



SEASONAL MORTALITY PATTERNS IN NON-HUMAN PRIMATES: IMPLICATIONS FOR VARIATION IN SELECTION PRESSURES ACROSS ENVIRONMENTS

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Examining seasonal mortality patterns can yield insights into the drivers of mortality and thus potential selection pressures acting on individuals in different environments. We compiled adult and juvenile mortality data from nine wild non-human primate taxa to investigate the role of seasonality in patterns of mortality and address the following questions: Is mortality highly seasonal

across species? Does greater environmental seasonality lead to more seasonal mortality patterns? If mortality is seasonal, is it higher during wet seasons or during periods of food scarcity? and Do folivores show less seasonal mortality than frugivores? We found seasonal mortality patterns in five of nine taxa, and mortality was more often tied to wet seasons than food-scarce periods, a relationship that may be driven by disease. Controlling for phylogeny, we found a positive relationship between the degree of environmental seasonality and mortality, with folivores exhibiting more seasonal mortality than frugivores. These results suggest that mortality patterns are influenced both by diet and degree of environmental seasonality. Applied to a wider array of taxa, analyses of seasonal mortality patterns may aid understanding of life-history evolution and selection pressures acting across a broad spectrum of environments and spatial and temporal scales.

KEY WORDS: Climate change, fitness, natural selection, paleontology, phylogenetic comparative analysis, seasonality.

Determining the selection pressures that act on individuals across different environments is crucial to understanding evolutionary processes. Throughout their evolutionary history, primates have inhabited a range of environments in dramatically different ecosystems (Reed and Fleagle 1995; Fleagle 1999). The varying selection pressures acting across these environments have played a central role in speciation (Coyne and Orr 2004) and led to a tremendous diversity of primate behaviors, diets, and morphologies (Fleagle 1984, 1999; Groves 2001; Strier 2007). The extent of environmental seasonality often varies across habitats and this variation has been widely implicated as a driver of life-history evolution and speciation (Boyce 1979; Wright 1999; Brockman and van Schaik 2005; Martin et al. 2009). An analysis of mortality patterns may provide insight into selection pressures acting in different environments, as well as aid in the interpretation of dietary strategies inferred from the fossil record. Primates are well suited for investigating the role of seasonality on mortality patterns and its implications for selection pressures, because their phylogeny is well resolved, facilitating comparative analyses. In addition, groups are followed over long periods so that conclusive, rather than inferred, mortality data are available. We examined mortality data in nine wild non-human primate taxa across three continents to understand how seasonal variation in rainfall and resource availability may act as selection pressures by influencing mortality.

Many factors contribute to primate mortality, including disease (Alexander 1974; Dunbar 1980; Milton 1996; Walsh et al. 2005; Kühl et al. 2008; Williams et al. 2008), predation (Cheney et al. 1981; Cheney and Wrangham 1987; Isbell 1994; Karpanty and Wright 2007; Teelen 2008; Irwin et al. 2009), injury during both interspecific and intraspecific interactions (van Schaik and Janson 2000; Cheney et al. 2006; Williams et al. 2008), and starvation (Dittus 1977, 1980; Dunbar 1980; Hamilton 1985). Resource availability for both primates and their predators, or other environmental variables, such as rainfall and temperature, may influence the importance of these different sources of mortality (Dunbar 1980; Richard 1985). Although the literature includes numerous

reports of the causes of mortality, mortality patterns are rarely analyzed over broad spatial or temporal scales and have not been compared across multiple species. If seasonal patterns in mortality are detectable, these could yield insight into the timing and drivers of selection pressures in primate populations (Richard 1985).

We expect causes of mortality to differ in the degree of seasonality they impose on mortality patterns, and for the relative contribution of these causes of mortality to overall mortality patterns to differ across species. For instance, primate habitats vary in the amount and seasonality of rainfall, which may lead to seasonal differences in resource availability (Janson and Verdolin 2005). There may be an increase in mortality during periods of resource scarcity related to increased competition for food, resulting in starvation in extreme cases (Dittus 1977, 1980; Hamilton 1985). In addition, it has been argued that leaves are a superabundant and evenly distributed resource over which primates will not have to compete (Isbell 1991; but see; Sterck and Steenbeek 1997; Snaith and Chapman 2005). During times of resource scarcity, foliage is likely more abundant and available than fruits (Wrangham 1980; Snaith and Chapman 2005), which may result in differences in seasonal mortality between folivores and frugivores.

Disease patterns are also commonly seasonal and may have important impacts on the behavior and life history of primates (Dunbar 1980; Nunn and Altizer 2006). Many vector-borne diseases increase in prevalence with increasing temperature and rainfall, as these affect arthropod vector distribution and abundance, parasite development, and parasite transmission rates (Harvell et al. 2002). Thus, elevated mortality during rainy seasons may be related to increased disease risk (Dunbar 1980; Milton 1996). Alternatively, seasonality of resources caused by a dry season may induce dietary stress as resource availability declines, depressing the immune system, increasing susceptibility to disease (Nelson 2004; Chapman et al. 2006), and potentially confounding the ultimate causes of mortality (i.e., starvation vs. disease). Such season-specific patterns in resource availability and disease susceptibility suggest that species living in more seasonal environments will exhibit more seasonal mortality patterns.

An analysis of seasonal mortality patterns can also aid in the interpretation of fossil assemblages. Vertebrate taphonomists are concerned with the ways in which the accumulation and preservation of fossils reflect palaeoenvironments (Behrensmeier 1980; Behrensmeier and Kidwell 1985; Alemseged 2003), the composition and abundance of source faunas and floras (Behrensmeier et al. 2000), and even social behaviors (Barnosky 1985; Berger et al. 2001; Muhlbachler 2003). The relationship between fossil assemblages and seasonality is a matter of major concern (Kurten 1983; Rogers 1990; Lyman 1994; Lubinski and O'Brien 2001), especially with regard to interpreting dental microwear, which is used to infer diet. Short-term (e.g., seasonal) variations in diet can result in differences in microwear fabrics, a phenomenon amply documented in extant species (Teaford and Oyen 1989; Teaford and Glander 1991, 1996; Merceron et al. 2010). As a result of this turnover, microwear will fossilize information pertaining to items consumed just before an individual's death (the so-called "Last Supper Effect"; Grine 1986). If primates typically die during the food-scarce period when their diets consist mainly of fallback foods (i.e., resources that are critical for a population's survival and that may present significant structural obstacles to comminution, but that are not preferred food items; Marshall et al. 2009), then the dental microwear preserved in the fossil record would be expected to over-represent those fallback regimes.

