Examining the Terminal Investment Hypothesis in Humans and Chimpanzees: Associations Among Maternal Age, Parity, and Birth Weight

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KEY WORDS   maternal investment; life history; *Homo sapiens*; *Pan troglodytes*

ABSTRACT   The terminal investment hypothesis (Williams [1966] Adaptation and Natural Selection; Princeton, NJ: Princeton University Press) holds that reproductive effort should increase over time in iteroparous species in which reproductive value declines with age. Attempts to model this hypothesis and test it in various species have produced mixed results. Clutton-Brock ([1984] Am. Nat. *123*:212–229) argued that simply testing for changes in propagule size with age fails to recognize that the costs of producing offspring of a given size may increase over the lifespan, hence absence of a positive correlation does not defeat the hypothesis. However, this interpretation is weakened by evidence of sequential increases in propagule size independent of age, as such changes reveal a capacity to increase absolute investment over time. Humans and chimpanzees meet the preconditions of the terminal investment hypothesis. Surveying the obstetrics literature, we show that the majority of published studies indicate that parity has a positive effect on birth weight, but age has no effect. Analyzing 436 captive chimpanzee births, we document a positive influence of parity and a negative influence of age. We therefore conclude that, though it is yet to be replaced by a more compelling alternative, the terminal investment hypothesis is not supported in these two species, as absence of a positive effect of age on birth weight cannot be interpreted in a manner congruent with the hypothesis. Am J Phys Anthropol 127:95–104, 2005.   © 2004 Wiley-Liss, Inc.

In a seminal book, Williams (1966), building on Fisher (1930), argued that, in iteroparous species in which reproductive value declines with age, reproductive effort should increase with age. This position, now sometimes called the terminal investment hypothesis, is premised on the assumption that reproduction is costly, and that allocation of resources occurs within a zero-sum framework. Put simply, the hypothesis holds that organisms should husband resources as a function of the remaining potential for reproduction. When remaining reproductive potential is high, organisms should invest conservatively in current reproduction so as to ensure that, in the future, available resources will suffice to exploit additional opportunities for reproduction. Conversely, when remaining reproductive potential is low, organisms should invest generously in current reproduction, as there are few or no future reproductive opportunities for which resources should be saved. A number of mathematical models have been formulated to explore Williams' proposal and while most support the idea, several counterexamples were also identified (reviewed in Caro et al., 1995; Roff, 2002).

In females, reproduction involves a direct investment in the tissue of offspring and supporting structures, creating an index of female reproductive ef-

fort, namely the size (and/or number) of the offspring produced. Many authors have therefore examined propagule size (and/or clutch size) in attempting to test or employ the terminal investment hypothesis (reviewed in Caro et al., 1995; Roff, 2002; see also Ericsson et al., 2001; Langley and Clutton-Brock, 1998; Weladji et al., 2002). However, Clutton-Brock (1984) has compellingly argued that propagule size alone may fail to capture the factor that lies at the heart of the proposal of Williams (1966), namely the relative costliness of the current level of investment. Clutton-Brock's important insight is that the costliness of a given increment of investment, and hence its impact on future reproduction, is not constant over the reproductive career. As a consequence, if one were to find that propagule size remained constant over maturation, while seeming

to contradict the predicted positive effects of age, this could in fact confirm them, as relative investment would actually be increasing, even though the outward result appears similar over time.

While relative costliness is the crux of the terminal investment hypothesis, it is extremely difficult to measure: Clutton-Brock (1984) pointed out, for example, that simply measuring propagule size while controlling for maternal body weight will not suffice, because larger animals may require less energy per unit body weight than smaller animals, or may be able to collect food more efficiently. One alternative, we suggest, is to compare age-related changes in propagule size with another sequential potential determinant of investment, parity. If parity exercises a positive influence over propagule size but maternal age does not, then it is difficult to argue that the occurrence of the same propagule size at two different ages should be interpreted as evidence of increased investment at the later age due to increased relative cost, as the organism is capable of sequentially increasing propagule size at a variety of ages, yet does not do so in response to changes in age alone.

Although the terminal investment hypothesis has been explored in females of a number of species, to date investigators have not applied this idea in research on humans and nonhuman primates. This is somewhat surprising given that other life-history perspectives have been extensively employed in investigations of humans and related species (Alvarez, 2000; DeRousseau, 1990; Hawkes, 2003; Hill and Hurtado, 1996; Kaplan et al., 2000; Kappeler and Pereira, 2003; Korpelainen, 2000; Mace, 2000; Nishida, 1990; Peccei, 2001; Pennington and Harpending, 1988; Strassmann and Gillespie, 2002; Van Schaik and Kappeler, 1997). In this paper, we follow the strategy outlined above in examining the terminal investment hypothesis, using 1) published findings on maternal determinants of birth weight in diverse human populations, and 2) original data on maternal determinants of birth weight in captive common chimpanzees, *Pan troglodytes*.

