



Factors Affecting Mortality, Fertility, and Well-being in Relation to Species Differences in Captive Orangutans

Leif Cocks

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Abstract For the past 20 years, field biologists have recognized Sumatran and Bornean orangutans as belonging to 2 separate subspecies. Primatologists have recently suggested that they may be full species and that the Bornean species could be divided into 3–5 subspecies. Statistical analyses of factors affecting the mortality, fertility, and well-being of captive orangutans have revealed some important differences between Bornean, Sumatran, and hybrid orangutans that could support the suggestion. Hybrid orangutans appeared to be genetically weaker, with much lower survival rates than pure subspecific individuals. The weakness also may have contributed to their higher rate of infant rejection. In addition, infertility was 3 times higher in Bornean orangutans than in Sumatran and hybrid orangutans.

Keywords hybrid · orangutan · species · zoos.

Introduction

For most of the 20th century, apart from acknowledging the place of origin of wild-born orangutans, zoos did not generally attempt to separate orangutans indigenous to different regions. However, field biologists frequently separated Bornean and Sumatran orangutans into separate subspecies. MacKinnon (1974) first described the physical differences between Sumatran and Bornean orangutans and a method of differentiation using hair samples. Seuanez *et al.* (1979) characterized the genetic differences of Sumatran and Bornean orangutans. As a result of these and other studies, most zoos managed Bornean and Sumatran orangutans as separate populations, but not before a sizeable number of hybrids had been produced. More recently, primatologists have described Bornean and Sumatran orangutans as 2

L. Cocks (✉)
Australian Orangutan Project, PO Box 1414, South Perth, WA 6951, Australia
e-mail: leif@orangutan.org.au

distinct species (*Pongo pygmaeus* and *P. abelii*), with Bornean species divided into 3 subspecies: *P. pygmaeus pygmaeus*, *P. pygmaeus wurmbii*, and *P. pygmaeus morio* (Groves 1999, 2004; Rijksen and Meijaard 1999; Warren *et al.*, 2001). Further, Rijksen (1978) described 2 different types of Sumatran orangutans based on differences in appearance and behavior.

While researching the factors affecting the well-being and survival of captive orangutans for my 1998 thesis, I noticed some unexpected statistical results with respect to Bornean and Sumatran species and specific hybrids. They may provide additional insight into the still debated question of orangutan classification and resultant captive management strategies.

Materials and Methods

My data came from two sources: *The International Orangutan Studbook* (Perkins 1994; Table I) and a survey I developed and sent to 214 institutions that had, or once had, orangutans. The cut-off census date was 1994 (Cocks 2007).

From the data I created a series of variables related to captive orangutan mortality, fertility, and well-being. Prognostic indicators have indicative power and included overall survival, infant survival (0–5 yr), infant rejection, stereotypic behavior, and maternal death and infertility. Captive husbandry variables have a predicted relationship to the prognostic indicator variables and included sex, population, chronology, adult body weight, diet type, social environment, enclosure type, occurrence of sterilization, region, time from last sibling, dam's rearing type, dam's maternal experience, individual's rearing type, age of dam at individual's birth, numbers of dam's previous offspring, average interbirth interval, and individual's age at birth of first offspring.

I used SPSS (6.0) for Windows to analyze the studbook data. Because there were censored (living individuals) and uncensored data (dead individuals), I used life tables for the analysis platform, by analyzing the probability of survival/death over

Table I Studbook and survey data used in this analysis

Studbook data	Survey data
International studbook	Adult weight
Number	
Facility name	Diet type
Location	Social grouping
Sire	Enclosure type
Dam	Occurrence of infertility
Date of birth	Dam's rearing type (human or mother)
Date of death (if applicable)	Dam's maternal experience
Sex	Individual's rearing type (human or mother)
Subspecies	Individual's maternal
	Experience
Wild or captive born	Occurrence of infant rejection
	Occurrence of stereotypic
	Behavior
	Occurrence of sterilization

Table II Percentage distribution of populations

Population	Number	Percentage
Bornean	736	37.3
Sumatran	652	33.0
Hybrid	290	14.7
Unknown ^a	297	15.0

^aThe specimens often died before I identified them and did not have offspring through which I could identify them before karyotyping was available. As the orangutans of unknown subspecies mostly died in infancy, very little data are available on the specimens, and I omitted them from my analyses.

fixed intervals of time. I used the Wilcoxon (Gehan) test statistic for survival variables and treated categorical data in 2 ways: I tested prognostic variables that I could not rank for association via Pearson chi-square and likelihood ratio analysis (Freeman 1987) and tested prognostic variables that I could rank for correlation via the Kendall and Spearman correlation coefficients (Freeman 1987). The significance level is .05 for all tests.