For many species, it is unknown whether seasonal patterns in mortality exist, primarily because of the scarcity of long-term mortality data. However, a number of studies support the hypothesis that mortality in primates is linked to environmental variables. For example, howler monkey (*Alouatta palliata*) mortality on Barro Colorado Island, Panama, is highly seasonal (Otis et al. 1981) and most deaths occur in the rainy season. This corresponds with the seasonality of botfly parasitism, rather than changes in diet (Milton 1996). Similarly, among gelada baboons (*Theropithecus gelada*), mortality was highest during the rainy season, rather than the period of food scarcity (Dunbar 1980). Mortality is high in Milne Edwards' sifakas (*Propithecus edwardsi*) at Ranomafana National Park in the drier winter months with fruit scarcity (Irwin et al. 2009), and is higher during years with major cyclones and a longer dry season than years with more evenly distributed rainfall (Dunham et al. 2008, 2010). Chacma baboons (*Papio hamadryas ursinus*) at the Moremi Game Reserve in Botswana have elevated mortality during the flooding season, predominantly due to predation (Cheney et al. 2004), whereas a population in the Namib Desert in Namibia had elevated mortality during severe droughts that resulted in malnutrition and starvation (Hamilton 1985).

We sought to understand mortality patterns in a wide range of non-human primates to provide a comparative basis for understanding the variety and timing of selection pressures in different environments. To our knowledge, a comparison of mortality patterns across primate species and their interaction with seasonal

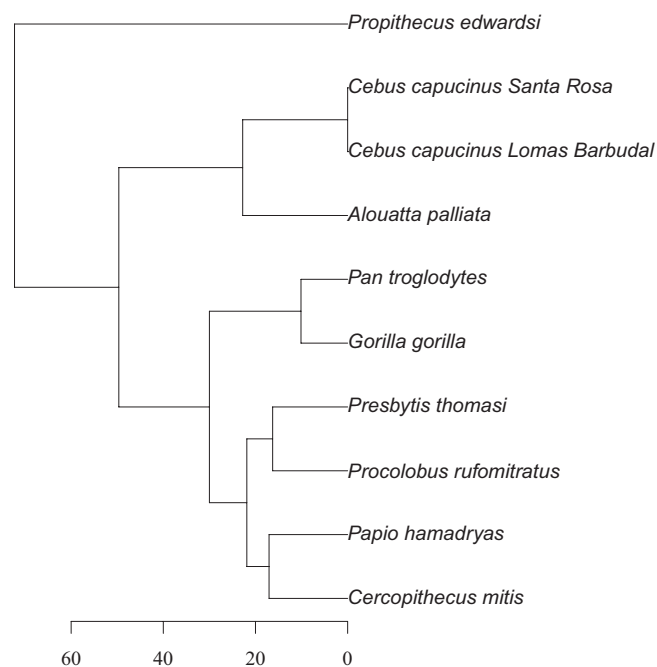


Figure 1. Phylogeny of the primate populations included in this analysis. Modified from a consensus tree (see text) from the 10kTrees project (Arnold et al. 2010), with the scale in millions of years.

resource scarcity and other environmental factors has never been performed. One reason is that there are few mortality data available to address the question. When data on primate mortality are available, they are typically presented in a way that does not facilitate examining seasonal patterns (e.g., life tables or survival studies: Pochron et al. 2004; Isbell et al. 2009; Cords and Chowdhury 2010; Bronikowski et al. 2011). Here, we compile and examine an extensive dataset on adult and juvenile mortality of nine wild non-human primate taxa representing diverse ecological conditions and spanning a broad temporal scale and range of the primate phylogeny (Fig. 1). These include primates from all major radiations, including one strepsirrhine (*P. edwardsi*), three New World monkeys (one *A. palliata* population and two *Cebus capucinus* populations), two cercopithecines (*Cercopithecus mitis* and *P. hamadryas*), one Asian colobine (*Presbytis thomasi*), one African colobine (*Procolobus rufomitratus*), and two African apes (*Gorilla gorilla* and *Pan troglodytes*). Diet varies across taxa, and our dataset includes five frugivorous and five folivorous populations (categorical diet classification follows that used by Nunn and van Schaik 2001). Rainfall seasonality also varies across sites, from marked seasonality to more evenly distributed rainfall throughout the year. We investigate five nonmutually exclusive hypotheses regarding the mortality patterns of primates: (1) mortality is highly seasonal across species, (2) mortality is higher during wet seasons than dry seasons, (3) mortality is higher during periods of fallback food consumption or food scarcity, (4) greater

environmental seasonality corresponds with more seasonal mortality patterns, and (5) folivores have less seasonal mortality than frugivores.

Methods

DATA COLLECTION

We present mortality data from seven study sites and three published studies (Milton 1996; Watts 1998; Cheney et al. 2004), for a total of 10 wild primate populations. Ecological conditions vary across sites, with rainfall ranging from 430 to 3200 mm per year. Rainfall has a highly seasonal distribution at some sites, but not others (Table 1).

The dataset includes only animals that were found dead (i.e., a carcass was found), or whose disappearance could confidently be registered as a death because at least one of three criteria was met: (1) an individual disappeared from the population that was a member of the nondispersing sex, (2) a juvenile disappeared before reaching the minimum known dispersal age, or (3) an individual was clearly ill or seriously wounded prior to disappearance. We included only those deaths that could be assigned to a given month of the year, using death dates with an error not exceeding ± 15 days, with the midpoint between the minimum and maximum date of death used in the analysis (with the exception of one dataset available from the literature: see below). Sampling effort for the study periods we included was generally equally distributed over all months of the year. Many species exhibit seasonal reproduction (Janson and Verdolin 2005) and elevated infant mortality immediately following birth (Altmann et al. 1977; Dunbar 1988; Wright 1995; Cheney et al. 2004; Isbell et al. 2009; Jin et al. 2009), so we focused on adult and juvenile mortality. Identification of infants differs among populations, and is described below.

