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Original Article

Infant and child death in the human environment of evolutionary adaptation

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ABSTRACT

The precise quantitative nature of the Environment of Evolutionary Adaptedness (EEA) is difficult to reconstruct. The EEA represents a multitude of different geographic and temporal environments, of which a large number often need to be surveyed in order to draw sound conclusions. We examine a large number of both hunter–gatherer ($N=20$) and historical ($N=43$) infant and child mortality rates to generate a reliable quantitative estimate of their levels in the EEA. Using data drawn from a wide range of geographic locations, cultures, and times, we estimate that approximately 27% of infants failed to survive their first year of life, while approximately 47.5% of children failed to survive to puberty across in the EEA. These rates represent a serious selective pressure faced by humanity that may be underappreciated by many evolutionary psychologists. Additionally, a cross-species comparison found that human child mortality rates are roughly equivalent to Old World monkeys, higher than orangutan or bonobo rates and potentially higher than those of chimpanzees and gorillas. These findings are briefly discussed in relation to life history theory and evolved adaptations designed to lower high childhood mortality.

1. Introduction

Evolution works in a forward direction, "solving" today's problems tomorrow (Dawkins, 1989). Bowlby (1982) coined the term Environment of Evolutionary Adaptedness (EEA) to refer to the environment in which an organism's current genotypes have been selected for. The human EEA is not a single time, place, or culture but rather a summation of all of the ancestral environments in which human evolution has occurred (Foley, 1995). The EEA may or may not be similar for separate traits (Irons, 1998). Traditional theory suggests that, for many human traits, the EEA is based on a combination of environments that were present during, or immediately preceding to, the paleolithic period (Tooby & Cosmides, 1992; Miller & Kanazawa, 2007). However, it is important to note that recent theories suggest that the last 10,000 years have played a significant role as a source of evolutionary adaptations and are hence part of the human EEA (Cochran & Harpending, 2009; Hartl & Clark, 1997; Irons, 1998; Yi et al., 2010; Tishkoff et al., 2007). Combining the last 10,000 years with the paleolithic gives a large time frame in which we must investigate the selective pressures present in the human EEA. What do we know about the evolutionary pressures that were present in this combined human EEA?

Detailed knowledge of the EEA is made difficult due to the paucity of evidence from our past. While we agree with others that this can be a serious limitation to the study of some aspects of the human EEA (Foley, 1995), we suggest that there are some areas in which the evidence for the EEA is quite robust. In particular, we believe that there is at least one aspect of the EEA that we can not only confidently describe qualitatively, but also be able to generate reliable quantitative estimates for infant and child mortality rates.

1.1. Infant and child mortality rates

One universal in the history of childhood stands above all others. The history of childhood is a history of death (Volk & Atkinson, 2008; Volk, 2011). Before modernized civilizations, across all times and cultures, children faced grim odds of survival. We suggest that infant and child mortality might be one of the most enduring features of the human EEA. To study this aspect of the EEA we have chosen to use the two most commonly used demographic markers in the study of child mortality: infant mortality rate (IMR), which is the likelihood of dying prior to age 1, and child mortality rate (CMR), which is the cumulative probability of dying prior to approximate sexual maturity at age 15. Life history models of human selective pressures over the course of the lifespan suggest that infant and child mortality may represent the period of human life subject to the strongest forces of evolutionary selection (Jones, 2009). Small changes in infant and child mortality rates can have dramatic consequences for both individual life histories and broader demographic trends (Bogin, 1997; Jones, 2009; Stearns, 2006; Wood, 1994). Therefore there is a strong theoretical incentive from life history theory to determine the likely values of IMR and CMR in the human EEA.

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Despite this strong incentive, it is perhaps not surprising that much of the work that has been done in evolutionary psychology has focused on adult behaviors such as mating and cooperation due to their prevalence and salience in modernized environments (e.g., Smith, 2010; Puts, 2010). The noted evolutionary psychologist Steven Pinker (2011) recently wrote that "[the decline in violence] may be the most important thing that has ever happened in human history." Mating, cooperating, and violence were all certainly associated with important evolutionary pressures that our ancestors faced. There are also behaviors and pressures that remain clearly visible to researchers today as modern Western adults still regularly witness or engage in mating, cooperation, and violence. The same cannot be said for infant and child mortality. With all due respect to Pinker, we believe that this may be due to one of the greatest of all human achievements—the dramatic reduction of IMR and CMR in the 19th–20th centuries (Stearns, 2006). Ironically, the 50-fold modern increase in child survival is a tremendous human achievement that may have obscured critical human selective pressures and adaptations (Volk & Atkinson, 2008). The staggering EEA levels of infant and child mortality are mostly foreign to many modern psychologists or social scientists outside of anthropology. They may even be relatively poorly understood by many evolutionary psychologists, although there is a growing awareness of their importance, particularly among those who study child evolutionary adaptations (e.g., Ellis & Bjorklund, 2005; Geary, 2010). We hope that the current paper illuminates a key evolutionary pressure that we suggest is under-appreciated by some evolutionary theorists and by many (though certainly not all) social scientists in general. In particular, we believe the provision of valid quantitative EEA data will be both revealing and of significant use to many social scientists, evolutionary or not.

2. Hunter–gatherer data

Unfortunately there simply is not enough direct paleodemographic archaeological data to make definite claims about the global patterns of infant and child mortality rates of our Paleolithic hunter–gatherer ancestors (Konigsberg & Frankenberg, 1994; Milner, Wood, & Boldsen, 2000; Lewis, 2007). Fortunately, there is a proxy for this kind of information—modern hunter–gatherers. We include modern hunter–gatherer societies in a study of the EEA as they are believed to be similar to their ancestral analogues in many aspects, including population demographics (Blurton-Jones, Hawkes, & O'Connell, 2002; Foley, 1995; Konner, 1977; Marlowe, 2010). Combined with existing Paleolithic data (e.g., Snow, 1948), modern hunter–gatherer populations can provide us with an estimate of ancestral infant and child mortality rates in hunter–gatherer cultures. We would like to caution that our data are drawn from hunter–gatherers who often currently live in marginalized territories that represent only a portion of potential environments in the EEA (Lee & Daly, 1999). This may be problematic as marginal environments could potentially inflate mortality levels. In response to this concern, we have attempted to maximize the diversity of environments we examine in an effort to average out the influence of any particular impoverished environment. We also included archaeological data from a hunter–gatherer population that lived in a resource-rich environment to serve as a check against modern hunter–gatherer data (Indian Knoll; Johnston & Snow, 2005).

