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ScienceDirect
Journal of Human Evolution 54 (2008) 34–42

Fertility and mortality patterns of captive Bornean and Sumatran orangutans: is there a species difference in life history?

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Received 25 August 2006; accepted 22 May 2007

Abstract

Across broad taxonomic groups, life history models predict that increased ecological predictability will lead to conservative investment in reproductive effort. Within species, however, organisms are predicted to have increased reproductive rates under improved environmental conditions. It is not clear how these models apply to closely-related species. In this paper, we examine predictions from these models as applied to variability in reproductive rates between the two species of orangutans, *Pongo pygmaeus* (Bornean) and *Pongo abelii* (Sumatran). Orangutans exhibit characteristics of a ‘‘slow’’ life history strategy with large bodies, late age at maturity, low reproductive rates, and long lifespan. Recently, researchers proposed that Sumatran orangutans may have an even slower life history than Bornean orangutans as a result of ecological and genetic differences (Wich et al., 2004). We examined this hypothesis by studying important aspects of life history of both species under conditions of relative ecological stability, in captivity. In this large dataset, there were no significant species differences in age of first or last reproduction, completed fertility, perinatal and postnatal mortality, or female longevity. Bornean orangutans in captivity did have significantly longer interbirth intervals, and male Bornean orangutans had higher survival past maturity. Our results do not support the hypothesis that selection has led to decreased reproductive effort under conditions of increased habitat quality in Sumatra (Wich et al., 2004), and instead suggest that phenotypic flexibility may be particularly important in explaining differences between closely related species.

Keywords: Reproductive parameters; Interbirth intervals; Reproductive ecology

Introduction

Life history adaptation can be viewed broadly as selection for ‘‘optimal’’ allocation of energy to the competing demands of maintenance, growth, and reproduction (Gadgil and Bossert, 1970). Thus, reproductive effort in mammals shares complex relationships with other variables such as body size, mortality rates, and ecological consistency. Primates exemplify selection for ‘‘slow’’ life histories characterized by late age at maturity, long lifespans, and long interbirth intervals (IBIs) (Charnov and Berrigan, 1993). Orangutans are at one extreme: among the largest and longest-lived of primates (Wich et al., 2004), they have the longest IBIs of any mammal regardless of size (Galdikas and Wood, 1990; Knott, 2001). Interestingly, field reports suggest that there may be significant variation in reproductive rates between the two orangutan species (*Pongo pygmaeus*, Bornean orangutan, and *P. abelii*, Sumatran orangutan), and that such variation may be linked to habitat differences between the two islands (Wich et al., 2004).

The available evidence suggests that IBIs in Sumatran orangutans are longer than in Bornean orangutans. Sumatran orangutans at Ketambe have a mean IBI of 111.5 months (9.3 years, $n = 23$), which is significantly longer than the mean IBI of 92.6 months (7.7 years, $n = 23$) for Bornean females at Tanjung Puting (Galdikas and Wood, 1990; Tilson et al., 1993; Wich et al., 2004). Although the samples are very small, reported mean IBIs of 98.4 months (8.2 years,

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doi:10.1016/j.jhevol.2007.05.014

$n = 8$ with estimated birth dates) from Suaq Balimbing in Sumatra (van Noordwijk and van Schaik, 2005) and 86.4 months (7.2 years, $n = 8$) from Gunung Palung in Borneo (Knott et al., in press) also support this difference.

Wich et al. (2004) hypothesized that the IBI difference is one indication of a general divergence in life history strategies that has resulted from differences in ecological stability between the Bornean and Sumatran habitats. Although Bornean and Sumatran orangutans were only recently classified as separate species, genetic studies estimate a divergence time of 1.1 to 5 million years (Xu and Arnason, 1996; Groves, 2001; Warren et al., 2001; Steiper, 2006). Recent ecological work emphasizes differences in habitat quality between the two islands. Consistent with the prevalence of rich volcanic soils on Sumatra, fruit is more readily available and stable in Sumatran study sites (Knott, 1998; Delgado and van Schaik, 2000; Fox et al., 2004; Knott and Kahlenberg, 2006). Thus, habitat quality and life history traits are theorized to form a gradient from west to east, correlating with other features such as cranial capacity, which is largest in *P. abelii* and smallest in the easternmost subspecies *P. pygmaeus morio* (Taylor and van Schaik, 2007).

Wich et al.'s (2004) hypothesis is consistent with the models of evolved life history differences between species. In comparisons across taxonomic groups, species with relatively rich habitat quality face lower mortality risks and reproduce at a slower pace (Gittleman, 1986; Charnov, 1991; Charnov and Berrigan, 1993). In such species, rather than maximization of reproductive rates, natural selection is expected to favor relatively slow reproduction and increased investment in survival and in individual offspring.

