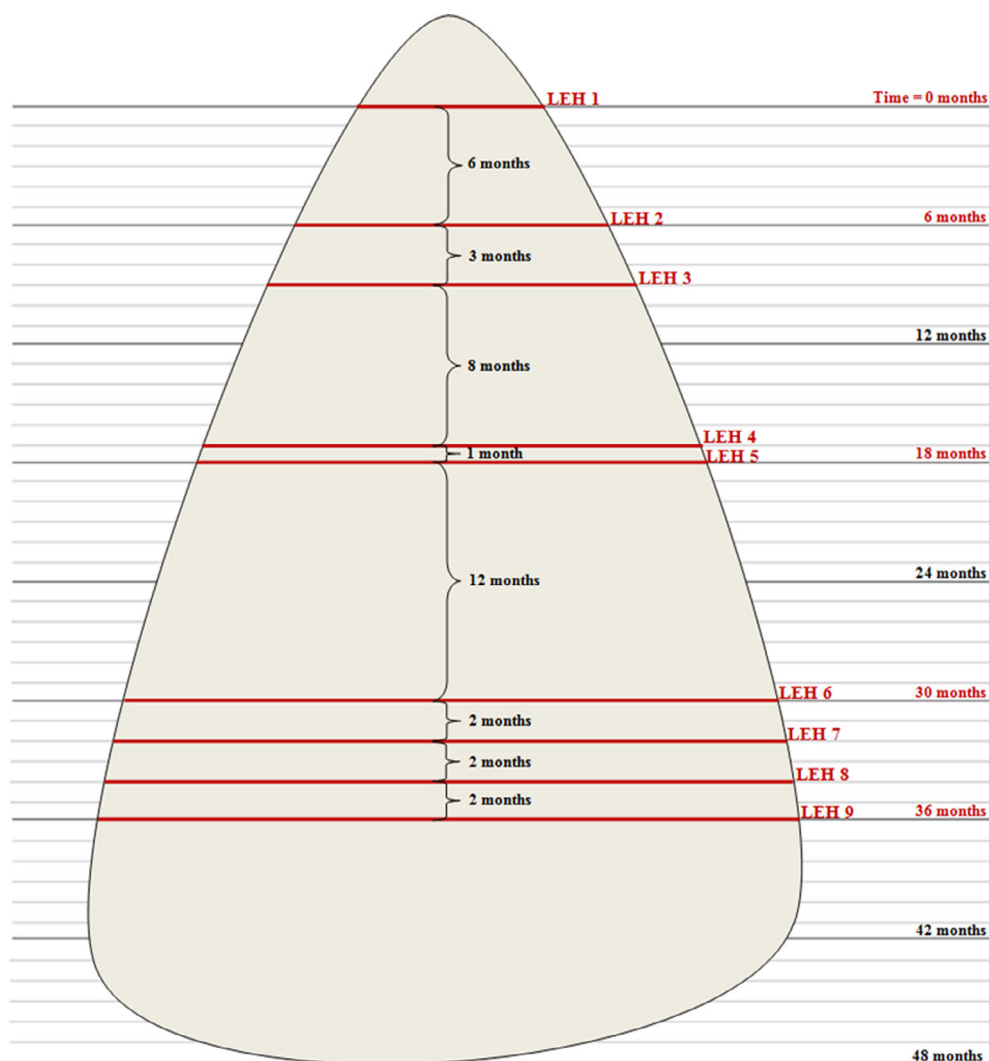
Each defect was recorded as either a linear enamel hypoplasia (LEH) or an accentuated perikyma (AP). The two are differentiated by the number of perikymata associated with the defect: if a defect appeared as a single, wide perikyma compared to those around it, it was reported as an accentuated perikyma. If multiple perikymata appeared larger than expected

and were associated with a depressed area of enamel thickness, it was considered a linear enamel hypoplasia. As the crown develops from the cusp tips to the CEJ, the earliest enamel defects are those closest to the tip and furthest from the CEJ (Figure 1). Accordingly, the initiation of each defect was recorded as the distance between the incisal border of a defect to the CEJ using the measuring microscope.

Enamel defects were recorded when they could be identified with a measuring microscope (50 $\times$ ), on the canine's antimeres, and with a hand lens (10 $\times$ ). Identifying each defect on the tooth's antimeres confirmed that the defect was systemic and not a localized defect (Goodman & Rose, 1990). After a minimum of 1 month following the first observation, each recorded defect was re-identified using the antimeres and a hand lens.

## 2.5 | Standard Perikymata profiles

To accurately identify cycles in defect expression, a technique must be employed that can evaluate the entire sequence of enamel growth and identify an underlying cycle of defects despite skipped cycles and/or defects that occur outside of the cycle (referred to here as non-cyclic



**FIGURE 1** A hypothetical individual's complete sequence of developmental defects. A 6-month cycle is evident (LEH 1, 2, 5, 6, and 9), though there are several extra, non-cyclic defects adding noise and driving the average amount of time between defects down to 4.5 months, with a mode of 2 months. Note that the 6-month cycle was skipped at the 12- and 24-month mark.

defects, Figures 1 and 2). To consider all defects within the context of their developmental time, time must be continuous and accounted for across the enamel surface. For this purpose, standard perikymata profiles (SPP) were developed so an individual's entire complement of dental defects could be considered in the sequence of crown development, even when surface wear obscured perikymata between defects (O'Hara, 2017).