Thus, in our article we expand upon the list of hunter–gatherer cultures by Hewlett (1991), with the important caveat that we purposely limited our sample only to those populations that had not been significantly influenced by contact with modern resources that could directly influence mortality rates, such as education, food, medicine, birth control, and/or sanitation. We further limited our analyses to populations based on sufficiently large sample sizes from reliable sources.

Examining hunter–gatherer IMRs and CMRs (see Table 1), we find that while there is variation, what stands out is the convergence of the data (see Figs. 1 and 2). The average IMR is $M = 26.8\%$ (SD = 6.9%), while average CMR is $M = 48.8\%$ (SD = 5.8%), with little skew (IMR = 0.246; CMR = −1.631) or kurtosis (IMR = 0.564; CMR = 3.821) and no outliers ($z < \pm 3.3$). Despite the rather large differences in culture, geography, and historical time frames, IMRs and CMRs appear to be quite high in the 18 hunter–gatherer societies presented in Table 1. This means that the children in these samples faced nearly even odds of surviving versus dying, the latter resulting in losing any chance to directly pass on their genes. This is true even for a hunter–gatherer population that lived in a rich resource-environment (Indian Knoll; Johnston & Snow, 2005). In agreement with life history theory (Hill, 1993; Stearns, Allal, & Mace, 2008; Jones, 2009), these high mortality rates clearly represent potentially strong and significant evolutionary pressures.

3. Historical data

As previously mentioned, human evolution did not stop 10,000 years ago. While it is unlikely that completely new complex adaptations have arisen within this time frame, we cannot completely discount the possibility that new adaptations have occurred in this time frame, or (more likely) that the expression of existing adaptations has not been altered (Cochran & Harpending, 2009; Irons, 1998). Thus it would be prudent to include more recent studies of infant and child mortality rates in our examination of EEA infant and child mortality rates. It is here that we depart from previous evolutionary anthropological studies of EEA rates of IMR and CMR (e.g., Hewlett, 1991; Marlowe, 2010) by incorporating historical data from the last 10,000 years to supplement our knowledge of the EEA. This is not merely an exercise in finding additional proxies for ancestral environments as is the case for hunter–gatherers. Rather, we suggest that these historical data represent a direct continuation of the actual human EEA, at least with respect to adaptations that would have the potential to alter infant or child survivorship.

When studying historical sources of mortality data, one must be cautious. It is usually the case that infant and child burial remains, death records, and written life histories are impoverished compared to their adult counterparts (Konigsberg & Frankenberg, 1994; Rawson, 2003; Walker, Johnson, & Lambert, 1988). This is due to the more rapid

Table 1
Hunter–gatherer infant mortality rates (IMR) and child mortality rates (CMR).

Culture	IMR	CMR	Source
!Kung	20.2%	49.4%	Howell, 1979; Hewlett, 1991
Aborigines	28%	n/a	Dugdale, 1980
Ache	21%	42%	Hewlett, 1991; Hill & Hurtado, 1989
Agta	34.2%	49%	Headland, 1989
Aka	20%	44.5%	Hewlett, 1991
Asmat	30%+	50%+	Van Arsdale, 1978
Batak	28.5%	48.2%	Eder, 1987; Hewlett, 1991
Chenchu	n/a	49%	Sibajuddin, 1984
Cuiva (Hiwi)	n/a	52%	Hurtado & Hill, 1987
Efe	14%	22%	Bailey & Peacock, 1988; Hewlett, 1991
Hadza	21.0%	46.1%	Blurton-Jones et al., 2002
Hiwi	24.5%	58.5%	Hill, Hurtado, & Walker, 2007
Indian Knoll (~2500 B.C.)	30%	56%	Johnston & Snow, 2005; Snow, 1948
Inuit	20%	45%	Malaurie, Tabah, & Sutter, 1952
Kutchin	17%	36.3%	Roth, 1981
Mbuti	33%	56.4%	Hewlett, 1991
Native Americans (600 AD)	n/a	44-64%	Thornton, 2000
Pumé	34.6%	n/a	Kramer & Greaves, 2007
Pygmy (Western)	n/a	45%	Walker et al., 2006
Semang	40.5%	n/a	Murdock, 1934
N	15	17	
Mean	26.8%	48.8%	