However, life history strategies also incorporate a norm of reaction as a means to accommodate random ecological effects (Ricklefs and Wikelski, 2002). Under life history models for short-term allocation of energy, large-bodied species like orangutans are expected to be able to increase their reproductive effort when energy intake is high (van Noordwijk and de Jong, 1986; Zera and Harshman, 2001). This responsiveness is mediated by the organism's physiology, particularly the endocrine system (Ketterson and Nolan, 1992; Ricklefs and Wikelski, 2002; Ellison, 2003; Knott, 2005). Reproductive ecologists describe strong positive links between energy availability and reproductive function (Wasser and Barash, 1983; Schneider and Wade, 2000). For example, intraspecies comparisons among primates generally reveal increased reproductive rates among captive or nutritionally-advantaged populations relative to populations living in natural ecological conditions (Asquith, 1989; Borries et al., 2001; Knott, 2001; Altmann and Alberts, 2003). This response is particularly elegant for the hominoids, in which reproductive function has a graded relationship with variance in energy balance (Ellison, 2003; Ellison et al., 1993; Knott, 2001, 2005; Emery Thompson, 2005; Emery Thompson and Wrangham, in review). Among wild orangutans at Gunung Palung, Borneo, Knott (1998, 1999) demonstrated that females had higher levels of ovarian hormones and increased conception success when their energy balance was most positive.

Thus, while interspecies models of life history predict a risk-aversive strategy of conservative reproductive effort with increased ecological certainty, models of phenotypic flexibility predict the opposite effect. Orangutans provide a valuable model for the study of contrasting life history predictions. In relation to other primates, they conform to predictions for the correlation between ecological stability and slow life histories. However, within populations, they meet predictions from reproductive ecology: energy availability correlates with increased reproductive rates. It is not clear how either model might apply to a contrast between the two closely-related orangutan species.

While preliminary evidence on orangutan interbirth intervals indicates slower reproductive rates with increased habitat quality (Wich et al., 2004), we find a number of problems with this argument (Knott et al., in press). First, sample sizes of wild orangutan birth intervals are still relatively small. The best published sample from Borneo (Tanjung Puting) consists of 12 complete (birth to birth) and 11 incomplete (no second birth at time of study) intervals from 11 female orangutans over 17 study years (Galdikas, 1985); the best Sumatran sample (Ketambe) is based on 16 complete and 7 incomplete intervals from 9 females over 32 study years (Wich et al., 2004). While these samples were sufficient to produce a statistically significant difference in complete birth interval length between populations, it is difficult to interpret differences observed over study periods that are short relative to the lifespan of the species. While infant mortality is reportedly low in the wild (Wich et al., 2004, Knott, unpublished data), the relatively solitary nature of these species makes it feasible that missed births and early perinatal deaths could skew estimates based on small samples. In addition, we cannot easily determine whether these are systematic differences between populations and species, or if they represent stochastic variation in habitat quality, demography, or forest disturbance.

A second problem is that life history theory predicts correlated differences in other life history traits (Eisenberg, 1981; Harvey and Clutton-Brock, 1985; Harvey and Zammuto, 1985; Read and Harvey, 1989; Charnov, 1991) that have not been observed yet in wild orangutans. No marked difference is evident in age of first birth between species (*Pongo pygmaeus*: 15.7 years, Tilson et al., 1993; *P. abelii*: 15.4 years, Wich et al., 2004), though these sample sizes are also very small. The few adult body weights that are available from the wild do not indicate a size difference: 86.3 (80–91) kg ($n = 4$) and 38.8 (33–45) kg ($n = 5$) for Bornean males and females, respectively, and 86.2 kg ($n = 1$) and 38.3 (34–43) kg ($n = 5$) for Sumatran males and females, respectively (Markham and Groves, 1990). Cranial analyses suggest more diversity in size and shape within the island of Borneo than between species (Groves et al., 1992; Taylor and van Schaik, 2007), as well as a strong influence of ontogenetic response to altitudinal differences (Courtenay et al., 1988). Most troubling, there is no suggestion as yet of a significant difference in either adult or juvenile mortality between species. Orangutans seem to have exceedingly low infant and juvenile mortality compared to other apes (Wich et al., 2004, Knott, unpublished data). While this is consistent with life history predictions about orangutans compared to other apes, there is no evidence that infant mortality differs enough to drive the evolution of life history differences between orangutan species.