DECLINES IN REPRODUCTIVE VALUE WITH ADVANCING AGE

Humans clearly meet the preconditions for the terminal investment hypothesis, as female fertility peaks in the mid-20s, and markedly declines by the late 30s (Dunson et al., 2002). Menopause creates a punctuated end to reproduction well in advance of the expected end of life under ancestral conditions (Blurton Jones et al., 2002; Hawkes et al., 1998; Hill and Hurtado, 1996; Kaplan et al., 2000). Likewise, in chimpanzees, fertility declines substantially after age 35 in both captive (Caro et al., 1995; Graham, 1979) and wild (Nishida et al., 2003) animals, despite a maximum lifespan of approximately 47 in wild populations and over 50 in captive populations (Hill et al., 2001; see also K. Gould, as cited in Bellino and Wise, 2003; Nishida et al., 2003). Field observations indicate that chimpanzees exhibit general signs of senescence beginning in their early 30s (Goodall, 1986; Hill et al., 2001; Huffman, 1990, p. 104), and endocrinological measures reveal reduced reproductive functioning in aged captive females (Gould et al., 1981). Although some births continue after age 40 in wild females, survivorship is very low (Sugiyama, 1994), suggesting that aging is accompanied by progressively declining reproductive abilities. Finally, as many as a quarter of wild females live 5 years or more following the birth of their last offspring, implying the existence of a menopause-like cessation of reproduction before the end of life (Nishida et al., 2003).

BIRTH WEIGHT, FITNESS, AND REPRODUCTIVE POTENTIAL

The use of birth weight as an index of female reproductive effort rests on two assumptions, namely, 1) there is a positive relationship between birth weight and offspring fitness (i.e., investing in increased birth weight pays fitness dividends), and 2) there is a negative relationship between birth weight and residual maternal resources (i.e., investing in increased birth weight entails costs to future reproduction; see Blurton Jones, 1978). In humans, birth weight clearly influences offspring fitness, as it is a significant determinant of infant morbidity and mortality (McIntire et al., 1999), motor and social development (Hediger et al., 2002), cognitive development (Matte et al., 2001; Richards et al., 2002; Sorensen et al., 1997), adult stature (Seidman et al., 1993; Sorensen et al., 1999; Leger et al., 1998), and in males, marriage as an adult (Phillips et al., 2001; Vagero and Modin, 2002).[1] Likewise, a variety of evidence supports the contention that, under ancestral conditions, increases in birth weight would have detracted from remaining human maternal reproductive potential. Normal pregnancy involves a substantial reduction in spinal bone mass density, as maternal bone is resorbed in order to provide calcium to the fetus (Black et al., 2000). Similarly, normal pregnancy frequently results in substantial hypoferremia (Hollán and Johansen, 1993), presumably a consequence of fetal demands for iron (Bentley, 1985). Given that the rate of consumption of both minerals is a function of tissue mass, it is likely that birth weight is positively correlated with the demands that pregnancy places on these maternal reserves. The more extensive any resulting maternal depletion, the greater the impact on future re-

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[1]In a highly altricial species such as our own, total postnatal investment normally exceeds total prenatal investment, suggesting that the age effects predicted by the terminal investment hypothesis ought to be most marked in regard to postnatal investment. Nevertheless, given the substantial impact of birth weight on highly fitness-relevant attributes, and given the wide range of variation in birth weights across individuals, prenatal investment constitutes a legitimate focus for tests of the terminal investment hypothesis despite human altriciality.

production is likely to be, an effect mediated via 1) the reduction of available resources, 2) the length of delay necessary to replenish them, or 3) an increased risk of morbidity and mortality as a consequence of depletion. Evidence indicative of maternal caloric depletion due to pregnancy is somewhat less clear, as investigators often do not measure the costs of gestation and lactation independently of one another. However, for present purposes, this conflation is not problematic, as larger infants presumably consume more milk, and thus inflict greater lactational costs on the mother. Reproductive depletion of maternal fat reserves or overall body mass has been demonstrated in some, but not all, studies of women in traditional societies (reviewed in Tracer, 2002; see also Khan et al., 1998). Finally, viewed with regard to the grossest phenomena, a number of studies of preindustrial populations reveal an inverse relationship between reproduction and longevity (Helle et al., 2002; Korpelainen, 2000; Lycett et al., 2000; Westendorp and Kirkwood, 1998).[2]