Each of our species was either frugivorous or folivorous based on the food category that dominated feeding time (following: Nunn and van Schaik 2001). For all species, we defined a food-scarce period. Where possible, we used site-specific plant phenology data to define this period. In other cases, we used feeding or weight loss data and observations from researchers working with the species at the site (Table 1). In addition, we delineated wet and dry seasons using long-term rainfall records combined with literature descriptions (Table 1). We describe specific details on the methods at each site below.

STUDY SITES AND SPECIES: DIRECT OBSERVATIONS

White-faced capuchins (C. capucinus)

S. Perry and L. Fedigan collected mortality data on *C. capucinus* from populations at two sites in northwestern Costa Rica: Lomas Barbudal and Santa Rosa National Park (site, population,

and methods described in Perry 2009 and Fedigan and Jack 2001, respectively). At Lomas Barbudal, year-round observations (i.e., monthly) occurred during 11 years (1992, 2001–2010). Many trees fruit in the dry season in this forest and the only time the monkeys seemed short of food was in May, which we defined as the food-scarce period (S. Perry, pers. obs.). Among the *C. capucinus* at Lomas Barbudal, some of the causes of mortality among juveniles and adults were anthropogenic (e.g., poaching, car accidents, and electrocution), but these deaths were not included in this analysis.

For *C. capucinus* at Santa Rosa National Park, we defined the food-scarce period using phenology records of common food plants (data and analysis available in Carnegie et al. 2011). Reliable recording of death/disappearance dates began in 1988, but we included only the 15 years in which there were no gaps in data collection. For both populations of *C. capucinus*, we excluded individuals younger than one year of age, the age at which individuals are no longer riding dorsally and after which suckling is infrequent (Fedigan et al. 2008).

Blue monkeys (C. mitis)

M. Cords collected mortality data in *C. mitis* from 1997 to 2009 in Kakamega Forest, Kenya (site, population, and methods described in Cords 1987; Pazol and Cords 2005; Ekernas and Cords 2007; Cords and Chowdhury 2010). We identified periods of fruit scarcity based on five years of phenological monitoring combined with vegetation surveys that contributed information about the abundance and size of different food trees (M. Cords, unpubl. data). We excluded young infants, defined here as individuals younger than one year old, the age of the youngest orphan to have survived independently (M. Cords, unpubl. data).

Chimpanzees (P. troglodytes)

J. Goodall, A. Pusey, and colleagues collected mortality data on *P. troglodytes* from 1960 to 2010, from two communities in Gombe National Park, Tanzania (for a description of the site see Wrangham 1977; Goodall 1986; for a description of the database see Strier et al. 2010). Phenology data were not available, so we identified the period of food scarcity as (1) months during which average female body mass decreased (Pusey et al. 2005), and (2) months in which fruits were observed to be less available and contributed less to the overall diet (Wrangham 1977; Goodall 1986; Pusey et al. 2005). We excluded individuals younger than two years because the period of high mortality associated with infancy in *P. troglodytes* drops off after reaching this age (Goodall 1986).

Thomas langurs (P. thomasi)

S. Wich, E. Sterck, and others collected monthly mortality data for *P. thomasi* from 1987 to 2001 at for the Ketambe research

Table 1. Details regarding study species, sites, sample sizes, and environmental variables.

Species	Study site	Diet	N deaths (years of study)	Annual rainfall (mm)	Rainfall seasonality (r-statistic)	Wet season	Food- scarce months(s)
<i>Alouatta palliata</i>	BCI, Panama	<i>Fol</i>	179 (7)	2600	0.320	May–Nov ¹	May–Dec
<i>Cebus capucinus</i>	Lomas Barbudal, Costa Rica	<i>Fr</i>	31 (11)	1600	0.536	May–Nov ²	May
<i>Cebus capucinus</i>	Santa Rosa, Costa Rica	<i>Fr</i>	20 (15)	1820	0.540	May–Dec ³	Oct–Mar
<i>Cercopithecus mitis</i>	Kakamega, Kenya	<i>Fr</i>	46 (13)	2000	0.198	Mar–Nov ^{4,11}	Mar–July and Nov
<i>Gorilla gorilla</i>	Karisoke, Rwanda	<i>Fol</i>	38 (25)	1810	0.115	Mar–May and Sep–Dec ⁵	Feb and Jun–Oct
<i>Pan troglodytes</i>	Gombe, Tanzania	<i>Fr</i>	112 (50)	1500	0.456	Nov–Apr ⁶	Weight loss: May–Nov Fruit scarce: Apr–May
<i>Papio hamadryas</i>	Moremi Game Reserve, Botswana	<i>Fr</i>	38 (11)	430	0.775	Nov–Mar ^{7,12} Flooding: Jul–Sep	Oct–Jun
<i>Presbytis thomasi</i>	Gunung Leuser, Indonesia	<i>Fol</i>	42 (15)	3230	0.088	Oct–May ^{8,11}	Fruit scarce: Sept–June Young leaf scarce: Apr–Oct
<i>Procolobus rufomitratu</i>	Kibale, Uganda	<i>Fol</i>	11 (10)	1700	0.122	Sep–Nov and Mar–April ⁹	Jan–Feb and May–Aug
<i>Propithecus edwardsi</i>	Ranomafana, Madagascar	<i>Fol</i>	23 (24)	2970	0.262	Nov–Mar ^{10,11}	Apr–Oct

Fr indicates predominantly frugivorous species whereas *Fol* indicates predominantly folivorous species (see text for details). Sources for annual rainfall, rainfall seasonality, and wet season distinction:

¹Milton (1996); Condit (1998); Janson and Verdolin (2005)

²Gordon et al. (1988); Frankie et al. (2005)

(Fedigan and Jack (2001); Campos and Fedigan (2009); L. Fedigan, unpubl. data

⁴M. Cords, unpubl. data; Ekernas and Cords (2007)

⁵Watts (1998); Janson and Verdolin (2005)

⁶Goodall (1986); Janson and Verdolin (2005); rainfall data recorded at Kasakela Station 942909 by the Directorate of Meteorology, Tanzania from 1989 to 1997, available via Jim Moore's Gombe Climatological Data webpage: <http://weber.ucsd.edu/~jmoore/apesites/Gombe/GombeClimate.html#Rain>

⁷McCarthy et al. (1988); Cheney et al. (2004)

⁸van Schaik (1986); Janson and Verdolin (2005)

⁹Struhsaker (1997); Janson and Verdolin (2005); Chapman et al. (2010a)

¹⁰Wright (1995); Janson and Verdolin (2005); King et al. (2011).