Here, we present life history data from captive orangutans in U.S. and international facilities as a means to experimentally control for ecological conditions. Specifically, we compare the ages of females and males at their first and last reproduction, IBIs, total numbers of offspring per female, infant mortality rates, and longevity between the two species. The life history hypothesis (Wich et al., 2004) predicts that, while captive orangutans may experience accelerated reproduction and greater survival overall, significant species differences in life history traits should be maintained; furthermore, differences in birth intervals should be accompanied by differences in correlated life history variables, such as maturation rates and survival. Alternately, the reproductive ecology hypothesis (Knott, 2001) predicts that, assuming no systematic differences in quality of care, captive Bornean and Sumatran orangutans should have accelerated reproductive schedules relative to their wild counterparts and show little or no species difference in life history traits.

While we have taken care in our methodology to minimize the influence of captive breeding manipulations on the data reported, we are aware that captive data on reproduction are problematic. However, because of the relatively recent designation as separate species, Bornean and Sumatran orangutans often shared facilities and caregivers and were even interbred. Therefore, we have no expectation that these species experienced different captive environments.

Methods

All data are from the *International Studbook of the Orangutan*, which contains information from 313 institutions worldwide on 2,566 captive orangutans, with birthdates between 1901 and 2005. Our data set included information from when the studbook was last published in 1994 (Perkins, 2001), as well as data compiled through 5 December 2005. These data included each individual's ID number, sex, species, dam and sire ID number, birth date, and death date when known. We also had a list of individuals (both males and females) known to have been sterilized, although it is a reasonable assumption that not all sterilized orangutans had been reported. All orangutans were classified by species as Sumatran, Bornean, hybrid, or unknown. We analyzed records for 881 Sumatran orangutans (446 females, 418 males, and 17 individuals of unknown sex) and 1,035 Bornean orangutans (499 females and 513 males, and 23 individuals of unknown sex).

Of these subjects, 39.9% ($n = 764$) were born in the wild. Wild-born individuals were typically acquired as juveniles, and their birth dates were estimated by zoo staff at the time of acquisition. Therefore, data from orangutans that spent their entire lives in captivity are the most reliable and relevant to our hypotheses. Thus, we excluded wild-born individuals from analyses that required age accuracy (age at first and last reproduction, lifespan, and total number of offspring by age category) but not from IBI analyses.

All life history analyses were calculated with ages and birth data as of 5 December 2005. Where feasible, we used Kaplan-Meier analyses for right-censoring data. Chi-square statistics reported for these analyses represent the outcome of Breslow Generalized Wilcoxon tests (SPSS, Inc.); this is the most conservative test, but can adequately accommodate these sample sizes and censoring proportions (Breslow, 1970; Benedetti et al., 1982). Results for female age at first and last reproduction reflect the ages at the time of the birth. Male age of reproduction refers to the approximate date of fertilization; the difference between the sire's birth date and the offspring's birth date was corrected for the 245 day mean gestation period for orangutans (Nowak, 1999).

Age at first reproduction

Age at first birth was evaluated with a Kaplan-Meier survival analysis. In order to best exclude the influence of primary sterility or the use of contraception on this analysis for females, we determined the latest age of first birth for a captive dam of known age (25.6 years) and excluded females that had not given birth by this age. Similarly, we excluded males that had not sired an offspring by the latest known age of first male reproduction (28.1 years).

Age at last reproduction

We calculated the mean age at last reproduction with the understanding that these values are likely to systematically underestimate the physiological capacity to reproduce (for both species) due to contraception practices. We included only males and females that had survived to the mean calculated age of first reproduction (16.0 years for females and 18.6 years for males) and had produced at least one offspring.

Birth rates

We calculated interbirth intervals using Kaplan-Meier analyses, including both open and completed intervals when the first infant survived for at least four years. We determined the maximum completed interval (203.2 months) and excluded the 33 (of 1,240) incomplete intervals that exceeded this length; these females were likely to have been sterile, isolated from mates, or contracepted.

As a second test, we calculated the number of offspring born to each dam according to her current age or age at death, and compared fertility of the two species for each decade of life using Mann-Whitney U tests. Although contraception and repeated infant removal may be expected to stretch our range of results in both directions, mean figures provide realistic estimates of orangutan fertility.

Infant mortality

We separated infant mortality into two categories: (1) prenatal and neonatal mortality, which we defined as all deaths occurring before (stillbirths or abortions) or during the day of birth, and (2) postnatal mortality, which we defined as all deaths of infants after the day of birth and before four years of age. These analyses included all infants born into captivity before 5 December 2001, thus excluding individuals for which it was unknown whether they survived to four years of age.