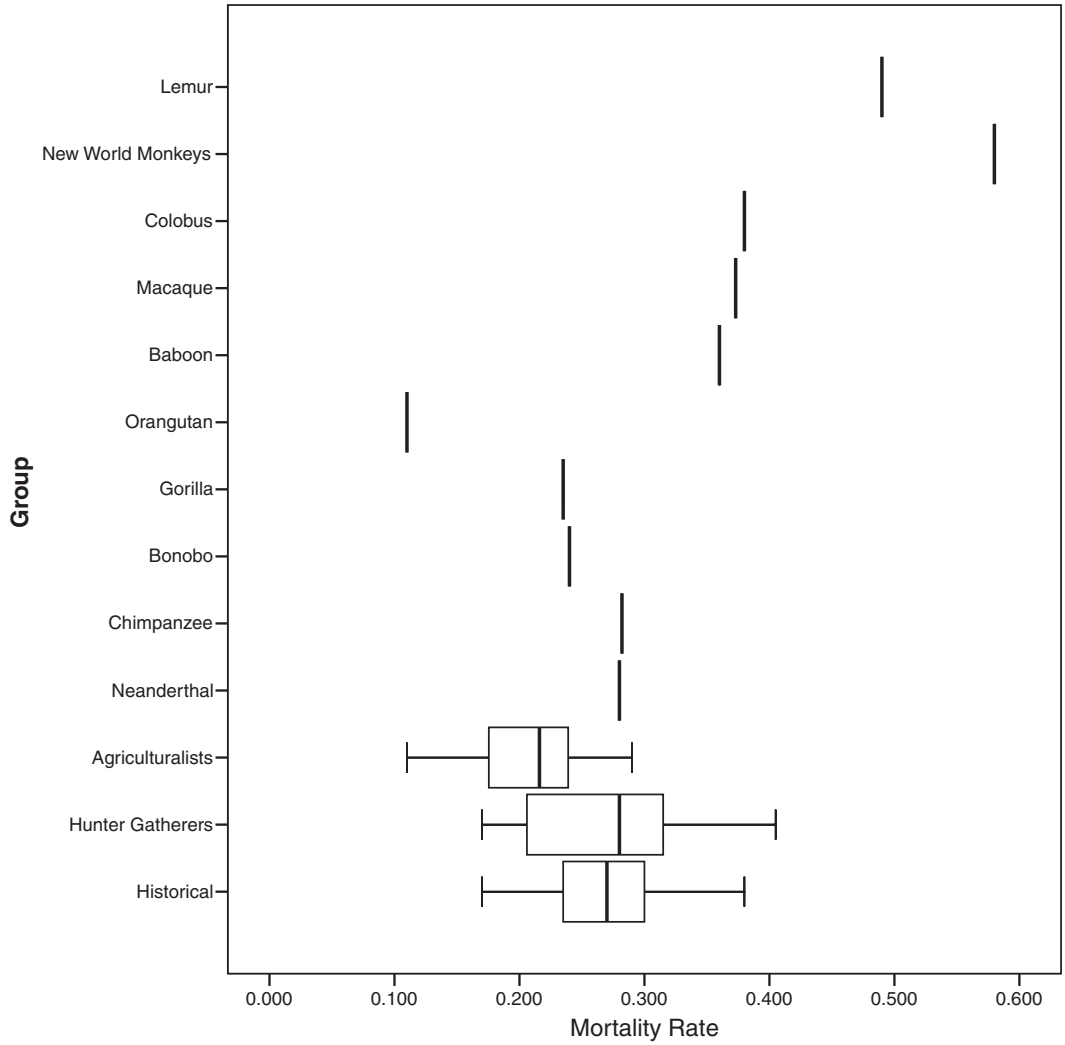

Fig. 1. Boxplot of infant mortality rate by group.

decay of children's smaller physical remains and the lower frequency of elaborate infant burials, death records, and written life histories (Lewis, 2007). Therefore, the historical infant and child mortality rates we present should be viewed as conservative estimates that generally err toward underestimating actual historic rates.

While there is a significant variation among the different cultures, the overall patterns of mortality remain surprisingly constant given the hundreds or thousands of both years and miles separating our historical samples (see Table 2). From the pre-Columbian Americas, to Ancient Rome, to medieval Japan, to the European Renaissance, roughly a quarter of infants died before their first birthdays and half failed to survive to adulthood. When the historic mortality rates from over 43 historical cultures are averaged, the average IMR is $M = 26.9\%$ (SD = 4.8%), while the average CMR is $M = 46.2\%$ (SD = 8.4%). What is immediately apparent is how similar these averages are to those found for hunter–gatherers in Table 1. Once again, the unity of the data is striking despite the enormous cultural, geographical, and temporal variations. In many ways, this unity is surprising given the vastly different ecologies within hunter–gatherers, let alone in comparison to the ecologies of our historical populations. Also, as with the HG data, there are no outliers and negligible skew (IMR = 0.349, CMR = 0.264) and kurtosis (IMR = −0.214; CMR = 0.811) in the data set. This similarity strongly suggests that these average mortality rates are reliable, enduring features of the human EEA. Overcoming these substantial IMR and CMR was a necessary prerequisite for adults, which makes their evolutionary influence even more significant (Williams, 1957; Jones, 2009; Roff, 1993). It does not matter if one has the potential to be the most talented and appealing adult if one fails to survive to adulthood. Therefore, infant and child mortality may have been one of the most, if not the most, important selective pressures faced by humans in the EEA (see Volk & Atkinson, 2008, for a quantitative comparison with adult pressures).

To put this figure in context, Table 2 also shows the approximate mean mortality rates in modern Western countries (IMR = 0.1%, CMR = 1%). The EEA average CMR thus represents a roughly 5000% increase compared to mortality rates in modern Western cultures. Children in modernized cultures face 99 to 1 odds of surviving compared to the 1 to 1 odds faced by their ancestors.

4. Agriculturalist data

For reasons soon to be discussed, we separately examine the mortality rates (MR) for 20 agriculturalist societies (horticulturalist and pastoralist societies) in order to further broaden the scope of our data (see Table 3). Again there were no outliers and low skew (IMR = −0.349; CMR = 0.264) and kurtosis (IMR = −0.214; CMR = 0.819) values. While these average rates ($M = 20.6\%$, SD = 4.8% for IMR, $M = 37.6\%$, SD = 9.7%, for CMR) are still much higher than