The position of each defect (in millimeters from the CEJ) was scaled to the standard tooth's crown height (O'Hara, 2017: Figure 1). The SPP was opened in ImageJ and the scale was set so that the known distance for the height of the columns was the SPP crown height. Once the scale was set, the standardized position of each defect was saved as a horizontal line on the image using the Ctrl+B function. Since each perikymata was numbered, the perikymata position that each defect was associated with was recorded from the minimum, mean, and maximum columns. The perikymata position of each defect was used to create a string of binary data (the IDS, individual defect sequence) where a "1" represents the onset of a defect and a "0" represents a perikymata that is not associated with the onset of a defect. Three IDSs were created for each individual: a minimum, mean, and maximum sequence of dental development. Finally, the number of perikymata was counted between each defect on the IDS.

## 2.6 | Rate of defect acquisition

Comparing the average number of defects per tooth is not very informative because each sex and species has a different "window of vulnerability" for acquiring defects (Guatelli-Steinberg, 2001, 2004; Guatelli-Steinberg et al., 2012; Guatelli-Steinberg & Skinner, 2000). The window of vulnerability is directly related to the lateral enamel formation time; a longer development time provides more opportunity for the acquisition of defects.

The amount of time between adjacent defects was calculated by counting the perikymata between them and multiplying by the species' perikymata repeat interval (Skinner, 2014; Skinner & Hopwood, 2004). The time represented by one perikymata depends on the number of days associated with that individual's underlying striae of Retzius. The repeat interval of a canine cannot be established without sectioning the tooth and counting the number of daily cross-striations between striae. Previously, this problem has been overcome by multiplying the number of perikymata by the modal repeat interval for the species (e.g., Skinner (2014) used RI = 10 days for *Pongo*). However, this method is problematic, as it does not represent the range of variation that exists for the species. This study reports a range of possible days between defects using RI = 8–11, as previously reported (Schwartz et al., 2001; Smith, 2016).

## 2.7 | Analyzing the time between adjacent defects

### 2.7.1 | Comparing to a random distribution

Dental enamel defects can be acquired for many reasons and could be formed at random intervals. Comparing the number of perikymata

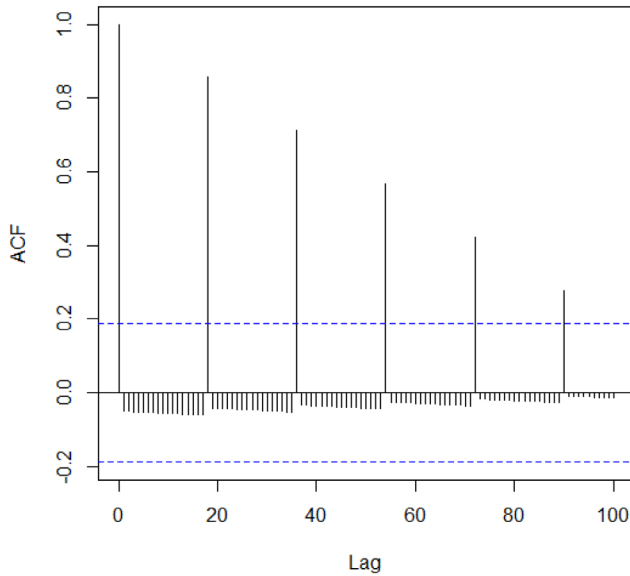
between defects to randomly generated distributions can establish whether the observed distribution could be caused by chance alone. If the amount of time between defects can be caused by chance, then an underlying cycle of physiological stress may not be necessary to explain the pattern of perikymata distribution (Skinner, 2014). If, however, cycles of physiological stress occur, we would expect the observed distribution of inter-LEH perikymata counts to have a narrow distribution, centered around the cycle periodicity while the randomly generated distribution of inter-LEH intervals may be broader and centered on a different perikymata mean. We seek to test whether central tendencies and distributions of inter-LEH perikymata counts could be a natural result of the number of perikymata related to the number of defects on a tooth. If so, randomly generated teeth with the same number of LEH as real teeth could produce inter-LEH perikymata distributions that match those of wild orangutans.

Attempts to compare the number of perikymata between defects to a randomly generated distribution have been performed before. Skinner (Skinner, 2014; Skinner & Skinner, 2017) took the total number of perikymata found on the surface of *P. pygmaeus* lower canines (~200) and used a table of random numbers to select two perikymata positions from 2–200. These authors identified the number of perikymata between the two positions and compared the distribution to the actual distribution of the number of perikymata between defects. Skinner (2014) found that the median time interval between defects for the randomly generated sample was significantly larger (2.64 years) than the observed interval (0.64 years) and concluded that the number of perikymata between defects for *P. pygmaeus* and *P. abelii* could not be explained by chance alone. However, by only selecting two perikymata positions for a span of 200 perikymata, Skinner's randomization criteria assumes that each tooth only had two defects. The more defects a tooth exhibits, the fewer perikymata can be found between any pair of defects. Later, Skinner (2021) incorporated multiple defects when randomly generating defects on chimpanzee canines. However, his method produced a right-skewed distribution in the number of perikymata between LEH by randomly selecting the position of the first LEH between 1 and 200 and then forcing LEH to be added until only one perikymata was left on the simulated tooth. For example, if the position of the first LEH was at perikymata #100, the second LEH could only fall between 100 and 200. If the second LEH was at perikymata #180, the third LEH must fall between 180 and 200. LEH were added until there was only one perikymata between the last LEH and the cervix. Thus, in Skinner's (2021) Figure 6, all 1000 generated teeth have 1 perikymata between at least one pair of defects. Again, Skinner found that the number of perikymata between LEH differed significantly from randomly generated LEH.