Longevity

We evaluated lifespans of captive-born orangutans using Kaplan-Meier survival analyses. We provide four estimates based on analyses of mean lifespan for individuals surviving (1) the first day of life; (2) the first year of life; (3) the period of infant dependency (4 years); and (4) until the mean age of reproductive maturity.

Results

Ages at first and last reproduction

Sumatran females had a mean age of first birth of 16.4 years, which was not significantly different from the age of first birth of Bornean females (15.5 yrs., Table 1, $\chi^2 = 0.47$, df = 1, $p = 0.49$). Similarly, male age of first reproduction did not differ significantly between species; Sumatran males sired their first offspring at an average age of 19.4 years, while Bornean males first reproduced at 17.8 years ($\chi^2 = 1.44$, df = 1, $p = 0.28$).

Female age of last reproduction averaged 26.2 years for Sumatran orangutans and 29.0 years for Bornean orangutans (Table 1). Male age of last reproduction averaged 26.3 years for Sumatran orangutans and 24.7 years for Bornean orangutans. Neither difference was statistically significant (females: $\chi^2 = 0.26$, df = 1, $p = 0.61$; males: $\chi^2 = 0.71$, df = 1, $p = 0.40$).

Interbirth intervals

Among Bornean mothers, captive-born individuals had significantly longer mean IBIs than wild-born individuals (captive-born = 75.3 months, wild-born = 57.8 months; $\chi^2 = 23.77$, df = 1, $p < 0.001$). The same was true for Sumatran mothers (captive-born = 69.2 months, wild-born = 53.7 months; $\chi^2 = 11.62$, df = 1, $p = 0.001$). We therefore treated IBIs from captive-born and wild-born individuals separately for between-species comparisons.

Among captive-born individuals, Bornean mothers had mean IBIs of 75.3 months ± 4.9 SE ($n_{\text{total}} = 108$, $n_{\text{censored}} = 27$), while Sumatran mothers had mean IBIs of 69.2 months ± 5.4 SE ($n_{\text{total}} = 122$, $n_{\text{censored}} = 27$). The birth intervals were significantly shorter for captive-born Sumatran than for Bornean mothers ($\chi^2 = 4.40$, df = 1, $p = 0.04$, Fig. 1a).

Among wild-born individuals, Bornean mothers had mean IBIs of 57.8 months ± 3.7 SE ($n_{\text{total}} = 249$, $n_{\text{censored}} = 46$), while Sumatran mothers had mean IBIs of 53.7 months ± 2.9 SE ($n_{\text{total}} = 308$, $n_{\text{censored}} = 46$). Thus, there was a smaller absolute difference in IBIs of wild-born mothers than we observed in captive-born mothers, and there was not a statistically significant species difference ($\chi^2 = 0.06$, df = 1, $p = 0.8$, Fig. 1b).

Fertility

Deceased, captive-born Sumatran mothers had a mean completed fertility of 2.8 offspring ($n = 34$, range = 1–11). Deceased, captive-born Bornean mothers had similar fertility: 2.5 offspring ($n = 20$, range = 1–6, U = 327.0, z = −0.241, $p = 0.81$). It is difficult to interpret differences in completed fertility in this manner because there are many mitigating factors; these include mortality or removal of infants and the reproductive span of the mother, taking into account her age at death.

To improve this analysis, we compared the fertility of mothers by age decade depending on their current age or age at death (Fig. 2). There was substantial variation within age groups, which reflects captive breeding practices such as contraception and removal of newborn infants. In this analysis, we found no significant differences within age groups between Bornean and Sumatran mothers ($p > 0.28$).

Infant mortality

Of the Bornean orangutans born into captivity, 13.1% (71 of 542) died during the day of birth, or before birth due to

Table 1
Comparison of age at first and last reproduction between Bornean and Sumatran males and females using Kaplan-Meier models

	Bornean orangutans (*P. pygmaeus*)						Sumatran orangutans (*P. abelii*)						Species comparison (Breslow test)		
	n of events	*n* censored	Mean				*n* of events	*n* censored	Mean				Chi-Square	df	*p*
			Estimate (yrs)	Std. error	95% Confidence interval				Estimate (yrs)	Std. error	95% Confidence interval				
					Lower bound	Upper bound					Lower bound	Upper bound			
Age at first reproduction (yrs)															
Captive-born females	88	158	15.5	0.56	14.4	16.6	101	183	16.4	0.55	15.3	17.4	0.47	1	0.49
Captive-born males	60	191	17.8	0.82	16.2	19.4	67	214	19.4	0.75	17.9	20.9	1.44	1	0.23
Age at last reproduction (yrs)															
Captive-born females	15	69	29.0	1.46	26.1	31.8	24	67	26.2	1.26	23.8	28.7	0.26	1	0.61
Captive-born males	12	42	24.7	1.17	22.4	27.0	23	37	26.3	1.75	22.9	29.7	0.71	1	0.40