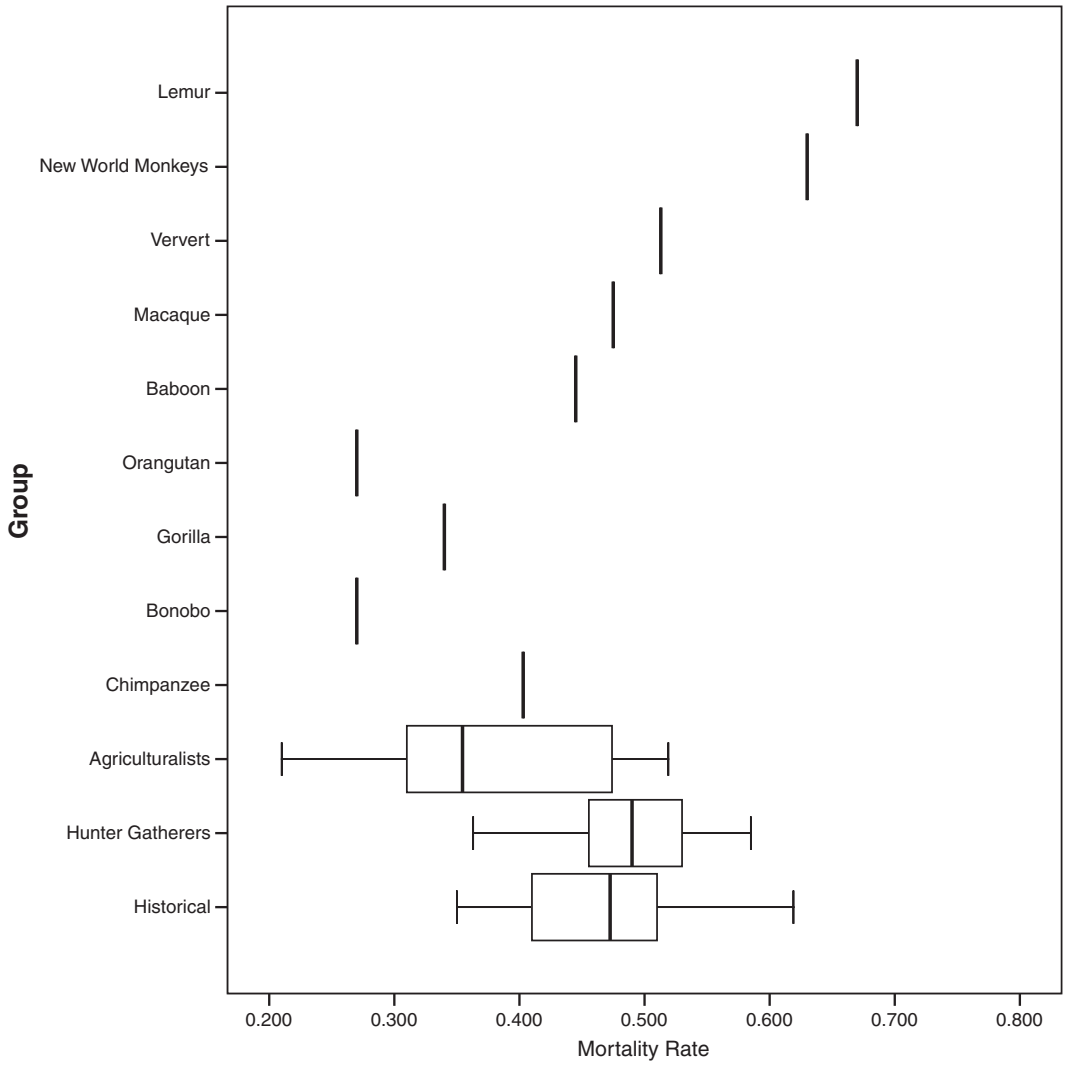

Fig. 2. Boxplot of child mortality rate by group.

modernized values (Table 2), when compared using a Student's *t*-test (Torres et al., 2002) they are significantly lower than either the historical or hunter–gatherer MRs (agricultural vs. historical IMR $t=-2.22$, $p=0.36$, CMR $t=-3.743$, $p<0.01$; agricultural vs. hunter–gatherers IMR $t=-3.928$, $p<0.01$, CMR $t=-3.599$, $p<0.01$). Some agriculturalist groups resembled hunter–gatherers in their mortality rates (e.g., Ayoreo, Semain, Yąnomamö), but the majority did not. We propose at least two possible reasons for this discrepancy. First, the advent of primitive agriculture may result in a decline in MRs due to advantages of that lifestyle such more reliable food security (Eshed, Gopher, Gage, & Hershkovitz, 2004). However, we believe that this is unlikely, as similar declines in MR are not seen in the numerous agricultural civilizations listed in Table 2. The second reason, which we believe to be more likely, is that modern agriculturalist cultures have deviated from the EEA because of positive exposure to modernized Western laws, education, sanitation, food, and medicines. There is now strong evidence that this exposure frequently occurs during the transition from hunter–gatherer to horticulturalist in modern times, and that it significantly decreases IMRs and CMRs (Roth, 1981; Kramer & Greaves, 2007). Indeed, all low mortality modern societies passed through a demographic transitory trend, first reducing CMR and then IMR, with Europe starting its transition to lower IMRs and CMRs in mid-18th century (Coale & Watkins, 1986). This historical trend appears similar to our agriculturalist data, where the trend compared to our EEA data is for a greater drop in CMR as compared to IMR. We therefore believe our data on agriculturalist populations are best considered as speculative data that are likely to be tainted by modern technologies and medicines and may represent ancestral populations transitioning to lower mortality rates due to external influences. We thus decided to exclude these data from our estimates of the EEA. However, even if these data are untainted, the average IMR of 21% remains over two orders of magnitude higher than the modern IMR, while the CMR is almost 40 times greater than modern Western CMR. Thus agriculturalist infant and child mortality rates still represent large selective pressures.

5. Nonhuman primate data

We include one final pool of data, non-human primates, in order to provide comparative data that can help determine how phylogenetically deep the human pattern is, and whether other primate species have faced similar selective pressures as ourselves. Prior to investigating the rates of mortality in other primates, it is necessary to define the various age categories used. For all primate species, IMR is typically defined in as the MR to 1 year of age. The Juvenile mortality rate (JMR), the rough equivalent of CMR in humans, is defined as the age of, or immediately prior to, puberty/adult fertility. For example,

Table 2
Historical civilized infant mortality rates (IMR) and child mortality rates (CMR).