¹¹The distinction between the wet and dry season is difficult to make and there is high interannual variability in this environment.

¹²We could test only the period Oct–Mar because mortality data were binned in three-month intervals (Cheney et al. 2004).

site in Gunung Leuser National Park, Sumatra, Indonesia (site, population, and methods described in Wich et al. 2007). *Presbytis thomasi* are generally folivorous (Steenbeek and van Schaik 2001), but young leaf production does not always display predictable seasonal patterns in this ecosystem (van Schaik 1986). In addition, *P. thomasi* prefer fruits when they are available (Steenbeek and van Schaik 2001). Fruit production peaks in July and August, which we assigned as the period of food abundance (van Schaik 1986). In addition, we tested whether there was decreased mortality in the period when young leaf flushes were most common (Nov–Mar: van Schaik 1986). We excluded infants younger

than 14 months, the age at which individuals can survive on their own (Sterck et al. 2005).

Red colobus (P. rufomitratu)

C. Chapman, L. Chapman, and colleagues collected data on *P. rufomitratu* mortality at Kibale National Park, Uganda between 2005 and 2011 (site, population, and methods described in Chapman and Lambert 2000; Chapman et al. 2007). We included two additional deaths reported for the same population during observations between 1970 and 1974 (Struhsaker 1975).

To assess the food-scarce period, we used phenology data of *P. rufomitratus* foods collected between January 2007 and September 2010 to determine food availability (C. A. Chapman and L. J. Chapman, unpubl. data). We excluded infants from the analysis, defined here as those individuals less than half the size of an adult female (Struhsaker 1975).

Milne-Edwards' sifakas (P. edwardsi)

P. Wright collected mortality data for *P. edwardsi* at Ranomafana National Park, Madagascar, between 1986 and 2009 (study site, population, and methods described in Wright 1995). Young leaves and fruits are more abundant during the wet season, so we defined this as the period of food abundance (Wright 1999). For *P. edwardsi*, we excluded infants, defined here as individuals that are not weaned (occurs at one year of age: King et al. 2011).

STUDY SITES AND SPECIES: LITERATURE DATA

Howler monkey (A. palliata)

We obtained data on *A. palliata* mortality from surveys for cadavers on Barro Colorado Island (BCI), Panama, conducted between 1986 and 1993 (study site, population, and methods described in Milton 1996). A total of 179 adult and juvenile *A. palliata* deaths were recorded (Milton 1996). Although this species is predominantly folivorous, fruits constitute a substantial (>40%) part of its diet when they are available (Milton 1979), and flower and fruit production peaks in the late dry season (Jan–Apr; Zimmerman et al. 2007). We therefore regarded this period as the season of food abundance. For *A. palliata*, we excluded infants, defined by Milton (1996) as being younger than one year of age.

Mountain gorilla (G. gorilla)

We obtained *G. gorilla* mortality data from the Karisoke Research Centre, in the Parc National des Volcans, Rwanda, and from long-term Karisoke records on *G. gorilla* demography and morbidity (site, population, and methods described in Watts 1998). Data collection began in 1967 and was continuous until 1991. Although the *G. gorilla* diet is fairly uniform throughout the year, these apes preferentially eat bamboo when new shoots are available; thus, we used the period of bamboo consumption as the time of food abundance (Watts 1998). For *G. gorilla*, births are nonseasonal and reported infant mortality rates are low (Watts 1991; 1998). We excluded all cases of infanticide, but published data include other cases of infant mortality (Watts 1998).

Chacma baboon (P. hamadryas ursinus)

We obtained *P. hamadryas* mortality data between 1992 and 2002 from the Moremi Game Reserve, Botswana (study site, population, and methods described in Cheney et al. 2004). Dates of death for five individuals who died from illness were not available, so we excluded these individuals from the analysis (Cheney et al. 2004).

Unlike the previous studies, in which the date of death could be confidently ascribed to a particular month, we had to partition *P. hamadryas* data into four three-month bins (Jan–Mar, Apr–June, July–Sept, and Oct–Dec: Cheney et al. 2004). The Moremi Game Reserve is a highly seasonal environment that undergoes yearly flooding after the rainy season, so we also tested whether mortality was higher during this period. Although plant phenology data are not available from this site, Cheney et al. (2004) describe food as being more plentiful following high rainfall, specifically in the months following July and August. For *P. hamadryas*, infants were defined by Cheney et al. (2004) as being younger than 12 months, thus we excluded these death dates from our analysis.

DATA ANALYSIS

We used circular statistics to test for seasonality in primate mortality because they permit analysis of data on a continuous axis and do not require any arbitrary decision about how to divide the year into repeating units (Batschelet 1981; Jammalamadaka and Sengupta 2001; Janson and Verdolin 2005). To illustrate the value of circular statistics, consider the following extreme example where, in a hypothetical species, 30 deaths occurred in December, and another 30 occurred in February. If one uses a linear framework and takes the standard division of a year from January–December and attempts to calculate the mean month of death for this species, one will get July. By contrast, if one divides the year based on an American academic calendar starting the year in September, one would obtain a mean month of death of January. Similarly, disparate results would result for most other descriptive statistics (e.g., variance and the coefficient of variation) and for many different statistical tests (e.g., Kolmogorov–Smirnov test). The mean vector length (r) obtained from circular statistical analyses is well suited as an index of seasonality, and the r -statistic is robust to differences in sample size facilitating the comparison of seasonality measures between species (Janson and Verdolin 2005). For mortality, when deaths are spread evenly across months (not seasonal), r is close to zero, whereas when deaths all occur at exactly the same time of year (extremely seasonal), r is one. We conducted Rayleigh tests to test a null hypothesis of a random distribution of primate deaths across the 12 months of a year (i.e., whether there is statistical evidence of directedness or seasonality to mortality). To test for bimodal distributions using the r -statistic, we doubled the angles calculated for each month (except for *P. hamadryas* for which data were in three month bins, which precluded the use of this test; Janson and Verdolin 2005). Because of uncertainty in death dates, we grouped data by month and used a correction factor for grouping ($c = 1.0115$, except for *P. hamadryas* for which data were in three month bins and $c = 1.1107$) when calculating r -statistics (Batschelet 1981).