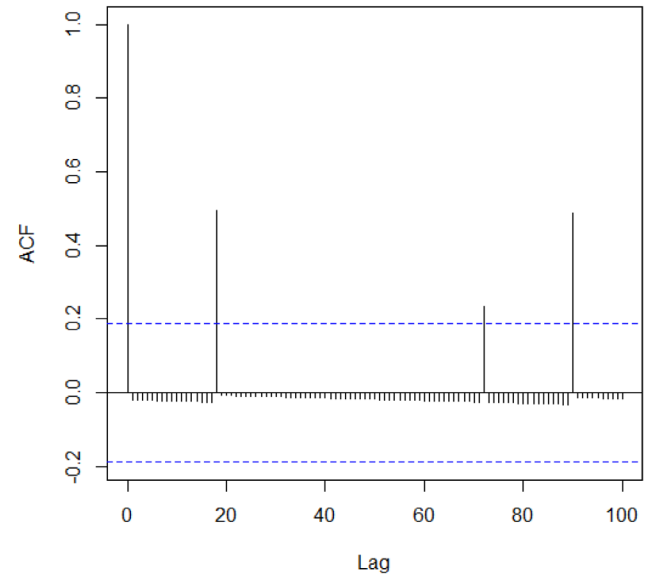
Here, a randomly generated sample of the number of perikymata between defects was based on the number of individuals and number of defects per tooth for a particular sex and species. Predetermining the number of defects per tooth to match the observed sample was an attempt to produce randomly generated LEH based on empirical observations. Using the R code "randompk" (Supplemental Information Section 1), perikymata positions for the number of individuals and the number of defects per individual were randomly generated.

**(a) Perfect cyclicity**

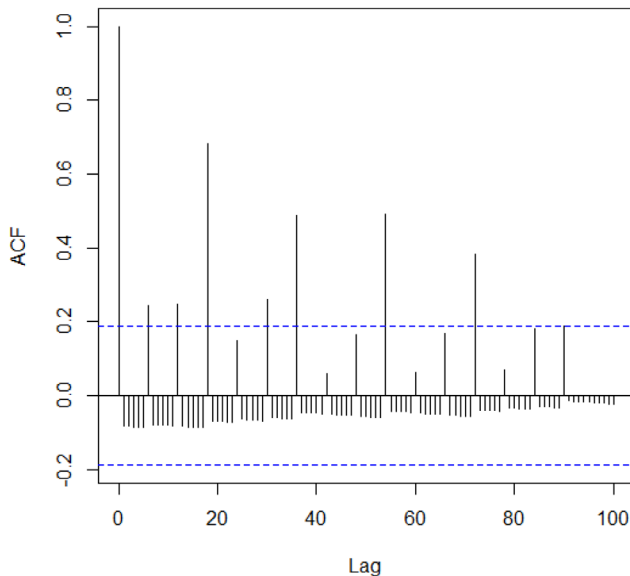
Total Defects: 7  
Cyclic Defects: 7 (*skipped phases: 0*)  
Non-cyclic Defects: 0  
Significant Lags: 18, 36, 54, 72, 90

**(b) Cyclicity with skipped cycles**

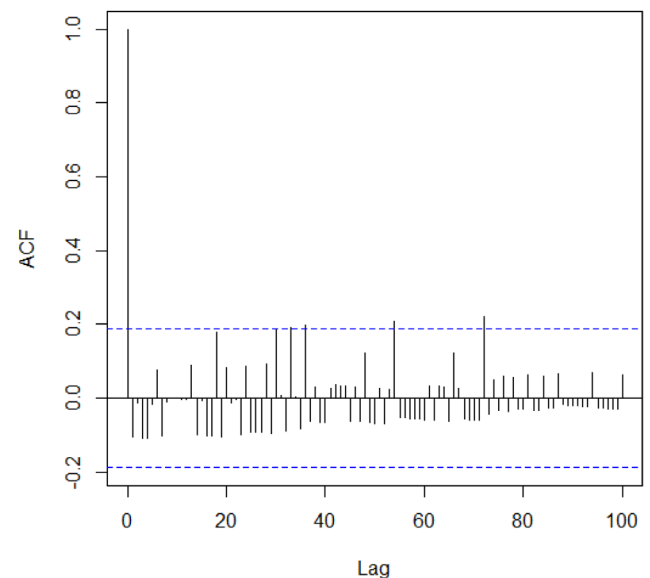
Total Defects: 4  
Cyclic Defects: 4 (*skipped phases: 3*)  
Non-cyclic Defects: 0  
Significant Lags: 18, 72, 90

**(c) Cyclicity with noise**

Total Defects: 10  
Cyclic Defects: 7 (*skipped phases: 0*)  
Non-cyclic Defects: 3  
Significant Lags: 6, 12, 18, 30, 36, 54, 72

**(d) Cyclicity with noise and skipped cycles**

Total Defects: 8  
Cyclic Defects: 5 (*skipped phases: 2*)  
Non-cyclic Defects: 7  
Significant Lags: 33, 36, 54, 72



**FIGURE 2** Autocorrelation Plots. There are four scenarios shown with different combinations of number of defects (a-d), skipped cycles (b, d), and extra non-cyclic cycles (c, d). All four scenarios reveal a cycle period of 18 because the common factor for the lags is 18 (ACF values is greater than the 95% confidence interval). When non-cyclic defects are included, some significant lags appear that are not factors of 18, but their correlation values tends to be lower than that of the cyclic defects.

The number of perikymata between each generated defect was calculated. This process was repeated three times to create three randomly generated samples. Then, each of the randomly generated samples was compared to the actual distribution of number of perikymata between defects using a Mann-Whitney  $U$  test.

## 2.7.2 | Comparing average time between defects across species

The median number of enamel defects (accentuated perikymata and LEH), perikymata between defects, and average number of defects per year were compared using Mann-Whitney  $U$  tests for the *Pongo* specimens. The tests were performed with all specimens, first using only males, and then only females.

To compare the average number of defects per year, the total number of defects was divided by each sex and species' lateral crown formation time (LCFT). LCFTs were calculated using the mean SPP estimate for the number of perikymata per decile. Details of how this metric was calculated can be found in Supplemental Information Section 2.