Time	Culture	IMR	CMR	Source
500–300 B.C.	Greece	25%–35%	n/a	Golden, 1990
400 B.C.–550 A.D.	Nasca (Peru)	34.7%	47.5%	Drusini, Carrara, Orefici, & Bonati, 2001
400–200 B.C.	Spain	25%	45%	Alesan, Malgosa, & Simo, 1999
200 B.C.–200 A.D.	Rome	30%	50%	Rawson, 2003
0 A.D.	Roman Egypt	33%	57%	Bagnall & Frier, 1994
200–400 A.D.	Rome	30%	n/a	Todman, 2007
300–550 A.D.	Teotihuacan	28.8%	49.4%	Storey, 1985
550–700 A.D.	Teotihuacan	32.4%	61.9%	Storey, 1985
600–1100 A.D.	Wari (Peru)	27.0%	52.5%	Drusini et al., 2001
1300–1400 A.D.	Japan	28%	48%	Nagoaka, Hirata, Yokota, & Mausu'ura, 2006
1500 A.D.	England	27%	n/a	Orme, 2001
1600–1700 A.D.	Sweden	25%–40%	50%	Human Mortality Database, 2008
1600–1700 A.D.	Finland	23%	n/a	Anderson, 1996
1600–1700 A.D.	France	24.4%–28%	40%–50%	Anderson, 1996; Lachiver, 1969
1650–1700 A.D.	England	17%	n/a	Anderson, 1996
1650–1800 A.D.	England, Quakers	35%	n/a	Landers, 1992
1650–1800 A.D.	Imperial China	26%	45%	Puyi, 1964
1670–1769 A.D.	France	27%	n/a	Charbonneau, 1970
1688–1742 A.D.	France	19%	n/a	Cohen, 1975
1692–1899 A.D.	Germany	35%	60%	Knodel, 1970
1700–1800 A.D.	Italy	25%	40%+	Oris, Derosas, & Breschi, 2004
1700–1800 A.D.	Japan	22%–25%	n/a	Oris et al., 2004
1700–1800 A.D.	Germany	22.8%	35%	Knodel & Hermalin, 1984
1700–1800 A.D.	China		40%+	Oris et al., 2004
1730 A.D.	Quebec	22.5%	n/a	Charbonneau, Desjardins, Légaré, & Denis, 2000
1749–1773 A.D.	Finland	27.5%	35% (at age 10)	Turpeinen, 1978
1751–1800 A.D.	Finland and Sweden	22%	41%	Gille, 1949
1776–1875 A.D.	Japan	28%	51%	Jannetta & Preston, 1991
1786-1865 A.D.	African-American Slaves	30-35%	n/a	Steckel, 1986
1800–1900 A.D.	Belgium	19%	41%	Oris et al., 2004
1800-1900 A.D.	Venice	28%	51%	Oris et al., 2004
1816–1850 A.D.	France	20%	44%	Preston & van de Walle, 1978
1820–1832 A.D.	West Indies	n/a	47%	Roberts, 1952
1836 A.D.	Ireland	23%	n/a	Anderson, 1996
1840–1852 A.D.	Iceland	25%–30%	n/a	Guttormsson & Garðarsdóttir, 2002
1850 A.D.	United States	21.6%	n/a	Haines, 2000
1875 A.D.	Poland	24.0%	55.3%	Budnik & Liczbińska, 2006
1888–1912 A.D.	Cocos Malay Islands	38%	n/a	Smith, 1960
1894–1900 A.D.	Brazil	24%	n/a	Sastry, 2004
1900–1909 A.D.	Mexico	30%	n/a	Feliciano, 2000
Late 19th–early 20th A.D.	Malta	25%	n/a	Walz, 2006
1910–1939 A.D.	Manitoba Cree	25%	n/a	Moffat & Herring, 1999
1950 A.D.	Afghanistan	28%	36%+	United Nations Data, 2008
	N	42	24	
	Mean	26.9%	46.2%	
Modern	Developed countries	>1%	1%	United Nations Data, 2008

this age is around 2 to 5 years for monkeys, 6 to 8 years for gorillas, and v8 for chimpanzees (Dyke et al., 1993; Goodall, 1986). It is important to note that, as with the horticulturalist data, the MRs of other primates can be seriously compromised by modern human influences (Köndgen et al. 2008). As with our human data, we have done our best to limit our primate data in general, and for great apes in particular, to stable populations that have not been seriously influenced by modern human activities such as poaching, zooanthropic disease transmission, and/or habitat loss. Populations that report mortality rates that have been significantly influenced by modern humans remain of interest for ecological and conservation purposes, but they may not be appropriate predictors of primate EEAs.

To begin with, the rough estimate of the 28% infant mortality of our closet relatives, Neanderthals, is remarkably similar to both historical and hunter–gatherer averages (see Table 4). The average IMR (23.1%) of other great apes is slightly lower than the historical and hunter–gatherer averages, but slightly higher than the agriculturalist averages. However, their average JMR (32.8%) remains much lower than the historical and hunter–gatherer averages. Chimpanzees, and potentially gorillas (who lack clear mortality to menarche data), appear to be the most similar to humans in terms of their IMR and JMR. The other great apes MR were substantially lower. Orangutans' very low IMR and JMR are most likely related to their lengthy average interbirth intervals (IBI) of 8 years (Wich et al., 2004). Bonobos' low IMR and JMR may be influenced by both low levels of infanticide and the artificial provisioning of food used by experimenters to aid in their observational studies (Furuichi et al., 1998). Old World monkeys have an average IMR of 36.1% and an average JMR of 42.7%. The IMR and JMR of New World monkeys (58% and 63%) and lemurs (49% and 67%) are the highest of all primates. Thus the pattern of human infant mortality appears to be similar to that of Neanderthals, chimps, and gorillas, but *not* to orangutans or bonobos (lower) and other primates (higher). In very rough terms, there appears to be a phylogenetic relationship with IMR and JMR as species more closely related to humans have more similar mortality rates. We appreciate that there may be different causes behind similar mortality rates in different species, and thus we strongly caution against using these data to draw direct phylogenetic conclusions. That said, our results do offer researchers a significant starting point in which to look for causal differences or similarities in the mortality rates of humans and apes (e.g., differences in parental care; Hrdy, 1999; Smith, 2005). Lastly, it is important to stress that reliable mortality rates from "pristine" primate populations are few and far between, and our primate samples are much smaller than our human samples, so a degree of caution is warranted about our primate data. With these caveats in mind it may be helpful to examine the causes of human infant and

Table 3
Agriculturalist infant mortality rates (IMR) and child mortality rates (CMR).