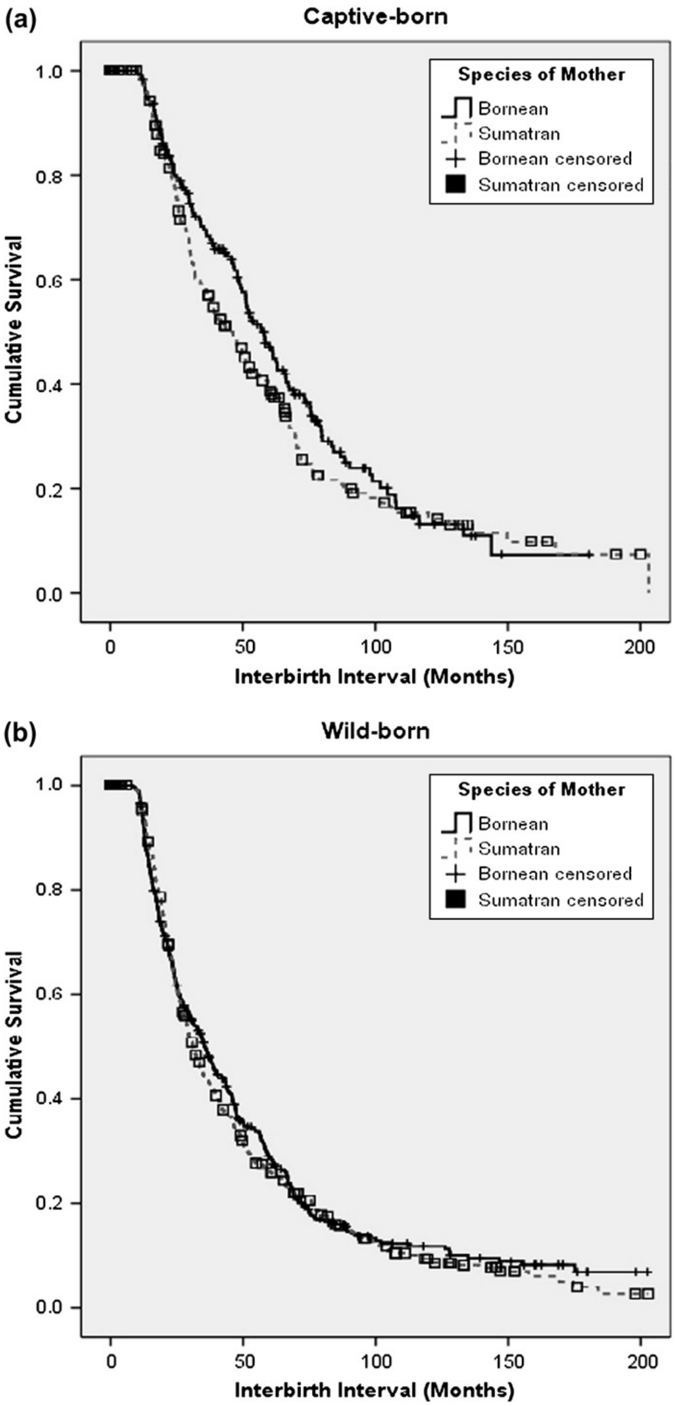

Fig. 1. Interbirth intervals of orangutan mothers, when first infant survived for at least 4 years, Kaplan-Meier analysis. (a) captive-born mothers, species comparison: $\chi^2 = 4.40$, df = 1, $p = 0.04$; (b) wild-born mothers: $\chi^2 = 0.06$, df = 1, $p = 0.8$. Y-axes reflect the cumulative proportion of intervals that remain open (i.e., no second infant born) at the time indicated by the X-axes. Breaks in the curve indicate completed birth intervals, while markers represent censored data (intervals that were incomplete at the time of data analysis).

stillbirths or abortions. Of the Sumatran orangutans, 10.6% (63 of 594) died before or during the day of birth. The distribution of prenatal and neonatal infant deaths between Bornean and Sumatran orangutans was not significantly different from chance ($\chi^2 = 1.49$, df = 1, $p = 0.22$).