To compare mortality between wet and dry seasons, or between food-scarce and food-plentiful periods, we conducted

G-tests on mortality grouped by month, with expected values related to the number of months that were wet versus dry, or in which food was scarce versus abundant (McDonald 2009). We used R 2.13.1 for all statistical analyses (R Core Development Team 2011).

To account for nonindependence of datapoints related to the shared evolutionary history of the species included in this analysis, we used phylogenetic generalized least squares (PGLS) regression (Felsenstein 1988; Rohlf 2001). PGLS uses an estimate of phylogenetic correlation, Pagel's λ , that varies between zero (indicating phylogenetic independence) and one (indicating species' traits covary in direct proportion to the degree of shared evolutionary history) and controls for this phylogenetic nonindependence of species values in a generalized least squares framework (Freckleton et al. 2002). We used the R packages "ape" and "caper" to conduct PGLS regressions and for all phylogenetic analyses (Paradis et al. 2004; Orme et al. 2011). We used the consensus tree of the taxa of interest from the 10kTrees project (Arnold et al. 2010). For those species or subspecies for which genetic data were not available, we used a well-established sister taxon that excluded all other species or subspecies in the analysis (e.g., *G. g. gorilla* was used in place of *G. g. beringei*). To incorporate the two populations of *C. capucinus*, we added a short branch of 10,000 years to the tip of the *C. capucinus* lineage (Fig. 1; Martins et al. 2002).

To test for a relationship between the degree of seasonality of the environment and the degree of seasonality of mortality, we conducted a bivariate PGLS regression of the *r*-statistic of rainfall on the *r*-statistic of mortality. In addition, because of the predicted impact of diet on the relationship between seasonality of environments and mortality patterns, we conducted a multiple PGLS regression of the *r*-statistic of rainfall and diet on the *r*-statistic of mortality. We treated diet as a dichotomous categorical variable (i.e., species were categorized as either frugivorous or folivorous; Table 1).

Results

Hypothesis 1: Mortality is highly seasonal across species.

Mortality was seasonal in *A. palliata*, *G. gorilla*, *P. hamadryas*, and *P. edwardsi* (Table 2). *Procolobus rufomitrat* had the highest *r*-statistic of mortality and although this *r*-statistic was not significant, the results of the *G*-tests further suggest mortality is seasonal in this species (Table 2). We did not detect significant seasonal mortality in *P. troglodytes*, *C. mitis*, *P. thomasi*, or *C. capucinus* (Table 2). *Procolobus rufomitrat* had the highest *r*-statistic of mortality ($r = 0.445$) and *P. troglodytes* had the least seasonal mortality. The two populations of *C. capucinus* had similar *r*-statistics of mortality (Lomas Barbudal $r = 0.198$, Santa

Rosa $r = 0.258$) and very similar patterns of mortality (Fig. 2), including a four-month stretch (Sept–Dec) in which only five of 51 deaths occurred (Lomas Barbudal: three of 31 deaths, Santa Rosa: two of 20 deaths). *Propithecus edwardsi* had a high *r*-statistic of mortality ($r = 0.382$) as did *A. palliata* ($r = 0.413$), *P. hamadryas* ($r = 0.409$), and *G. gorilla* ($r = 0.297$), whereas *C. mitis* ($r = 0.154$) and *P. thomasi* ($r = 0.189$) exhibited much lower seasonal mortality patterns (Table 2).

We detected evidence for a bimodal pattern to mortality, with an increase in the *r*-statistic after doubling the angles associated with each month (see methods), for the *C. capucinus* population at Lomas Barbudal ($r = 0.380$, $P = 0.009$) and *G. gorilla* ($r = 0.438$, $P = 0.0005$). Although there was an increase in the *r*-statistic for *P. troglodytes* ($r = 0.120$, $P = 0.191$) when testing for bimodality, the difference from the unimodal *r*-statistic was minimal and the distribution of deaths was still not significantly seasonal. In the case of *G. gorilla*, the bimodal pattern to mortality may be linked with the bimodality of rainfall. For the population of *C. capucinus* at Lomas Barbudal, the bimodal pattern to mortality does not appear to be related to rainfall or food availability (Fig. 2 and the following two sections).

Hypothesis 2: Mortality is higher during wet seasons than dry seasons.

Three of the 10 populations (*P. rufomitrat*, *A. palliata*, *G. gorilla*) had elevated mortality during the wet season. *Propithecus edwardsi* had elevated mortality during the dry season, and *P. hamadryas* had elevated mortality during the annual period of flooding (Fig. 2; Table 2). Four of the five folivorous species had seasonal mortality (three in the wet season and one in the dry season), whereas only one of the five frugivorous populations had seasonal mortality (during the period of flooding).

Hypothesis 3: Mortality is higher during periods of fallback food consumption or food scarcity.

Two species (*A. palliata* and *P. edwardsi*) had elevated mortality during the food-scarce period, whereas three species (*P. hamadryas*, *P. rufomitrat*, and *G. gorilla*) had elevated mortality during the food-abundant period. Both species with elevated mortality during the food-scarce period also exhibited an effect of rainfall on mortality (Fig. 2, Table 2).

Hypotheses 4 and 5: Greater environmental seasonality leads to more seasonal mortality patterns, and folivores have less seasonal mortality than frugivores.

There was no significant relationship between the degree of rainfall seasonality (the *r*-statistic of rainfall) and the degree of seasonality of mortality (the *r*-statistic of mortality) when diet was not included as factor in the model ($R^2 = 0.0007$, $F_{[2,8]} = 0.005$, $P = 0.995$, $\lambda < 0.001$). When diet was

Table 2. By-species results for tests of seasonality in mortality patterns.