## 2.8 | Identifying cycles using autocorrelation

Autocorrelation is a time series analysis that can identify cycles even when phases are skipped and extra, non-cyclic defects are present (Figures 1 and 2). The autocorrelation function takes a string of time-series data (here, the IDS), compares it to itself in a series of iterative analyses, and calculates the correlation between the original data and the copied data for each iteration (Venables & Ripley, 2002). The original time series data set is copied and compared to itself; since it is an exact copy, the correlation is  $r = 1.00$ . This initial comparison is called "lag 0" and always returns the same result. Lag 1 follows the same procedure, but the copied dataset is shifted down one time step (in the case of the IDS, one perikymata position). The correlation between the original IDS and the copied and shifted IDS is calculated. For each subsequent "lag" position, the entire time series is shifted down another time step and the correlation is re-calculated. This is continued until the copied and shifted IDS reaches the last time-point on the original IDS. A line graph of the autocorrelation value associated with each lag is plotted and used to identify significant lags (Figure 2). "Significant lags" are those with autocorrelation values (ACF) that exceed the 95% confidence interval and therefore indicate that the probability of such a correlation occurring randomly is significantly unlikely (Venables & Ripley, 2002). When multiple statistically significant lags exist for a single time series, the period (or duration) of a cycle can be identified by identifying a common factor for the significant lag positions (Figure 2).

An R code, "GsSID" (Supplemental Information Section 2), took each IDS and identified the significant lags (those with a correlation value greater than the 95% confidence interval, Figure 2). Common factors for significant lags were reported for each analysis as the

duration of potential cycles (the cycle periodicity). This process was repeated each tooth in the sample.

Autocorrelation analysis makes it possible to identify cycles even when certain phases are skipped and extra defects exist. Autocorrelation is a robust analysis, but its ability to identify cycles is reduced with multiple skips and non-cyclic defects. For example, in Figure 2, the autocorrelation values only barely surpass the 95% confidence interval. To reduce some of the potential noise in the dataset and make the results directly comparable to earlier studies, the accentuated perikymata were removed from the IDS and the autocorrelation was run a second time for every individual in the sample (except for those specimens that only had LEH and no accentuated perikymata). Finally, for a conservative analysis, the first defect, both with and without the accentuated perikymata, was deleted and the remaining time series set was analyzed for a third and fourth time. The cycle periodicity for each individual's four sets of autocorrelation analyses was tallied.

## 3 | RESULTS

### 3.1 | Standard perikymata profiles

The standard perikymata profiles and the data used to generate them can be found in Supplemental Information Section 3. A decile was left blank on the SPP if perikymata counts for that decile had only been possible for a single individual. A SPP was only generated if five or more deciles could be included. It was not possible to generate standard perikymata profiles for *P. abelii* females. *P. abelii* females were evaluated for perikymata, but only three deciles could be included.

### 3.2 | Number of defects per tooth and rate of acquisition

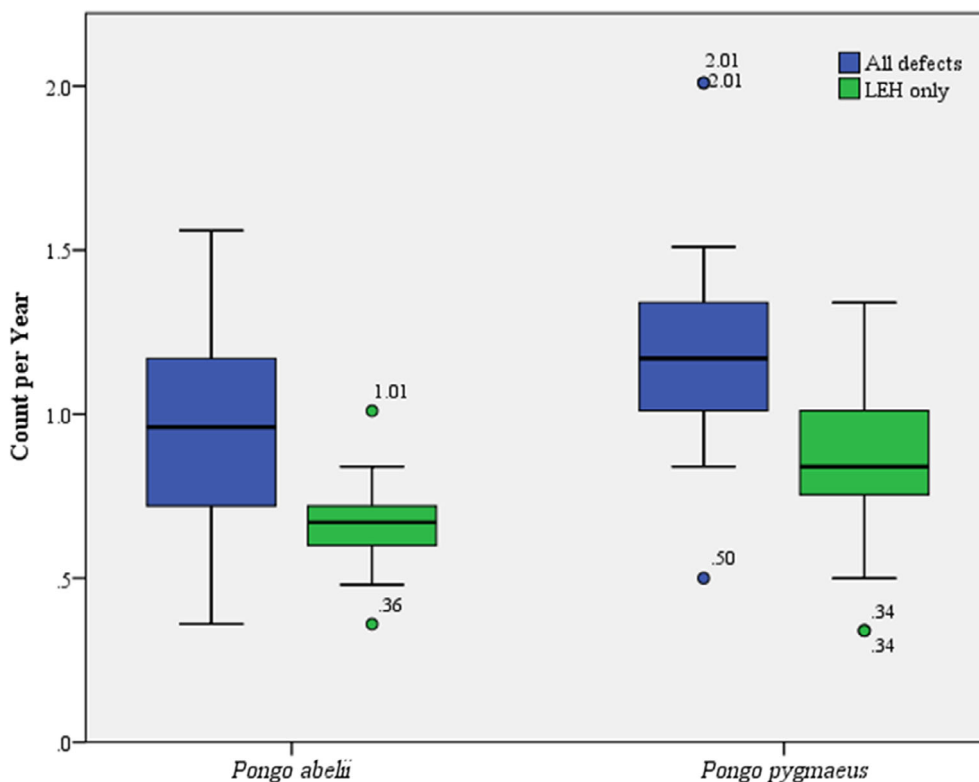
Descriptive statistics for the total number of defects (accentuated perikymata and LEH) per tooth can be found in Table 2. Table 2 identifies the average number of defects acquired per year for each sex and species. The number of defects found per tooth was divided by the LCFT identified for its sex and species in Table S5. When the window of opportunity for acquiring defects is taken into account, the rate of acquisition becomes clearer. If dental defects were being acquired semi-annually, a rate of 2 defects per year would be expected. However, no species or sex gets close to a rate of 2 defects per year (Table 2, Figure 3). The possibility of an annual rate of defect acquisition has some support. *P. pygmaeus* males, and *P. abelii* females all average close to 1 defect per year (1.02, 1.01, and 1.07, respectively).