Results

The sample of wild Bornean orangutans is estimated to be almost 10 times larger than the Sumatran sample (Singleton *et al.* 2004). In captivity, the Sumatran sample in 1943–1994 was 88% the size of the Bornean sample. In addition, there are hybrid orangutans (Table II).

I found a survival difference when comparing the 3 orangutan populations via the Wilcoxon (Gehan) test statistic ($p=.0007$, $df=2$; Fig. 1). There is no statistical difference in the survival of the Bornean ($n=729$) and Sumatran ($n=606$) subspecies ($p=.7385$, $df=1$), but hybrids ($n=289$) have a lower survival rate than either Bornean ($p=.0002$, $df=1$) or Sumatran orangutans ($p=.0017$, $df=1$).

I found similar results in infant survival rates (Fig. 2). There is a significant difference in overall infant survival for the 3 populations ($p=.0079$, $df=2$). The survival of Bornean ($n=196$) and Sumatran ($n=181$) infant orangutans did not differ

Fig. 1 Effect of population on survival.

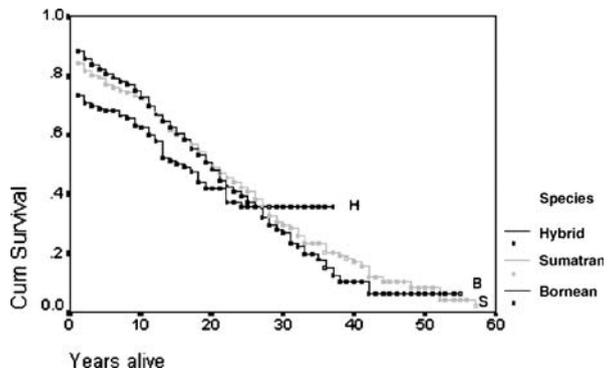
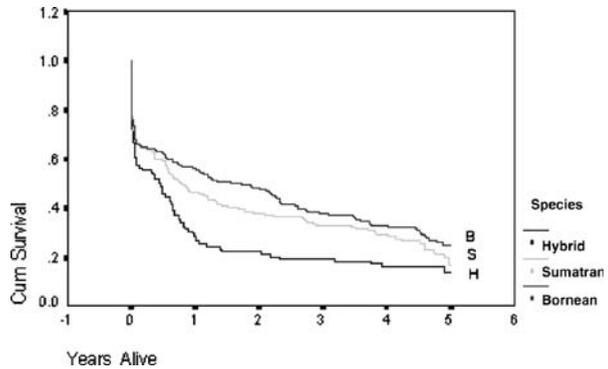


Fig. 2 Infant survival in 3 sample populations.



($p=.3633$, $df=1$), but infant survival in hybrids ($n=108$) is significantly lower than in Bornean ($p=.0024$, $df=1$) and Sumatran ($p=.0199$, $df=1$) species.

At 13%, the incidence of infertility was 3 times greater in the Bornean species than in the Sumatran species (4%; $p=.02209$, $df=1$) or hybrid population (4%; $p=.02318$, $df=1$; Fig. 3).

The Bornean species had an occurrence of 25% of maternal deaths compared to 23% for Sumatran and 15% for hybrid populations (Fig. 4). Hybrids appear to have a lower rate of maternal death, but the differences between hybrid and Bornean and hybrid and Sumatran samples are not statistically significant (Pearson chi square $p=.32239$, $df=2$; likelihood ratio analysis $p=.30069$, $df=1$).

At 80%, hybrid female orangutans have a higher percentage of infant rejection than those of either Bornean (29%; $p=.01018$, $df=1$) or Sumatran (36%; $p=.01077$, $df=1$) female orangutans (Fig. 5). Bornean and Sumatran female orangutans did not differ in their infant rejection rates ($p=.4620$, $df=1$).

The occurrence of stereotyped behaviors was nearly evenly distributed across the 3 orangutan populations (13.9% in Bornean, 8.6% in Sumatran, and 10.7% in hybrids; Fig. 6). Pairwise comparisons of each population are not statistically significant (Pearson chi square $p=.58762$, $df=3$; likelihood ratio analysis $p=.35126$, $df=3$).

Fig. 3 Effect of population on infertility.