Culture	IMR	CMR	Source
Ayoreo	26.2%+	51.0%	Diez & Salzano, 1978
Bambara	23.8%	n/a	Hewlett, 1991
Bari	11%	21.4%	Hewlett, 1991
Datoga	20.8%	33%	Borgerhoff Mulder, 1992
Dusun	17.1%	36.2%	Salzano, Neel, & Mayburry-Lewis, 1967
Fulani	21.1%	n/a	Hewlett, 1991
Gainj	16.5%	33.6%	Wood, 1987
Kapauku	n/a	34.7%	Popsil, 1963
Kipsigis	25.4%	31.0%	Borgerhoff Mulder, 1988
Lese	17.9%	26.9%	Hewlett, 1991
Masai	53%	n/a	De Vries, 1987
Ngbaka	24%	29.7%	Hewlett, 1991
Nyimba	21.6%	n/a	Levine, 1988.
Plateau Tonga	16%	n/a	Colson, 1958
Pumé	13.2%	n/a	Kramer & Greaves, 2007
Sebei	n/a	38.2%	Goldschmidt, 1976
Semai	23.4%	47.4%	Hewlett, 1991
Talensi	n/a	51.9%	Fortes, 1943
Tamang	20.4%	38.9%	Fricke, 1984
Tikopia	28.6%	n/a	Firth, 1983; Hewlett, 1991
Twareg	22.8%	n/a	Hewlett, 1991
Yąnomamö	21.8%	51.9%	Early & Peters, 1990; Hewlett, 1991; Neel & Weiss, 1975
N	19	14	
Mean	20.6%	37.6%	

child mortality rates, particularly as compared to the causes of IMR and JMR in other primates.

6. Causes of infant and child mortality

To fully understand the evolutionary implications of infant and child mortality rates, we need to have some understanding of their causes (i.e., the underlying evolutionary events/pressures that cause infant and child mortality). Unfortunately, completely determining the cause of infant or child death is not always possible even in modern hospitals, let alone for non-modern populations (Bryce, Boschi-Pinto, Shibuya, Black, & WHO Child Health Epidemiology Reference Group, 2005; Lewis, 2007). We are thus left with educated estimates from various EEA-like populations. Hill et al. (2007) found that among Hiwi forager's infant deaths that approximately 30% of deaths were caused by congenital problems, 30% from disease (mostly gastrointestinal (GI) or respiratory in nature), 30% from violence (i.e., infanticide, mostly targeted at female infants), and 10% from accidents. For child death, 70% were caused by disease, 10% from congenital problems, 10% from violence, and 10% from accidents. The authors note that the Hiwi have exceptionally high mortality levels due to violence, especially post-Western-contact (Hill et al., 2007). Thus, these percentages may not represent the more general hunter–gatherer values. Even with the high rate of violent deaths, most deaths were caused by GI or respiratory disease. In a broader survey of eight hunter–gatherer and agriculturalist cultures (forest Ache, settled Ache, !Kung, Tsimane, Agta, Hiwi, Machi-guenga, and Aborigines), 65% of the child deaths were due to illness (again primarily GI and respiratory), 9.5% to congenital problems, 8% to accidents, and 17% to violence (Gurven & Kaplan, 2007). If the two most aggressive groups (forest Ache and Hiwi) are excluded, the percent of child deaths due to violence drops to 5%. Among the historical EEAs, illness is again the major cause of infant and child death, with infanticide/abandonment being an important secondary cause (Rawson, 2003; Cunningham, 2005; Budnik & Liczbińska, 2006). As in agriculturalist and hunter–gatherer cultures, GI and respiratory diseases remain the primary modern causes of infant death (especially in countries with high mortality rates; Bryce et al., 2005). We did not come across explicit

Table 4
Primate infant mortality rates (IMR) and juvenile mortality rates (JMR).

Primate	IMR	JMR	Source
Neanderthal	~28%	n/a	Trinkhaus, 1995
Chimpanzee	28.2%	40.3%	Goodall, 1986; Wrangham, Clark, & Isabirye-Basuta, 1992 Sugiyama, 1994, 2004
Bonobo	16%–32%	27%+	Furuichi et al., 1998; De Lathouwers & Van Elsacker, 2005
Gorilla	23.5%	34% at weaning, 47.5% (age 8)	Harcourt, Fossey, & Sabater-Pi, 1981; Schaller, 1963; Watts, 1989; Yamagiwa & Kahekwa, 2001;
Orangutan	11.00%	27%	Debyser, 1995; Van Noordwijk & van Schaik, 2005; Wich et al., 2004
Baboons (*Papio cynocephalus*, *Papio hamadrayas*, *Papio ursinus*)	36%	44.5%	Altmann, Altmann, Hausfater, & McCuskey, 1977; Jolly, 1973; Sigg, Stolba, Abegglen, & Dasser, 1982; Cheney et al., 2004
Macaques (*Macaca sylvanus*, *Macaca fuscata*, *Macaca mulatta*, *Macaca sinica*)	37.3%	45%–50%	Ménard & Valet, 1996; Takahata et al., 1998; Melnick, 1981; Dittus, 1977, 1981
Colobus monkey (*Colobus guereza*)	38%	n/a	Dunbar & Dunbar, 1974
Ververt monkey (*Cercopithcinae aethiops*)	n/a	51.3%+	Hauser, 1988
Smaller New World monkeys (*C. faccus*, *L. rosalia*, *S. fuscicollis illigeri*, *S. fuscicollis* hybrids, *S. oedipus*)	58%	63%	Dyke et al., 1993
Lemurs (*Lemur catta*, *Propithecus verreauxi*, *Propithecus diadema edwardsi*)	49%	67%	Gould, Sussman, & Sauther, 2003; Richard, Dewar, Schwartz, & Ratsirarson, 2002; Wright, 1995

infant or child mortality rates caused by non-human predation, so this was presumably a relatively minor cause of infant and child mortality, although it certainly can occasionally occur (Wrangham, Wilson, Hare, & Wolfe, 2000). There is some evidence that predation may have played a larger role for earlier hominids (Hart & Sussman, 2005), but this may be the largest difference in mortality causes between *Homo sapiens* and our primate relatives, for whom predation plays a much greater role, alongside infanticide (Anderson, 1986; Cheney et al., 2004). Indeed, predator-caused mortality rates have been observed to be as high as 40% in baboons (Bulger & Hamilton, 1987) and 65% in chimpanzees (Boesch & Boesch-Acherman, 2000). Additionally, there are numerous, well-documented, predator-induced severe group size declines for most primate species that have been studied in detail for a sufficient period of time (Hill & Dunbar, 1998; Hart & Sussman, 2005), an event that has never been documented in any human population. It is interesting then that humans have a higher CMR than any other ape species. This may be a consequence of our lengthier childhoods that simply expose us to greater opportunities to die (primarily by disease or violence). This emphasizes how important childhood must have been to our species given its increased cost in terms of higher mortality rates. It also emphasizes the possible importance of novel (or altered) mortality pressures on humans as compared to other apes, as well as the need to better understand when and why such shifts occurred.