A t-test revealed no difference between species in the average number of total defects acquired per year (Table 3). However, a statistically significant difference was identified in the average number of LEH acquired per year: *P. pygmaeus* averaged 0.86 LEH per year while *P. abelii* only acquired an average of 0.69 (Table 3, Figure 3).



**TABLE 2** Number of defects per tooth and calculated defects per year

Species	Sex	All defects				LEH only			
		Total per tooth		Per year		Total per tooth		Per year	
		Mean	Median	Mean	Median	Mean	Median	Mean	Median
<i>P. abelii</i>	F	6.40	6	1.07	1.01	4.60	4	0.69	0.74
<i>P. pygmaeus</i>	F	6.86	6	1.19	1.17	5.11	5	0.86	0.84
<i>P. abelii</i>	M	7.56	7	0.91	0.84	5.11	5	0.61	0.60
<i>P. pygmaeus</i>	M	8.42	8	1.01	0.98	5.58	6	0.77	0.67

**FIGURE 3** Average developmental defects acquired per year

### 3.3 | Analyzing the time between adjacent defects

#### 3.3.1 | Number of perikymata between defects

The number of perikymata between adjacent defects was estimated using SPPs. Descriptive statistics were calculated for the entire species and for the sexes separately (Table 4). Mann-Whitney *U* tests revealed no significant difference in the number of perikymata between defects between *P. abelii* and *P. pygmaeus* (Table 4). A histogram of the percent of observations of the number of perikymata between defects illustrates how similar the distributions of *P. pygmaeus* and *P. abelii* are to one another (Figure 4).

#### 3.3.2 | Comparing to a randomly generated distribution of defects

Perikymata positions, descriptive statistics for each randomly generated set of defects, and the details of the Mann-Whitney *U* tests can

be found in Supplemental Information Section 3. Table 5 reports the *p*-values of the Mann-Whitney *U* tests comparing the actual number of perikymata between defects to the number counted for three sets of randomly generated defects. For every sex and species evaluated here, the average observed number of perikymata between defects failed to differ from a randomly generated data set at least once (Table 5), making it impossible to reject the possibility that the observed perikymata counts between defects was due to chance alone.

### 3.4 | Identifying cycles using autocorrelation

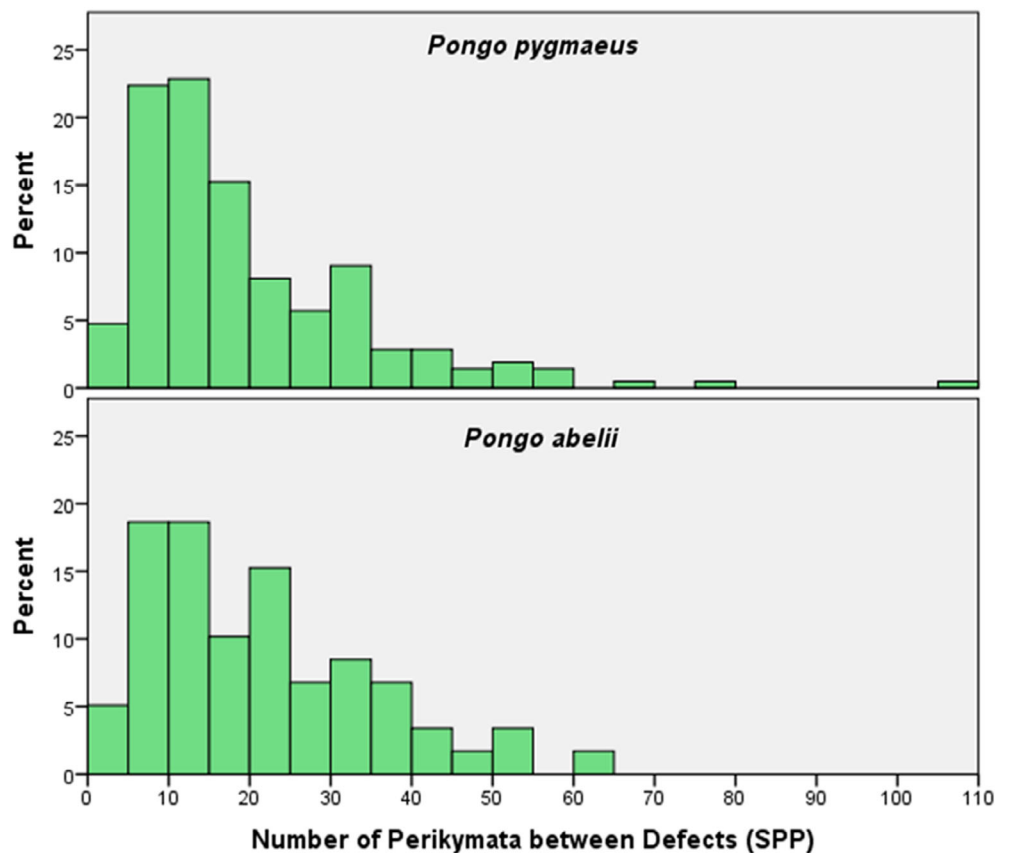
Supplemental Information Section 4 contains all the autocorrelation plots, significant lags, and potential cycle periodicities for every individual in this study and summary tables for each species (Tables S12 and S13). Table 6 details the number of individuals per species that exhibited each cycle periodicity (number of perikymata per cycle). The threshold for including a cycle periodicity in Table 6 was set

**TABLE 3** Comparison of observed number of defects and LEH per year.

Defects	Species	<i>n</i>	Mean	St. dev.	<i>t</i>	Sig.
All defects	<i>P. abelii</i>	14	0.97	0.33	−1.809	0.080
	<i>P. pygmaeus</i>	19	1.19	0.36		
LEH only	<i>P. abelii</i>	14	0.67	0.17	−2.314	0.027*
	<i>P. pygmaeus</i>	19	0.86	0.27		

\**p* > 0.05.**TABLE 4** Number of perikymata estimated by SPPs between defects.