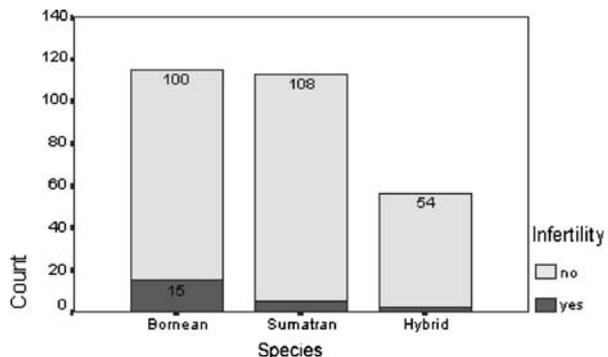
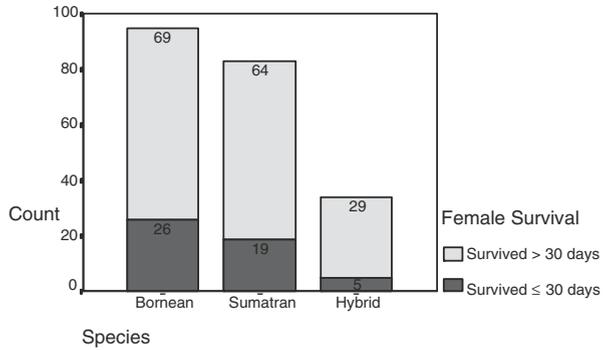


Fig. 4 Effect of population on maternal death.



Discussion

There are 2 orangutan species: Bornean and Sumatran. In the wild, the species appear to have different behaviors. Rijksen (1978) and Singleton (2000) have attributed the Sumatran orangutan’s heightened sociability to the more clumped distribution and greater productivity of their food resources in the Sumatran rain forest. I hypothesized that behavioral, genetic, and other differences of the 2 species might influence the health and longevity of captive individuals. Further, subspecific hybrids were frequently produced in captivity, and I posited that the hybridization might have an effect on the longevity and health of hybrids.

Between 1946 and 1994, 32% of captive orangutans, of known species, were Bornean and 33% were Sumatran. In the wild, the numbers of Bornean orangutans are estimated to be *ca.* 3 times greater than that of Sumatran orangutans (Wilkins 1995). It appears from the captive numbers that zoo personnel prefer to keep the more endangered species or that more specimens have been imported from Sumatra.

Hybrid orangutans, all of which are captive bred, represent 15% of the captive population. Most zoo staff now prevent the individuals from reproducing, so they

Fig. 5 Effect of population on infant rejection.

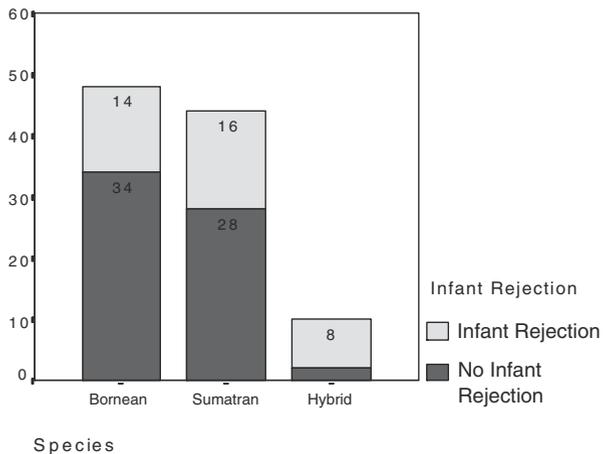
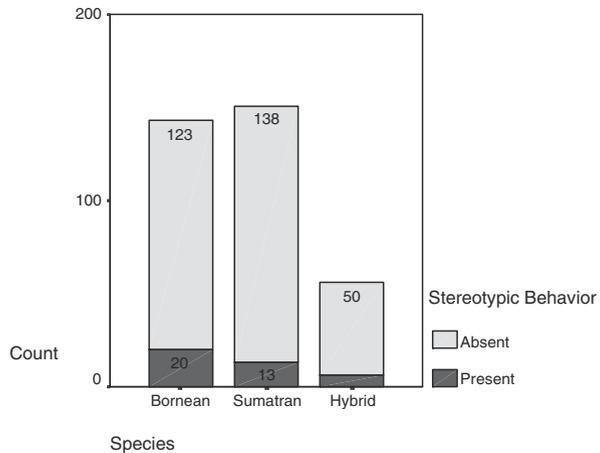


Fig. 6 Effect of population on stereotypic behavior.



have no direct role in specific conservation. From this perspective, they occupy captive positions that could arguably be better filled by individuals of pure species.

There was little difference in survival between the 2 species, but hybrids had a significantly lower survival rate than either species. There was no evidence of a difference in infant mortality between the 2 species. However, hybrid infants have a significantly higher infant mortality than either of the 2 subspecies.