Related to the question of what caused infant and child mortality is the question whether or not there is any evidence that the EEA rates of mortality could have been ameliorated by behavioral adaptations. If not, if IMR and CMR were behaviorally unavoidable, and all individuals suffered equally (and randomly), this could mean individual differences in behavior were not sufficient to mediate mortality rates in the EEA. This in turn would suggest that IMR and CMR might have exerted a psychologically static evolutionary pressure in the EEA that might not be of adaptive concern, at least to psychologists, as evolution is necessarily based on differential reproduction/transmission of genes (Dawkins, 1989). In other words, for IMR and CMR to be of relevance to behavioral psychologists (and related scientists), there must have existed some links between behavior and changes in IMR and/or CMR in the EEA.

This indeed appears to be the case, as there are a number of factors that alter mortality rates at both inter-individual and inter-population levels. Not surprisingly, previous research has found that anything that increases the amount or quality of direct investment in a child decreases that child's probability of dying. As a marker of general resources available to parents, socio-economic status is negatively related to IMR and CMR between populations (Preston & van de Walle, 1978) and within populations (Houweling & Kunst, 2010). More specifically, an increase in the quality and quantity of food decreases mortality (Gage 1994; Houweling & Kunst, 2010). An increase in alloparental support can also decrease mortality levels (Hawkes, O'Connell, & Burton-Jones, 1989; Sear, Steele, McGregor, & Mace, 2002, Sear & Mace, 2008), while maternal care is perhaps the strongest predictor of infant mortality (Hrdy, 1999). Firstborns tend to suffer from higher infant mortality rates (Cohen, 1975), perhaps due to the inexperience of their parents (Smith, 2005). Interestingly, this does not appear to affect child mortality rates (Cohen, 1975), perhaps because older children are less susceptible to first-time parents' mistakes. It does appear that in stressed populations, mothers with higher IQ's may have higher child survival rates (Čvorović, Rushton, & Tenjevic, 2008). Family size is also positively related to mortality rates, presumably because (all else being equal) in larger families each child has access to fewer resources (Cohen, 1975; Knodel & Hermalin, 1984). Intact biological families also tend to have lower mortality rates (Cohen, 1975), although this is not a universal finding. Hygienic practices surrounding newborns can also have profound impacts on mortality rates by regulating the amount and type of pathogens that infants are exposed to (Wood, 1983). Other behavioral factors that affect MRs include breastfeeding (eg: Golding, Emmett, & Rogers, 1997; Victora et al., 1987; Volk, 2009), reduced interbirth intervals (Hobcraft, McDonald, & Rutstein, 1983, Palloni & Millman, 1986, Alam, 1995, Bøhler & Bergström, 1995) and polygyny (e.g., Omariba & Boyle, 2007). Thus we feel confident repeating our assertion that infant and child mortality represented serious and salient forces in the evolution of human behaviors.

We should note that a competing hypothesis is that humans have responded to high levels of infant and child mortality via greater fertility rather than reduced mortality. This would represent a shift from a slow to a fast life history strategy (Bogin, 1996, 1997, 1999). While we lack data to directly test this hypothesis, we believe it to be less significant that mitigating mortality for three reasons. First, the most direct route to greater fertility, having multiples at birth, is associated with a dramatic (4–5×) increase in the odds of mortality and/or serious handicap (Kleinman, Fowler, & Kessel, 1991). Second, the significant costs and risks of human pregnancy impose a significant baseline cost on any fast strategy when compared to a slow strategy (Bogin, 1996, 1997, 1999). Third, indirect evidence comes from modern human behavior where individuals choose to raise fewer, more competitive, high-quality children rather than maximizing the number of offspring despite relatively low odds of child mortality even in very large modern families. We suggest that this "keeping up with the Joneses" behavior reflects an underlying evolutionary preference for quality (slow/mortality) over quantity (fast/fertility). Nevertheless, one should not underestimate the potential evolutionary benefits of increasing fertility. Fortunately, for the simplicity of theoretical considerations, the mechanisms for increasing fertility are often the same as those for decreasing mortality (e.g., increasing parental resources).

7. Discussion

An understanding of the EEA is crucial for the study of human behavior from an evolutionary perspective. Although the study of the EEA is fraught with challenges, we propose that there are certain aspects of it that can be reliably elucidated. We have argued that there is one such critical feature of the human EEA for which we have robust quantitative data: infant and child mortality rates.

We combined archaeological, anthropological, historical, and primate data to create a broad, yet detailed, qualitative overview and quantitative estimate of infant and child mortality in the human environment of evolutionary adaptedness. Although there are limitations to our historical, paleodemographic, cross-cultural, and cross-species mortality estimates (see above), our findings of EEA IMR and CMR are exceptional in their relative congruence (see Figs. 1 and 2). Average infant and child mortality rates for *H. sapiens sapiens* were similarly high across an enormous range of cultures, geographic locations, and times in our EEA. These rates appear to be higher than the aggregate mortality rates for other great apes (especially for children versus juvenile apes). This is slightly less so when compared to Neanderthals, chimpanzees and gorillas, which suggests the possibility of phylogenetic influences on mortality rates.

That said, humans may have had lower levels of predation than other great apes for an evolutionary significant period of time. This means that the other causes of infant and child mortality, such as disease and infanticide, should be more salient evolutionary pressures for *H. sapiens* than for related species such as gorillas or chimps. Individual differences in socio-economic status, parental care, family structure, and cultural practices (e.g., religion) are just some of the behavior-related factors that influenced sub-adult mortality rates. It must be stressed that the evidence of specific causes of mortality is less concrete than the evidence for the overall MRs. This evidence nevertheless provide a useful framework of where and what to begin looking for when searching for potential adaptations. However,

particularly among psychologists, infant and child mortality is rarely explicitly acknowledged as an important selective pressure.