Species	Sex	<i>n</i> (pairs)	Mean	Standard deviation	Kolmogorov–Smirnov sig.	Mann–Whitney <i>U</i>	Sig.
<i>P. abelii</i>	M	59	20.46	13.76	0.003*	5728	0.376
<i>P. pygmaeus</i>	all	210	19.11	14.62	0.000*		
	F	123	17.84	12.64	0.000*		
	M	87	20.91	16.95	0.000*		

\**p* > 0.05.**FIGURE 4** Number of perikymata between defects for *P. pygmaeus* and *P. abelii*.**TABLE 5** Randomly generated distributions compared to the actual distribution

	Sex	Random 1	Random 2	Random 3	All random
<i>P. abelii</i>	M	0.180	0.031*	0.249	0.016*
<i>P. pygmaeus</i>	F	0.068	0.003*	0.000*	0.007*
	M	0.011*	0.085	0.164	0.094

**TABLE 6** Autocorrelation: number of individual developmental sequences (IDSs) that expressed cyclicity of any number of perikymata (4–64, bolded)

	4	5	6	7	8	9	10	11	12	13	15	16	17	18	19	24	32	41	48	64
<b>% of n with cycles of any length</b>	<b>5</b>	<b>2</b>	<b>2</b>	<b>2</b>	<b>2</b>	<b>2</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>2</b>	<b>2</b>	<b>1</b>	<b>2</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>
<i>P. abelii</i>	(6 of 9)																			
<i>P. pygmaeus</i>	(14 of 31)																			
	66.7%																			
	45.2%																			

deliberately low: a cycle periodicity only needed to be found in one of the four sets of autocorrelation analyses run for each individual to be included (all defects, only LEH, all defects excluding first, and only LEH excluding the first).

In some cases, it was possible to identify multiple cycles within a single tooth, many of which were multiples of each other (e.g., 8, 16, and 32 perikymata, as  $8 \times 2 = 16$  and  $16 \times 2 = 32$ ). When multiple cycle periodicities were identified, all possibilities were reported on Tables 8 and 9 because it is impossible to know which may be the “true” cycle for that individual (e.g., *P. pygmaeus* 145321, Table 7) and it is also possible for an individual to express multiple, overlapping cycles with different periodicities (Macho et al., 1996). Table 7 highlights the cycle periodicities that would fall within the range of 3-, 6-, 12-, and 18-month long cycles and identifies the number of individuals from each species that expressed cycles falling within the defined ranges.

Six of the nine individuals (66.7%) in the *P. abelii* sample evinced cycles; cycles of any duration were impossible to identify in the other three individuals (Table 6, “% of sample with cycles”). Of the cycle periodicities identified for *P. abelii*, a periodicity of four perikymata was the most frequent (five of the six individuals for which cycles were identifiable and 55.5% of the total *P. abelii* sample). A periodicity of four perikymata corresponds to a cycle duration of 32 to 44 days. The second-most common periodicities were six, seven, eight, and 16 perikymata, each of which had been identified in a total of two individuals. Periodicities of six to eight correspond to 48–66, 56–77, and 64–88 days, respectively.

Cycles were identified in less than half of the *P. pygmaeus* individuals (45.2%). Like *P. abelii*, the most common cycle periodicity identified was four perikymata. A cycle periodicity of four perikymata was found in nine individuals, 29% of the *P. pygmaeus* sample. The next most common cycle periodicities were seven, six, and nine perikymata, respectively. The ranges for the corresponding number of days for cycle periodicities of four, six, and seven, are the same for those described for *P. abelii*. A cycle periodicity of nine perikymata would correspond to a cycle duration of 72–99 days.

Of all the orangutans, only one *P. pygmaeus* individual (MCZ 5211) has a cycle periodicity that falls within the range expected for a yearly cycle of physiological stress (Table 7). *P. pygmaeus* and *P. abelii* individuals both express cycles that fall within the expected ranges for cycles of 3, 6, and 18 months (Table 7). Only six of the 31 *P. pygmaeus* individuals (19.4%) have a cycle periodicity that falls within the range of 6 months, indicating a cycle of that length is neither ubiquitous, nor common in the species.

## 4 | DISCUSSION

### 4.1 | *P. pygmaeus* versus *P. abelii*

A series of descriptive, comparative, and time-series analyses were performed to compare the timing of dental developmental defects between the two species. Due to sexually dimorphic crown formation

**TABLE 7** Cycle periodicities potentially falling within 3, 6, 12, or 18 months

Range of days based on 28-31 day months	Range of cycle periodicities based on repeat interval			
	3 months 84-93 days	6 months 166-186 days	12 months 336-372 days	18 months 504-558 days
RI = 8-11	8-11 perikymata	16-23 perikymata	31-46 perikymata	46-69 perikymata
<i>P. abelii</i>	3	2	0	1
50960	M 11			
143587	M 8			
143593	M 8	16		64
578647	M	16		
<i>P. pygmaeus</i>	6	6	1	1
5211 <sup>a</sup>	M		41	
5296x <sup>a</sup>	M 8			
11111	F	19		
37358 <sup>a</sup>	M 9, 11	17		
145309	F 9			
145321	F 8, 9	16		48
153823	M 9, 10	19		
153833	F 8	18		

<sup>a</sup>Kinabatangan River, Camp Abai, Borneo.