(N deaths)	Deaths in food-scarce period				Deaths in wet season		
	Mortality seasonality (<i>r</i> -statistic)	Deaths observed (%)	Deaths expected (%)	<i>G</i> -test results	Deaths observed (%)	Deaths expected (%)	<i>G</i> -test results (<i>G</i>)
<i>Alouatta palliata</i> (179)	0.413***	84	67	26.77***	79	58	33.46***
<i>Cebus capucinus</i> Lomas Barbudal (31)	0.198	7	8	<i>ns</i>	65	58	0.50 <i>ns</i>
<i>Cebus capucinus</i> Santa Rosa (20)	0.258	40	50	0.81 <i>ns</i>	60	67	0.39 <i>ns</i>
<i>Cercopithecus mitis</i> (46)	0.096	44	50	0.78 <i>ns</i>	76	75	0.03 <i>ns</i>
<i>Gorilla gorilla</i> (38)	0.297*	32 ¹	50	5.28*¹	82	58	9.37**
<i>Pan troglodytes</i> (112)	0.077	WL:56 FS:21	58 17	0.20 <i>ns</i> 1.71 <i>ns</i>	54	50	0.57 <i>ns</i>
<i>Papio hamadryas</i> (38)	0.409**	45 ¹	75	15.75***¹	WS:32 ² FL:55	50 25	5.28*² 15.75***
<i>Presbytis thomasi</i> (42)	0.189	FS:88 LS:67	83 58	0.75 <i>ns</i> 1.23 <i>ns</i>	55	67	2.56 <i>ns</i>
<i>Procolobus rufomitratu</i> s (11)	0.445	18 ¹	50.0	4.82*¹	82	42	7.48**
<i>Propithecus edwardsi</i> (23)	0.400*	78	58	4.07*	22 ^b	42	4.08*²

WL indicates period of weight loss, FS indicates period of fruit scarcity, and LS indicates period of young leaf scarcity. WS indicates wet season whereas FL indicates period of flooding (see text for details). Bold values indicate significant results with *** $P < 0.001$, ** $P < 0.01$, and * $P < 0.05$. Nonsignificant results are indicated with *ns*.

¹Fewer deaths during food-scarce period than expected.

²Mortality was higher than expected in the dry period.

included in the model, the overall model was significant ($R^2 = 0.636$, $F_{[3,7]} = 8.880$, $P = 0.009$, $\lambda < 0.001$), as were both factors (diet: $T = 4.210$, $P = 0.004$; *r*-statistic rainfall: $T = 3.223$, $P = 0.015$). Folivores exhibited more seasonal mortality than frugivores, and greater seasonality of environments was associated with higher seasonal mortality in both frugivores and folivores (Fig. 3).

Discussion

Nearly half of the primate species examined exhibited seasonal mortality, although none of the *r*-statistics approached the seasonality observed for other aspects of life-history traits (e.g., *P. edwardsi* has an *r*-statistic for births of 0.887, and the highest *r*-statistic of mortality in the current study was 0.445; Janson and Verdolin 2005). Even for the most seasonal patterns of mortality, deaths still occurred throughout the year. The occurrence of deaths throughout the year likely reflects the multiple causes of mortality such as predation, disease, and injury, which may act

independently and be differentially influenced by environmental seasonality.

Where it occurred, seasonal mortality was tied to rainfall patterns. We found only limited support for the hypothesis that mortality is higher during periods of food scarcity. Contrary to our prediction, three of the five species that demonstrated seasonal mortality in relation to diet actually had elevated mortality during the food-abundant period. Also contrary to our prediction, seasonal mortality patterns appeared to be more common in folivorous than frugivorous species.

In addition, we found that mortality was more seasonal in more seasonal environments when diet (i.e., frugivore vs. folivore) was included in the model explaining variance in mortality patterns (Fig. 3). The PGLS analysis showed that folivores exhibited more seasonal mortality than frugivores at any given degree of rainfall seasonality. Interestingly, the small values of Pagel's λ estimated in the PGLS regressions suggest that there is not a strong phylogenetic component to this relationship. Either this relationship is ecologically based, or small sample sizes may have limited