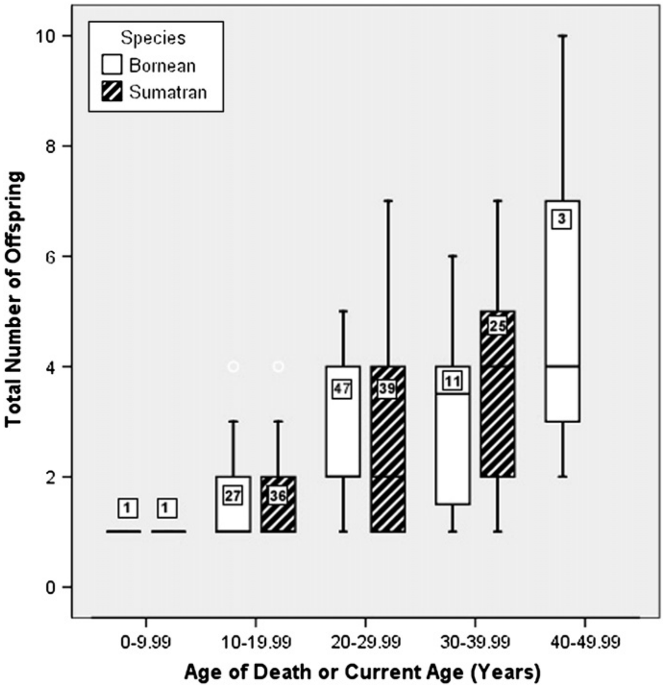

Fig. 2. Total number of offspring born to each captive-born dam, classified by age of death or current age. Boxes indicate the range between first and third quartiles; horizontal line designates the median; vertical spans indicate the range of values; and the boxed number is the number of mothers ($p > 0.28$).

Likewise, the proportion of postnatal deaths was similar between species. Of Bornean infants who survived their first day of life, 90 of 440 (20.5%) died before the age of 4 years. Of their Sumatran counterparts, 22.4% (113 of 504) died before they reached 4 years of age. Again, the distribution of infant deaths between species did not differ from that expected by chance ($\chi^2 = 0.42$, df = 1, $p = 0.52$).

Longevity

Table 2 summarizes data on the mean lifespan by species. The lifespans of captive-born Bornean females tended to be longer than those of Sumatran females, but survival analyses indicated no significant differences ($p \geq 0.13$; Fig. 3a). Perinatal and postnatal mortality did not cause lifespans to differ significantly between Bornean and Sumatran males. However, Bornean males that survived past maturity had significantly longer lifespans than Sumatran males ($\chi^2 = 11.03$, df = 1, $p = 0.001$). The difference in expected mean lifespan at maturity was only 1.3 years, although the models in Fig. 3b indicate that the greater trend was for approximately 10–20% greater survival rates in adult Bornean males. Although many wild-born males were suspected to be older, the eldest Bornean male of known age was 33.7 years, while the eldest Sumatran male of known age was 40.8 years; thus, the possible Bornean male mean lifespan in this model is truncated relative to the Sumatran sample.

Discussion

We examined the demography of captive orangutan populations to determine whether, under similar ecological

Table 2
Comparison of longevity of Bornean and Sumatran orangutans using Kaplan-Meier models

	Bornean orangutans *(P. pygmaeus)*						Sumatran orangutans *(P. abelii)*						Species comparison (Breslow test)		
	n of events	*n* censored	Mean				*n* of events	*n* censored	Mean				Chi-Square	df	*p*
			Estimate (yrs)	Std. error	95% Confidence interval				Estimate (yrs)	Std. error	95% Confidence interval				
					Lower bound	Upper bound					Lower bound	Upper bound			
Captive-born females															
Survived at least 1 day	84	153	28.0	1.39	25.2	30.7	118	151	23.6	1.04	21.5	25.6	1.41	1	0.24
Survived at least 1 yr	58	153	31.4	1.39	28.7	34.1	85	151	26.8	1.02	24.8	28.8	1.64	1	0.20
Survived at least 4 yrs	47	153	33.1	1.37	30.4	35.7	72	151	28.3	0.99	26.4	30.2	2.31	1	0.13
Survived to maturity (16.0 Yrs)	23	153	37.1	1.33	34.5	39.7	33	151	33.0	0.92	31.2	34.8	0.91	1	0.34
Captive-born males															
Survived at least 1 day	104	122	19.3	1.01	17.4	21.3	149	109	18.8	1.03	16.8	20.8	0.36	1	0.55
Survived at least 1 yr	65	122	23.3	1.00	21.4	25.3	103	109	22.8	1.06	20.7	24.9	0.85	1	0.36
Survived at least 4 yrs	49	122	25.4	0.95	23.5	27.2	84	109	24.9	1.06	22.8	27.0	1.04	1	0.31
Survived to maturity (18.6 Yrs)	15	122	30.6	0.74	29.1	32.0	48	109	29.3	1.05	27.3	31.4	11.03	1	0.001

conditions, there was any evidence of systematic divergence in life history strategies between Sumatran and Bornean orangutans. We found no statistical species difference in the age of first or last reproduction in males or females, in perinatal and postnatal mortality rates, or in the completed fertility of mothers. Lifespans of the two species were similar under captive conditions, although captive-born Bornean males lived significantly longer past the age of maturity than Sumatran males. In addition, Bornean mothers had longer IBIs than Sumatran mothers; this difference was small, but significant.