**TABLE 8** Differences between males and females

Species		Number of defects acquired per year		Number of Perikymata between defects	
		Mean ± SD	Sig.	Mean ± SD	Sig.
<i>P. pygmaeus</i>	F	1.19 ± 0.37	0.085	17.84 ± 12.64	0.247
	M	1.01 ± 0.35		20.91 ± 16.65	

**TABLE 9** One month cycles

	<i>n</i>	Individuals with cycles of any periodicity	Individuals with periodicities within a 1-month range	1-month periodicities that are sub-factors of another periodicity
<i>P. abelii</i>	9	6	5	3 (60%)
<i>P. pygmaeus</i>	31	14	9	4 (44.4%)

times, the number of defects per tooth should only be compared by sex. Females averaged fewer defects per tooth and more defects per year for both species, which is expected given their shorter crown formation times and windows of vulnerability.

Both *P. pygmaeus* and *P. abelii* averaged close to one defect per year (0.97 and 1.19, respectively) (Table 4). Additionally, there were two *P. pygmaeus* individuals that acquired defects at a rate of 2.01 per year. However, this evidence is not sufficient to conclude that the orangutan species experience physiological stress events annually or semi-annually because the distribution of defects across the course of development is not taken into consideration. This analysis establishes the rate of defect acquisition, not the regularity. *P. pygmaeus* was found to acquire LEH at a significantly higher rate than *P. abelii* (Table 3).

*P. pygmaeus* males averaged 20.91 ± 16.95 perikymata between defects while *P. abelii* males averaged 20.46 ± 13.76 perikymata between defects (Table 4). Approximately 21 perikymata corresponds to 168-231 days (RI = 8-11). Table 7 indicates that the range of days for a six-month cycle duration should fall between 166 and 186 days. However, Figure 4 demonstrates that the distribution of the number of perikymata between defects is highly skewed for *P. pygmaeus* and *P. abelii*, and the distribution is not clustered tightly around the mean. Thus, the median and modal number of perikymata between defects may be more informative: *P. abelii* has a median of 16 and mode of 15, *P. pygmaeus* has a median of 14.5 and a mode of 8. It should also be noted that it was possible to generate the same distribution of the number of perikymata between defects randomly. For the individuals acquired in 1937 at Camp Abai along the Kinabatangan River, one

showed a yearly cycle of defect expression and two others exhibited cycles that may represent 3- or 6-month cycles (Tables 7 and S13). This does not suggest common or frequent cycles even within conspecific individuals.

Autocorrelation results revealed cycles of any duration in 66.7% of *P. abelii* individuals and 45.2% of *P. pygmaeus* individuals. Within each species, though, no major trends emerged. Neither species had a cycle periodicity shared by all the individuals in the group. The most frequent cycle periodicity for both species was 4 perikymata (32–44 days, or slightly more than 1 month). Cycle periodicities of 6, 12, and 18 months have been identified before (Skinner, 2014; Skinner & Hopwood, 2004). These studies have regularly found cycles of LEH of 6, 12, and 18 months in chimpanzees, gorillas, and orangutans from Africa and Asia, and across several environments by estimating the amount of time between adjacent pairs of LEH either with crown height proportions or perikymata counts. While a few individuals expressed cycle periodicities that could fall within the range of those intervals, they could only be found in 2/9 and 7/31 individuals, indicating that such cyclicity are not the norm for *P. abelii* or *P. pygmaeus*.

Most studies have found significant differences between the orangutans of Borneo and Sumatra either in average number of LEH (Guatelli-Steinberg et al., 2012), number of perikymata between defects (Skinner, 2014), defect depth (Skinner & Skinner, 2017), presence of ketones in urine (Wich et al., 2006), or in cranial capacity (Taylor & van Schaik, 2007), and these studies have suggested that variable ecological factors between the two islands may drive some of these differences. The difference between the islands is further supported in this study by the fact that the average number of LEH acquired per year is greater for Bornean orangutans compared to Sumatran. However, every other set of analyses revealed that no statistically significant differences exist between *P. pygmaeus* and *P. abelii*.

No differences were found in the number of defects, number of perikymata between defects, or the cycle periodicities for the two species. The average rate of LEH acquisition was calculated by dividing the number of LEH by the LCFT; the statistic generated for each tooth assumes that LEH occur across the entire LCFT and this assumption may be erroneous, as all of the defects may have occurred in any fraction of the LCFT. Thus, this study concludes that there are no consistent differences in the timing of developmental enamel defects for orangutans from Borneo and Sumatra.

## 4.2 | Sex differences

In this study, females tended to acquire defects at a higher rate than their male conspecifics and tended to have fewer perikymata between defects. Female *P. pygmaeus* averaged greater rates of defect acquisition than the males (Table 8), but the difference was not significant. It could be argued that the significant differences in the rate of acquisition and time between defects are due to discrepancies in repeat intervals between the sexes. When Bromage et al. (2012) found a range of perikymata repeat intervals within a species, males tended to have higher repeat intervals than females. However, if males have higher

repeat intervals than females, then the discrepancy in the amount of time between defects would only increase because the number of defects would be multiplied by a higher number of days, revealing more time between defects. Thus, it can be concluded that differences do exist in timing of developmental defects between males and females.

There is an argument that males are less buffered from stress than females and therefore have less resilience against physiological stress; this idea is typically referred to as either male vulnerability or female buffering (reviewed in Guatelli-Steinberg and Lukacs (1999)). With increasing levels of environmental stress, males should be more susceptible to physiological stress and retain enamel defects more frequently than females (Guatelli-Steinberg & Lukacs, 1999). Conversely, Dirks et al. (2010) argues that higher counts of accentuated striae in a female baboon may indicate that female offspring receive less maternal investment than male offspring and are more susceptible to stress. Here, females acquired defects at higher rates and had fewer perikymata between defects, lending some support to the idea that females are more vulnerable to physiological stress than males and/or may receive less maternal investment. However, this observation may be the result of internal growth geometry such that females have more tightly packed perikymata or more obtuse striae angles, making enamel defects appear deeper and perhaps more easily observable (McGrath et al., 2019; M. C. O'Hara & Guatelli-Steinberg, 2020).