It is ironic then that the very basis for of this paper, the EEA, comes from one of founders of modern evolutionary psychology—John Bowlby. Bowlby (1982) was keenly aware of the importance of ancestral child mortality, which his theory of attachment is meant to be a response. Parenting is certainly a key potential adaptation toward reducing mortality rates. In particular, research by evolutionary anthropologists strongly suggests that besides the unusual level of paternal care shown by humans (Geary & Flinn, 2001), alloparenting (care from someone other than the child`s parents) is a crucial adaptation toward improving child survival (Blurton-Jones, Hawkes, & O'Connell, 2005; Hawkes, O'Connell, Blurton-Jones, Alvarez, & Charnov, 1998; Hrdy, 1999, 2009; Marlowe, 2010; Weiner & Gallimore, 1977). Despite arguments to the contrary (Ariès, 1962), parents did not stop loving their children or treating them like commodities once agriculture made them valuable working commodities. The selective pressures of infant and child mortality ensured that attentive parental care remained a crucial feature of human behavior throughout the last 10,000 years (Rawson, 2003; Cunningham, 2005).

However, parenting is not the sole aspect of adult behavior to which infant and child mortality is relevant. Research on both mating and cooperation may benefit from insights regarding child and infant mortality. The importance of parental care may be a key aspect in the choice of long-term partners (Buss & Schmidt, 1993). Choosing a partner for good genes may also be particularly salient (Puts, 2010; Scheib, Gangestad, & Thornhill, 1999), as one chooses an individual who is not simply a fit adult, but someone who has genes that may promote the survival of one`s offspring. Although this has been tested in animals (Grammer, Fink, Møller, & Thornhill, 2007), we are not aware of any human mating research that has explicitly examined the relationship between mate choice and child survival rates. Barber (2000) found that female sociosexuality at the population level increased with the risk of infectious disease, and that female sociosexuality was inversely related to the spread of HIV; results that are most parsimoniously explained by a good genes model (Møller & Alatalo, 1999).

For research on cooperation, it may be that an increase in child survival is a key function of cooperation, such as sharing food or defending a territory (Geary & Flinn, 2001; Hill & Hurtado, 2009). Studies of coalitional formation could, for example, use protecting children as a factor when designing experiments. Males who cooperate with, and trust each other, may be less likely to commit infanticide over perceived paternity issues. Women who cooperate may be able to provide the valuable alloparenting that is sometimes required for offspring to survive. Indeed, life history theorists have suggested that this may be part of the function of menopause—the switch from parenting to provisioning kin and allies (Bogin, 1996, Hawkes et al., 1998).

It should be noted that behavioral adaptations are highly unlikely to be confined to adults. As evolutionary developmental theorists have increasingly suggested, infancy and childhood appear to be adaptations in their own right, not simply preparatory phases for adulthood (Bjorklund, 1997; Pellegrini & Smith, 2005; Konner, 2010). That is, children are adapted to meet the needs and demands of childhood and are not simply incomplete or under-developed adults (Bjorklund, 2007; Konner, 2010). Indeed, childhood appears to be a uniquely human life history adaptation (Bogin, 1996, 1997, 1999). Therefore children should possess unique adaptations that reduce their odds of dying. Infants clearly posses such innate mechanisms designed to increase their survival. Infant crying is a clear solicitation of parental care, and one that is generally effective (Furlow, 1997; Soltis, 2004). Infant facial cues also appear to motivate adults to provide parental care (Alvergne, Faurie, & Raymond, 2009; Volk & Quinsey, 2002). Also, while men place a greater emphasis on cues of resemblance (Dubas, Heijkoop, & van Aken, 2009; Volk & Quinsey, 2007), both sexes are positively motivated by cues of youth, small size, cuteness, and health (Alley, 1983; Volk, Lukjanczuk, & Quinsey, 2007). Children also appear to show adaptive timing and learning of fears that coincide with new environmental threats. For example, a fear of heights does not develop when the child is carried high off the ground by parents (a fear that would interfere with the delivery of vital parental care). It develops only after the child has learned self-locomotion, when the child is suddenly much more prone to falling accidents (Gibson & Walk, 1960; Campos, Berthenthal, & Kermoian, 1992). Children in a number of societies forage for their own food, supplement the parental care they receive with their own efforts (e.g., Marlowe, 2010). Indeed, Zeller (1987) suggests that this self-provisioning may have played an important role in hominid evolution. Finally, children may also use aggression to obtain vital resources for themselves at the expense of others when environmental conditions are poor and/or parental care is negligible (Hawley, Little, & Rodkin, 2007; Volk, Camilleri, Dane, & Marini, 2012a). As mentioned previously, it is important to recognize that these child adaptations need not have ended 10,000 years ago (Cochran & Harpending, 2009). For example, Volk, Camilleri, Dane, and Marini (2012b) argue that novel environmental pressures in "civilized" cultures over the past 10,000 years may have influenced the forms, functions, and frequencies of childhood bullying, as well as psychopathy.

8. Future research

The above list of "evidence for an adaptation" is not meant to be exhaustive or limiting. Rather, it is meant to illustrate only a handful of the myriad potential applications relevant to the selective forces that IMR and CMR played in our EEA. The temporal primacy of infant and child mortality in the lifespan, their ubiquity through virtually all ancestral environments, their potential phylogenetic history, and the very high odds of childhood genetic failure mean that there are very strong qualitative and quantitative reasons for believing infant and child mortality is a critical selective pressure in the human EEA. It is our hope that we have communicated the significance of infant and child mortality, and its potential implications for human mental evolution. Our paper is meant to serve not only as a reliable estimate of an important evolutionary pressure in the EEA, but also as a call for researchers to consider how infant and child mortality may have played a role in shaping the evolution of the human mind. In particular, a more thorough investigation of factors that mediated IMR and CMR is critical to understanding the nature of the selective forces operating on the IMR and CMR EEA, and we encourage further exploration of these factors. These factors connect with the need for further research into the questions of why are mortality rates so relatively constant across such a range of cultural, temporal, and ecological conditions.

The quantitative nature of our data, along with its strong reliability and validity, means that researchers can use our IMR and CMR estimates to confidently devise and test a host of evolutionary theories in a variety of disciplines. Individuals studying life history now have numerical values that they can use with confidence. Behavioral researchers can not only use our quantitative estimates as well, but also draw on our qualitative estimates of the causes and factors associated with IMR and CMR to test existing hypotheses and to generate new ones. We thus hope that the tragedy of high levels of infant and child death in the past can help modern infants, children, and adults, by leading to more informed and complete evolutionary theories of human behavior.

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