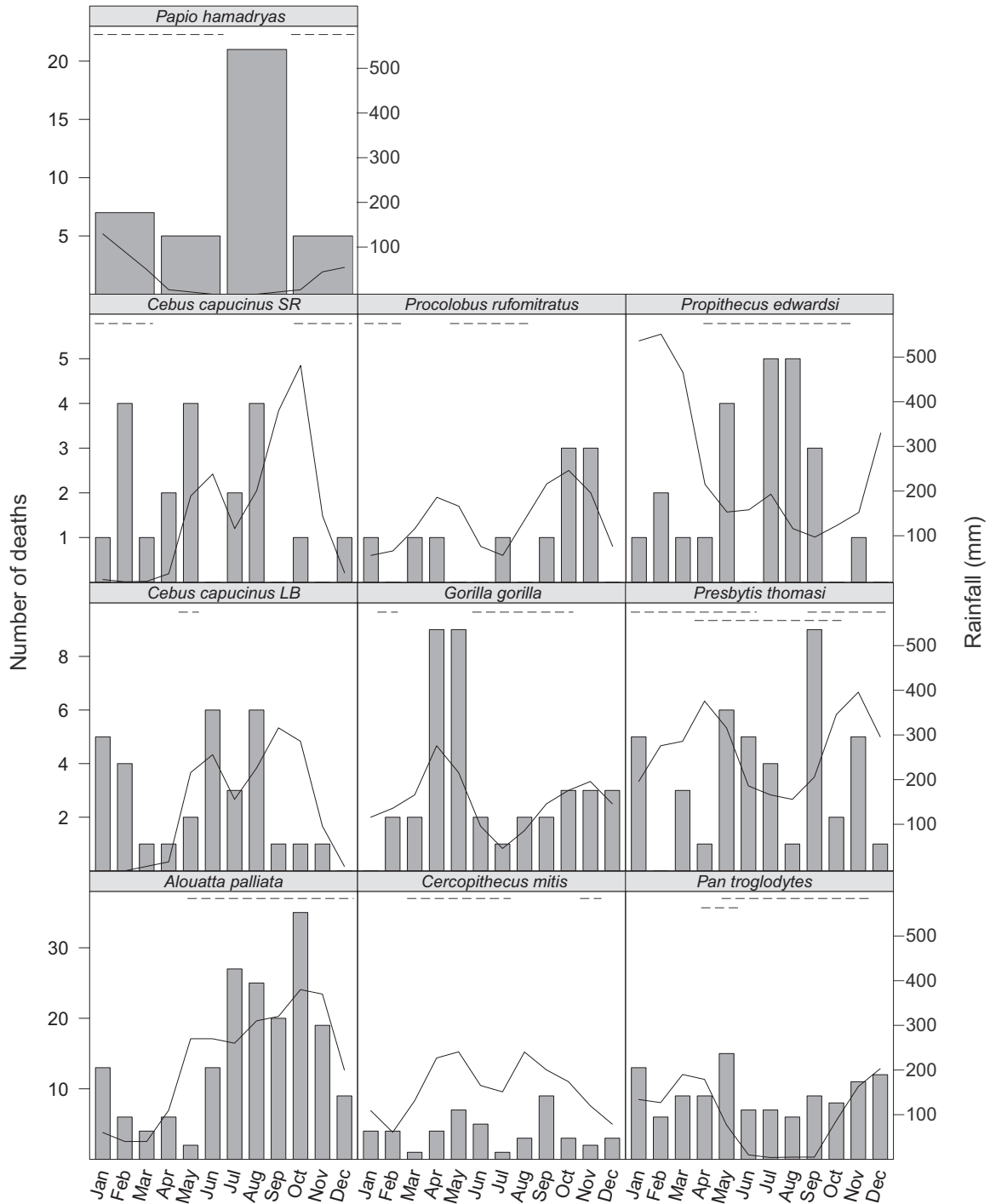


Figure 2. The number of deaths in each month for the 10 populations included in the current study. Bars indicate number of deaths with the axis on the left. The solid line indicates the monthly rainfall in mm, with the axis on the right. The food-scarce period is indicated by the dashed line at the top of each population’s graph, and the population is indicated in the header above the graph. For *Presbytis thomasi*, the topmost dashed line indicates the period of fruit scarcity, whereas the lower indicates the period of young leaf scarcity. For *Pan troglodytes*, the topmost dashed line indicates the period of weight loss, whereas the lower line indicates the period of fruit scarcity.

our ability to detect a significant phylogenetic signal. Our dataset did not include folivores in environments that were as seasonal as the environments occupied by the frugivores, although there was considerable overlap in the seasonality of environments of

the species in both dietary categories. The apparent pattern of folivores exhibiting more seasonal mortality patterns than frugivores is perhaps more striking, given that the folivorous species tended to come from less seasonal environments than

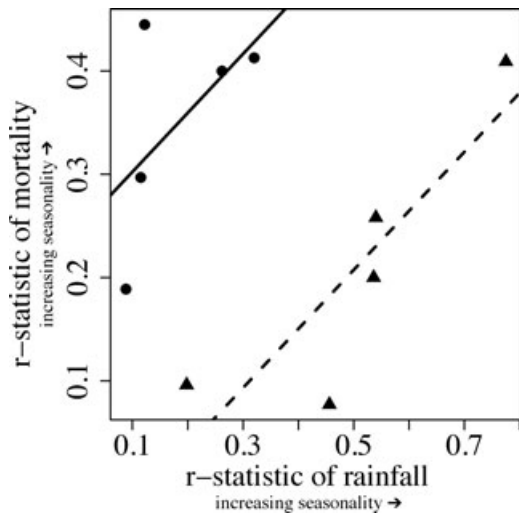


Figure 3. The relationship between the seasonality of mortality (the r -statistic of mortality) and the seasonality of the environment (the r -statistic of rainfall) for the 10 primate taxa in the dataset (see Methods for details). Circles represent folivorous species and triangles represent frugivorous species. The lines represent the results of the multiple PGLS regression of the r -statistic of rainfall and diet on the r -statistic of mortality (dashed lines: frugivorous species, solid line: folivorous species).

the frugivorous species. The different relationships between the seasonality of the environment and seasonality of mortality exhibited by frugivores and folivores is intriguing and suggests that dietary strategy is tied to the selection pressures exerted by seasonality in different environments.

IMPLICATIONS FOR SELECTION AND ECOLOGY

The pattern of increased mortality in the wet season observed for some of the populations may result from seasonal exposure to diseases. Increased moisture has been associated with increased parasitism both within (Huffman et al. 1997; Chapman et al. 2010b; van Dijk et al. 2010) and between species (Nunn and Altizer 2006: pp. 92–95). Analysis of human diseases has revealed a strong association between parasite diversity and latitude, which is driven in large part by climatic variables, including temperature and precipitation (Guernier et al. 2004). Similarly, a comparative analysis across primates demonstrated that white blood cell counts, a measure of immune function, exhibit a strong positive correlation with rainfall (Semple et al. 2002). The findings of Semple et al. (2002) suggest that disease exerts a strong selective force on populations, and that the nature of this selection is mediated by ambient rainfall. Even if the direct cause of death were predation, animals suffering the ill effects of disease would likely be most vulnerable (Penteriani et al. 2008; Genovart et al. 2010).

In *P. edwardsi* and *P. hamadryas*, the majority of deaths are caused by predation and both species exhibit strongly sea-