## 4.3 | High frequency of 1-month cycles

Although no species-wide trends in cycle periodicity were found in this study, the most common periodicity was close to one-month (e.g., 4 perikymata). Dirks et al. (2010) evaluated the amount of time between accentuated striae across an individual's development and found approximately monthly patterns of physiological stress in a male and female baboon. However, it is unlikely that one-month cycles are biologically meaningful by themselves. A closer look at the cycle periodicities that produce month-long cycles reveals that they are low integer values that are often sub-factors of other common factors used to identify multiples in the significant lags (Table 9). In fact, in nearly half of all individuals for whom one-month cycle periodicities were identified, larger cycle periodicities that were multiples of the one-month periodicity were identified (Table 9). In some cases, such as *P. pygmaeus* 37358, a cycle periodicity of 4 was identified because 4 is the only factor for the significant lags 60 and 116 (see Supplemental Information Section 4). While a periodicity of 4 perikymata could exist in such an instance, it is unlikely that it explains a meaningful cycle. Thus, this 1-month trend is likely an artifact of the math required to identify cycles and not indicative of any monthly environmental or ecological perturbations.

Throughout this study, individuals evinced cycles of unique periodicity. While no trend was noted that would indicate these cycles fall along 3-, 6-, 12-, or 18-month durations, they may still be meaningful. They indicate that, within an individual, regular cycles of defect expression may exist even if the periodicity is not environmentally meaningful. Individuals may also have a unique physiological threshold

for becoming ill and be more susceptible to certain stressors. The existence of such individual-scale cycles may still be biologically or medically meaningful and could be further investigated with known life histories, trace element analysis, and isotopic techniques.

#### 4.4 | Caveats

The analyses and conclusions presented here are limited to juvenile non-human primates. While lower canines are best for studies such as this one because they take the longest to develop, they represent only a very small fraction of an individual's life. This study cannot comment on the patterns of susceptibility in adult primates. However, a study of barium in orangutan molars shows approximately yearly periods of nursing for 7–8 years after birth, some of which are associated with accentuated striae (Smith et al., 2017). The one individual in our sample that showed an approximately yearly pattern of stress was MCZ 5211 (Table 7), which was collected during the same field season and from the same location as one of the individuals (MCZ 5290) in the Smith et al. (2017) study, although MCZ 5211 was an adult and MCZ 5290 was a juvenile at the time of death. Either way, this pattern of yearly bouts of breastfeeding was not identified on the surface of the teeth as linear enamel hypoplasia or accentuated perikymata. This suggests that mothers may be successfully buffering young orangutans with breastmilk during difficult periods to the extent that physiological perturbations do not become extreme enough to produce surface defects.

For species with a range of reported perikymata repeat intervals, the exact amount of time between defects and cycle periodicity in days cannot be known without sectioning each tooth. Not knowing the repeat interval for each individual in the sample makes it difficult to know, for example, whether the 41-perikymata cycle periodicity (which falls within the range of a yearly cycle) found in the *P. pygmaeus* specimen 5211 actually represents 324, 369, 410, or 451 days ( $RI = 8, 9, 10, \text{ and } 11$ , respectively). If specimen 5211 has a repeat interval of 9 days, then a yearly cycle of defect expression can be said to exist for this individual (369 days). If specimen 5211 has a repeat interval of 11 days, then the cycle demonstrated by this individual (451 days) is ecologically inconclusive (approximately 15 months).

## 5 | CONCLUSION

This study systematically evaluates whether developmental defects of enamel occur with regular cyclicity in *Pongo* from the islands of Borneo and Sumatra. Although significant differences were identified in the rate of defect and LEH acquisition, neither species exhibited consistent cyclicity in their defects. A few individuals demonstrated potential cyclicity in defect expression, but cyclicity was neither common nor shared across all or even most individuals within a species. It seems that while a few individuals may develop defects annually or semi-annually, they are not representative of the species as a whole. Additionally, the distribution of the number of perikymata between defects could be generated randomly.

This study confirms that it is possible to statistically identify cycles of defect expression using autocorrelation. While autocorrelation analysis did not reveal species-wide trends of overarching cycles of vulnerability between species or by environment in this study, the techniques utilizing standard perikymata profiles and autocorrelation analysis provide a robust and accurate method to analyze the timing of developmental defects. The potential for autocorrelation in other samples is promising. Macho et al. (1996) identified near-yearly cycles in accentuated striae expression in *Theropithecus oswaldi* teeth and Smith et al. (2017) identified near-yearly cycles of breastfeeding in the enamel and dentine of *Pongo*. Those studies had the benefit of sectioning teeth and knowing the individual's perikymata repeat interval. Future studies should seek to validate these methods using a sample that comes from a well-known, strictly seasonal environment with well-defined seasons and physiological stressors. Understanding the rhythmicity and predictability of developmental defects will help identify seasonal patterns of physiological stress/susceptibility in archeological and paleoanthropological remains.

#### AUTHOR CONTRIBUTIONS

**Mackie O'Hara:** Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); project administration (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Scott W. McGraw:** Conceptualization (supporting); writing – review and editing (equal). **Debbie Guatelli-Steinberg:** Conceptualization (supporting); funding acquisition (lead); methodology (supporting); project administration (supporting); supervision (lead); writing – original draft (supporting); writing – review and editing (equal).

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#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

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