Thus, our data on orangutans of known age suggest no major differences in life history parameters between Bornean and Sumatran individuals under captive conditions. The small differences that do exist are in the direction opposite to that predicted by Wich et al. (2004) and by the preliminary wild data, suggesting that any genetic change may have led to increased, not decreased, reproductive effort with increased habitat quality. The convergence of life history parameters between captive individuals of the two species supports the role of energy availability as a primary determinant of reproductive capability, as suggested by models of reproductive ecology. However, we cannot rule out the alternate hypothesis that each species has evolved a different norm of reaction in response to ecological change. Under this scenario, life history parameters might converge because Sumatran orangutans experience a more intense response to increased energy availability than do Bornean orangutans. However, this is unlikely because wild studies have suggested that Sumatran orangutans show little reproductive responsiveness to minor variation in food availability (Wich et al., 2006).

Curiously, while we found little evidence for species differences, we found that wild-born individuals had faster reproductive rates than captive-born individuals. This difference likely reflects breeding initiative on the part of zoo management. Caregivers have intentionally promoted the reproduction of orangutans born in the wild more than those born in captivity because they provide a greater contribution to the genetic diversity of the captive population (Perkins, pers. comm.).

Our results provide important contrasts to data from orangutans living their entire lives in the wild. The 4.5–6 year IBI that characterized the captive population is shorter than even the lowest estimates from wild populations (7.2 yrs., Gunung Palung, Knott et al., in press; 6.1–6.5 yrs, Kutai/Kinabatangan, Wich et al., in press). While wild interbirth interval figures may be inflated by unobserved births, even the shortest birth intervals recorded are over 5 years (Knott, 2001). Faster reproductive rates have been observed in captive versus wild chimpanzees (Tutin, 1994; Knott, 2001). Bonobo and gorilla IBIs, on the other hand, change little in captivity versus the wild (Tutin, 1994; de Lathouwers and van Elsacker, 2005; Robbins et al., 2006). This may indicate that these species have decreased plasticity in life history variation. However, it has been suggested that reduced feeding competition relative to chimpanzees leads bonobos and gorillas to reproduce near their maximum rate in wild populations (de Lathouwers and van Elsacker, 2005). Alternatively, provisioning in wild bonobo poplations (de Lathouwers and van Elsacker, 2005) and captive breeding problems in gorillas (Sievert et al., 1991) might be expected to reduce the observed IBI difference in these species between captivity and the wild.

Contrary to expectation, our data on the infant and adult mortality of captive orangutans did not indicate improved survivorship over the wild. Thirty percent of captive offspring died at birth or before the age of 4 years. By comparison, infant mortality reported from Ketambe, in Sumatra, was 11% for females and 3% for males (*P. abelii*, Wich et al., 2004). At Gunung Palung, Borneo, no infant deaths have been recorded in over 45,000 hours of observation (Knott, unpublished). However, early data from Suaq Balimbing, in Sumatra, suggest infant mortality commensurate with that of the captive population (Wich et al., 2004). Studies of other captive catarrhines, including chimpanzees and gorillas, have illustrated a general