The reason for the results could be either that zoo personnel selectively neglect hybrid individuals or that hybrids are inherently weaker than the 2 species are. As early as 1982, de Boer and Seuanez warned of the possible negative consequences of orangutan hybridization.

To determine which argument is a better explanation for my results, I repeated analyses for specific survival using orangutan data only from the North American region, where zoos operate under the authority of the Orangutan Species Survival Plan (SSP). By SSP mandate, hybrid orangutans have never been kept off-exhibit or, with the exception of prohibitions on breeding, otherwise managed differently compared to Bornean or Sumatran orangutans (Perkins 1995). Most likely due to pressure from animal rights groups, North American zoo personnel have paid special attention to providing equal treatment of hybrid and pure orangutans.

There was no difference in the survival of Bornean or Sumatran orangutans in North America, but the survival of hybrid orangutans was significantly below that of the 2 species (Cocks 1999). I suspected that there might be a relationship between the reduced survival of hybrids and the geographic location of the zoo because zoos in developing regions have been less strict about preventing hybridization of Bornean and Sumatran orangutans. Zoos in developed regions have also sometimes sent unwanted hybrids to zoos in developing regions. Only 34% of hybrid orangutans lived in zoos in developing countries (Table III). Hybrids in both developed and developing regions showed reduced survival, so there is scant indication of a link between the zoo's geographic location and hybrid survival rates (Cocks 1999). Thus, the data suggest that the lower survival rate of hybrid orangutans is due to reduced fitness associated with hybridization.

Table III Distribution of orangutans in zoos in developed and developing regions of the world

	Percentage developed region	Percentage developing region
Bornean	59 (<i>n</i> =434)	41 (<i>n</i> =302)
Sumatran	76 (<i>n</i> =480)	24 (<i>n</i> =152)
Hybrid	66 (<i>n</i> =191)	34 (<i>n</i> =99)

The taxonomy of orangutans has profound implications for conservation plans and for captive management. Genetic (Chemnick and Ryder 1994), dermatoglyphic (Boedtani and Smits 1994), and other (Groves 1999) evidence supports recognition of 2 distinct species-Bornean and Sumatran-but other taxonomic viewpoints exist. Andrew (1999), e.g., advocates a monotypic orangutan species. Muir's (1998) DNA analyses reveal as much difference between the various Bornean populations as exists between Bornean and Sumatran orangutans. Muir maintains that there were 10 occasions over the past million years or so when land bridges connected Sumatra and Borneo, allowing the transfer of genetic material between some populations and preventing the simple division of orangutans into 2 species based on island of origin.

If Muir's (1998) view is correct, then primatologist should manage at least some of the Bornean orangutans as genetically separate populations to avoid the negative effects of hybridization. It is interesting to note that the only significant difference I observed is the higher infertility of Bornean orangutans when compared to both Sumatran and hybrid individuals. Infertile offspring is common result of crossbreeding incompatible populations. Infertile Bornean orangutans could also possibly result from the captive breeding of distinct populations of Bornean orangutans, which would support Groves' (2004) recommendation that the Sumatran and Bornean orangutans should be separate species, with the Bornean species containing 3 subspecies.

In addition to having reduced survival rates, hybrids have a significantly higher frequency of infant rejection (80%) than Bornean (29%) and Sumatran (36%) orangutans do. As suggested by their shorter life spans, hybrids may have a host of mental and physical ailments that negatively impact on females' abilities to raise their infants. The high occurrence of maternal rejection could also be due to caretakers giving hybrids insufficient attention to ensure reproductive success.

Many pure orangutans were wild born (32%), but all hybrid orangutans are captive born. Arguably, because hybrid individuals are the product of the captive environment, they might, as a group, display more of the problems caused by captivity, including an inability to raise infants. However, I found no significant change in infant rejection over time, and most wild-born individuals enter captivity as partially hand-reared infants. As adults, hand-reared individuals are more likely to reject their offspring than mother-reared individuals are, which suggests that higher infant rejection is a result of hybridization. Significant difference occurs in stereotypic behavior for the 3 samples, suggesting that higher hybrid infant rejection is more closely associated with physical rather than mental weakness, though reduced viability apparently does not increase the occurrence of maternal death in hybrids.

Bornean orangutans are more solitary than Sumatran orangutans (MacKinnon 1974). Hence in captivity, Bornean orangutans may suffer from higher levels of social stress more easily than their Sumatran and hybrid counterparts. Severe social stress produces infertility in primates (Wildt 1996). Though I found a higher

occurrence of infertility in Bornean orangutans, I found no difference in the incidence of stereotyped behaviors for the 3 populations, supporting my argument that higher infertility in Bornean orangutans may be a consequence of captive breeding between distinct populations.

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