Chimpanzee females exhibit patterns of bone loss explicable in terms of the demands of pregnancy (Sumner et al., 1989). Although published findings do not yet allow for definitive statements on maternal depletion in chimpanzees, it is eminently plausible that the situation resembles that in humans, given the many similarities in gestational dynamics between the two species, importantly including the mean ratio of birth weight to maternal weight (approximately 6% in both species; Dufour and Sauther, 2002). Likewise, while the available literature does not address the relationship between birth weight and offspring fitness in chimpanzees, this too is a highly plausible assumption, made more so by direct parallels between the human literature and results in other nonhuman primate species (e.g., Gunderson et al., 1989). With high confidence that humans display the features that constitute preconditions for testing the terminal investment hypothesis, and reasonable confidence that the same is true of chimpanzees, we therefore turn to an examination of the relationship between age, parity, and birth weight in these two species.

EXAMINING THE TERMINAL INVESTMENT HYPOTHESIS IN *HOMO SAPIENS*

Consistent with its significant public health implications, a large corpus of research examines the determinants of birth weight in humans. Searching the PubMed and Biosis databases, and using a snowball citation strategy, we identified publications containing information on the effects of maternal age and parity on birth weight. Because age and parity are necessarily correlated, in order to ensure that the influence of each was being measured inde-

pendently, we only included studies in which the effects of age and parity were assessed separately. Because the methods of analysis employed differed substantially across studies, systematic meta-analysis of these studies is problematic. Instead, results are presented for inspection in Table 1.

In addition to the studies summarized in Table 1, a number of other investigations contain results that, though relevant, are not easily tabulated. McKeown and Gibson (1951; n = 19,414; England) found that parity positively affects birth weight through the third birth but not thereafter, while age has no effect on birth weight. Sheferaw (1990; n = 1,707; Ethiopia) reported that parity is positively correlated with birth weight through parity 5 and beyond, but age is not systematically correlated with birth weight. Camilleri and Cremona (1970; n = 2,607; Malta) reported a positive effect of parity through the tenth birth, but no clear effect of age. Namboodiri and Balakrishnan (1959; n = 12,640; India) reported that parity is positively correlated with birth weight, although the effect diminishes at high parities; in contrast, there is a trend toward a negative effect of age. Rehan and Tafida (1979; n = 1,460; Hausa, Nigeria) found a high positive correlation between parity and birth weight, but none between age and birth weight. Bardham (1966; n = 1,011; Bengal, India) reported a substantial positive effect of parity (particularly in male infants), but a slight negative effect of age. Millis and Seng (1954; n = 18,425; Singapore Chinese) reported a notable positive effect of parity (again greater in males), with diminishing effects beyond parity 7, but they found no overarching age effects. Loeb (1965, p. 34–36; n = 837,786; USA) presented results suggesting that parity is positively correlated through the second birth for all age groups, and through the fifth and higher for all age groups except those who began childbearing before age 19; in contrast, except for women of parity 5 and over, age makes a positive contribution to birth weight only in the mid-20s and thereafter has either no effect or a slightly negative one. Selvin and Janerich (1971; n = 1,524,229; USA) similarly presented data indicating that parity has a positive effect except in women who begin reproduction very early; age has multiple effects, namely, 1) the maximum birth weight for each parity class occurs at increasing ages for each successive parity (a pattern suggesting that there is an optimal age at which to begin reproduction), and 2) within each parity below parity 6, age has a convex effect (e.g., an initial positive effect followed by a negative effect, with the peak as early as age 20–24). MacLeod and Kiely (1988; n = 36,056; USA) found initial positive effects for both parity and age, with negative effects after parity 3 and after age 35. Dhall and Bagga (1995; n = 3,293; North India) reported a significant positive effect of parity for the second birth, but none thereafter, and a significant positive effect for age, but only below 20 years. Finally, Muslimatun et al. (2002; n = 296; Indonesia) reported

TABLE 1. Summary of results from 19 studies in which effects of parity and maternal age on birth weight were examined independently