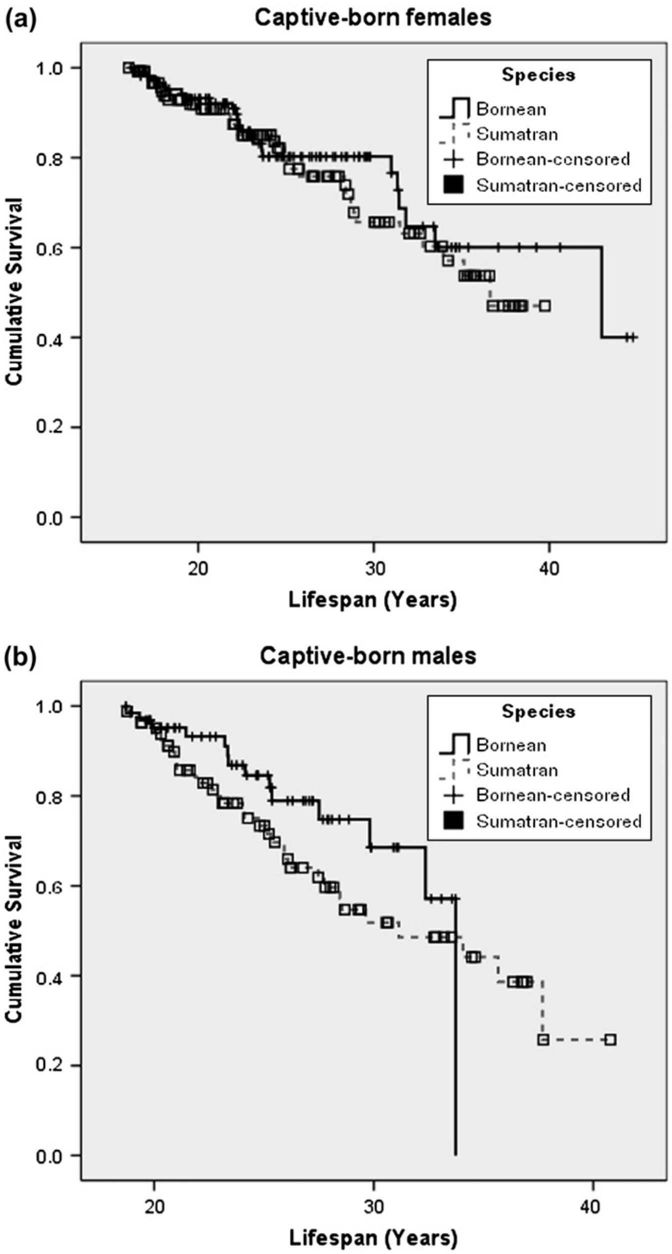

Fig. 3. Survivorship plots of captive orangutans that survived to maturity (16.0 yrs. for females, 18.6 yrs. for males), Kaplan-Meier analysis. (a) captive-born females, species comparison: $\chi^2 = 0.91$, df = 1, $p = 0.34$; (b) captive-born males: $\chi^2 = 11.03$, df = 1, $p = 0.001$). Censored data points reflect the ages of individuals still living at the time of data analysis.

tendency for high early-infant mortality that can often be attributed to maternal incompetence (Davenport, 1979; Seal et al., 1985; Beck and Power, 1988; Courtenay and Santow, 1989; Latinen, 1989; Debyser, 1995).

Can it really be true that despite provisioning and veterinary supervision, captive animals have decreased survivorship? We propose that in this case, it is the wild data that must be approached with caution. Due to the dispersed social organization of orangutans, researchers are likely to miss deaths that occur within the first months of life in individuals who are followed irregularly. The data on longevity of wild orangutans should also be considered tentative, as all ages of older individuals are estimated with large potential error. Age estimation is particularly difficult for males due to sexual bimaturism and delay of development for as long as 20 years after maturity (Kingsley, 1982; Schürmann and van Hooff, 1986; Leigh and Shea, 1995; Maggioncalda et al., 1999; Utami et al., 2002; Knott and Kahlenberg, 2006). Indeed, the age structure of males in the Ketambe demography (Wich et al., 2004) is irregular, with more old individuals than might be suggested by the existing population of younger individuals; this suggests that some ages may be overestimated. Pending the development and strengthening of orangutan field sites across a diversity of habitats, we suggest that more data be collected on the range of ecological and life history variability within each orangutan species before final conclusions about between-species differences can be drawn.

Finally, while these analyses do not support genetically-determined life history differences between orangutan species, they do aid in understanding the unique evolution of human life history. Under conditions of ample food availability and low energy expenditure, orangutan birth intervals (4.5–6 years) are considerably longer than those of even ecologically-stressed human populations (3–3.5 years, Howell, 1979; Hill and Hurtado, 1996). Therefore, it appears that the norms of reaction for reproductive rates are not overlapping in these species. Although these hominoids share characteristics of large body size, late age at maturity, and long lifespan, human evolution has led to a dramatic increase in the ability to devote energy to reproductive effort. As theorists have suggested (Kaplan et al., 2000; Wrangham et al., 2000; Knott, 2001; Aiello and Key, 2002), explanation of this marked shift in life history strategy lies at the heart of understanding the evolution of our species.

Acknowledgements

We thank the members of the zoological community who have cooperated to produce the *International Studbook of the Orangutan*. The SSP and studbook are currently maintained at Zoo Atlanta. We thank Susan Antón, David Pilbeam, and three anonymous reviewers for helpful suggestions on the manuscript.

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