sonal mortality (Wright 1998; Cheney et al. 2004; Irwin et al. 2009; Wright et al. 2009). Among *P. troglodytes*, *G. gorilla*, and *A. palliata*, the majority of deaths have been attributed to disease and parasitism, with *G. gorilla* and *A. palliata* exhibiting strongly seasonal mortality (Milton 1996; Watts 1998; Williams et al. 2008). Given that 58% of the *P. troglodytes* deaths of known causes in the Kasekela community have been attributed to disease, and other studies have shown seasonal (albeit conflicting) patterns in disease and parasitism (Goodall 1983; Gillespie et al. 2010; Lonsdorf et al. 2011), it is perhaps surprising that we detected no seasonal mortality in chimpanzees. This is especially intriguing given the large size of our study sample. Several factors may contribute to the lack of seasonal mortality observed. First, the Gombe chimpanzees have recently been shown to have a high prevalence of SIVcpz (Keele et al. 2009). If SIV-induced mortality is nonseasonal but important, it might drive the lack of seasonal mortality observed in this population. However, deaths in humans with acquired immunodeficiency syndrome (AIDS) are often seasonal, possibly because of susceptibility to other diseases that are seasonal (Lin and Nichol 2001). Second, the Gombe chimpanzee communities were initially provisioned and occasionally medicated throughout the study; both of these interventions may have contributed to the lack of seasonality, although the data encompass a lengthy period after provisioning ceased (Pusey et al. 2008). Third, the fission–fusion societies of chimpanzees, the use of medicinal plants, and other behavioral, physiological, or social adaptations of chimpanzees might reduce disease risk during the rainy season (Huffman and Wrangham 1994). Lastly, it is possible that different sources of mortality vary in their seasonality and in when they exert their greatest effect, combining to create a nonseasonal pattern to mortality. For example, the chimpanzees at Gombe hunt more often in the fruit-abundant dry periods (Stanford et al. 1994). This hunting could increase the probability of acquiring diseases from their preferred colobus prey during the dry season, whereas wet season mortality may be high due to heightened risk of parasitism (Gillespie et al. 2010). Further studies on the seasonality of specific causes of death may help explain the observed patterns.

Contrary to expectation, we found that folivores exhibit more seasonal mortality than frugivores. Although early studies suggested that folivores may not be resource limited because leaves are abundant, recent studies suggest that folivores exhibit within-group competition over resources and are in fact resource-limited (Koenig 2000; Snaith and Chapman 2005; Snaith and Chapman 2007; Borries et al. 2008; Harris et al. 2010). In addition, young leaf flushes are often seasonal events and all folivores in the current study, with the exception of *G. gorilla*, exhibited some degree of seasonal frugivory. Leaf-eating primates also ingest larger volumes of food than frugivores, leading them to ingest more parasites whose infectious stages contaminate leaf

materials. Comparative studies have indicated that the degree of folivory is positively correlated with diversity of helminth species across primate species (Nunn et al. 2003; Vitone et al. 2004). Thus, the higher seasonal mortality apparent in folivores may result from a combination of seasonal abundance of pathogens combined with a greater exposure to pathogens owing to diet. Frugivores may also be better adapted physiologically, behaviorally, or socially to energy fluctuations in the environment because of the seasonal availability of many fruits (Jones 2011); these adaptations may render them less prone to seasonal mortality. The different mortality patterns associated with alternative dietary strategies suggest differential selection pressures are acting on species with different diets. The varying selection pressures exerted by seasonality on frugivores and folivores may be a mechanism driving diversification of dietary strategies among primates.

The available data forced us to use rather broad categorical variables for assessing food availability and environmental seasonality. Although it would likely be informative, we were unable to evaluate interannual variation in the current analysis. In addition, we were unable to assess the degree of food scarcity across sites and how variation in food scarcity relative to the animals' requirements influences the degree of seasonal mortality. Future studies should incorporate these factors as continuous variables measured on a finer scale, which will increase statistical power and allow for tests of the interaction between factors. Due to limitations of our data, we were also unable to incorporate infant mortality into the current analysis. However, age-structured models suggest that human fitness may be particularly sensitive to changes in prereproductive survival probabilities (Jones 2009), and understanding infant mortality patterns represents an important area of future research. Although we have done our best to control for variation in sampling methods between species and sites, the slow life history of primates means that sample sizes are generally small. Further, long-term studies will be useful in confirming these results and clarifying the particular causes of the seasonal mortality patterns documented here.

The seasonal nature of mortality in some primates suggests that climate change may contribute to changing mortality patterns (Dunham et al. 2008, 2010), potentially altering selection pressures. Increases in seasonality and extreme weather events are predicted with climate change (Frich et al. 2002; Tebaldi et al. 2006; Kharin et al. 2007), especially in the tropical environments that many primates inhabit (IPCC 2001). One-third of primate species are currently threatened with extinction (IUCN 2010) and changes in plant phenology patterns along with shifts in disease dynamics associated with climate change have already been documented for many plant and animal species (Parmesan and Yohe 2003; Parmesan 2006). Increases in primate mortality and changes to mortality patterns are also expected (Pedersen et al. 2007). However, climate change may also reduce certain vector-

borne diseases in some tropical areas (e.g., Paaijmans et al. 2009); understanding the interaction between climate change and disease dynamics presents a promising area of future research. Identifying the regions where changing seasonality of climate will coincide with and potentially amplify mortality patterns may provide a means of setting conservation priorities.

IMPLICATIONS FOR PALEONTOLOGY

We found limited support for the idea that microwear patterns in the fossil record will over-represent periods of food scarcity. The primates we examined did not die preferentially during periods of food scarcity, and several species actually exhibited elevated mortality when food was abundant. In addition, despite the "Last Supper Effect" (Grine 1986), the distribution of mortality across seasons, even when there was a seasonal pattern, suggests that microwear studies incorporating teeth from many individuals may capture the entire diet of a species. Chimpanzees are perhaps the best model for the diet of our hominin ancestors, and yet the chimpanzees of Gombe demonstrated the least seasonal mortality of all species, further suggesting that microwear will not over-represent a given period of the year in the hominin fossil record.

Taphonomic processes play a role in fossil preservation and fossil assemblages may therefore not represent the same seasonal pattern as the animals that die. Fossils may be more likely to be preserved when animals die in a particular season of the year (e.g., in the rainy season or during periods of flooding), which would influence the types of microwear patterns preserved in the fossil record. Our findings suggest that these effects may be more universally important than seasonal mortality in influencing the fossil record and its interpretation.

SUMMARY

We found that primate mortality was seasonal in approximately half the primate species examined, and it was more often tied to seasonal patterns of rainfall than seasonal patterns of food availability. These results suggest that selection pressures on some populations may be strongest during the wet season. We also found that more seasonal environments were associated with increased seasonal mortality and that the nature of this relationship is influenced by dietary strategy, with folivores exhibiting more seasonal mortality patterns than frugivores. Climate change may exacerbate the observed effects and patterns reported here. Application of these methods to a broader array of vertebrate taxa would further elucidate the role of seasonality in mortality patterns.

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Supporting Information

The following supporting information is available for this article:

Appendix S1. Supplemental Acknowledgements.

Supporting Information may be found in the online version of this article.

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