Citation	Population	N (births)		P	β coefficient	B coefficient	Partial r	Mean square ratio
Rogers et al., 1987	Hong Kong	8,802	Parity	<0.001		42.5		
			Age	<0.001		6.8		
Feleke and Enquoselassie, 1999	Ethiopia	4,047	Parity	<0.0001		28.81		
			Age	<0.05		8.11		
Madebo, 1994	Ethiopia	1,260	Parity	n.s.				
			Age	<0.001		20.21		
Clegg and Clegg, 1989	Fiji	56 (Indian)	Parity	n.s.				
			Age	<0.005		20.6		
Yudkin et al., 1983	Israel	14,219	Parity	n.s.				
			Age	<0.001		6.0		
Shami and Khan, 1980	Pakistan	524 (males)	Parity	<0.001			0.4841	
			Age	<0.01			−0.3018	
Karn and Penrose, 1952	UK	6,419 (females)	Parity	<0.05			0.173	
			Age	<0.05			−0.035	
Karn and Penrose, 1952	UK	6,697 (males)	Parity	<0.05			0.166	
			Age	<0.05			−0.043	
Fabia, 1973	Canada	7,712	Parity	<0.001	45.55			
			Age	n.s.				
Eriksson et al., 1997	Sweden	524 (males)	Parity	<0.0001		263.41		
			Age	n.s.				
Andersson et al., 2000	Sweden	851 (females)	Parity	0.0001		46.2		
			Age	n.s.				
Kulmala et al., 2001	Malawi	581	Parity	0.003		190		
			Age	n.s.				
Clegg and Clegg, 1989	Fiji	90 (Melanesian)	Parity	<0.05		3.65		
			Age	n.s.				
Malik et al., 1997	India	1,000	Parity	<0.001		69		
			Age	n.s.				
Peters et al., 1983	UK	16,989	Parity	<0.001				66.2
			Age	n.s.				
Peters et al., 1983	UK	16,792	Parity	<0.001				71.3
			Age	n.s.				
Nyaruhucha and Msimbe, 1993	Tanzania	331	Parity	n.s.				
			Age	n.s.				
Shami and Khan, 1980	Pakistan	470 (females)	Parity	n.s.				
			Age	n.s.				
Petridou et al., 1996	Greece	2,538	Parity	n.s.[1]				
			Age	n.s.				

[1] Not significant after parity 2.

that parity positively influences birth weight, significantly so between the first and second births, but age has no effect.

Discussion

The terminal investment hypothesis predicts that reproductive effort should increase with age. Of the 19 investigations summarized in Table 1, only 5 reveal a positive effect of age, and one of these 5 (Clegg and Clegg, 1989) employs a questionably small sample. Three studies report a negative effect of age, and the remaining 11 find no significant age effects. Likewise, of the 12 studies summarized above, only 1 (MacLeod and Kiely, 1988) reports clear evidence of a positive influence of age on birth weight once maturity is reached and, in seeming violation of the premise of the terminal investment hypothesis, this effect is reversed after age 35, some 15 years before menopause (Greendale et al., 1999). Several studies report negative effects of age.

Because relative reproductive effort might increase with age even if absolute investment remains unchanged or declines, in order to assess the capacity to increase absolute investment over successive births, we also explored the effect of parity on birth weight. In contrast to the negligible or negative effects of age, 13 of 19 studies summarized in Table 1 reveal a positive correlation between parity and birth weight, and none report a negative effect of parity. Likewise, of the 12 additional studies described above, 7 present evidence of a clear positive impact of parity, 2 present evidence indicating that such an effect occurs in the first few births but not thereafter, and 1 indicates that parity has a positive effect at low values, and a negative effect at high values.[3]

Our survey included investigations of the determinants of birth weight in genetically, culturally, and economically disparate human populations, and hence the overarching patterns that emerged are

[3] In addition to the studies discussed above, Juntunen et al. (1997) presented evidence suggesting that parity has a consistently positive effect on birth weight throughout the reproductive career in women who bear a very high number of offspring, and Seidman et al. (1988) presented additional evidence of parity's impact on birth weight.

unlikely to be the consequence of parochial factors. To summarize the results of our survey, while most studies report that age has little or no effect, and some report a negative effect, the opposite is generally true with regard to parity. These patterns suggest that, in humans, it is not reasonable to interpret the absence of an increase in birth weight with advancing age within the framework of increases in the relative costliness of investment postulated by Clutton-Brock (1984), as the sequential elevation of offspring size with successive births is indicative of a capacity to increase absolute investment over time.

Skeptics might argue that parity effects could themselves reflect the pattern predicted by the terminal investment hypothesis: if parity and age were highly correlated in ancestral populations, natural selection could conceivably have exploited parity-related physiological changes as indices of age, and hence an evolved mechanism might attend to such changes in adjusting investment in light of remaining age-related reproductive potential. However, studies of contemporary forager women reveal substantial interindividual and intergroup variation in lifetime fertility (Blurton Jones et al., 1992; Hill and Hurtado, 1996; Kirchengast and Winkler, 1996; Pennington and Harpending, 1988). Given that there is every reason to suppose that equivalent levels of variation in lifetime fertility were present in ancestral populations, parity would have constituted such a crude proxy for age that the allocation of reproductive investment on the basis of parity would not have effectively met the adaptive challenge described in the terminal investment hypothesis. To illustrate this, consider woman A, who reached menarche early and/or had short interbirth intervals, and woman B, who reached menarche late and/or had long interbirth intervals. At a given age, woman A has a substantially higher parity than woman B. If parity were used as a proxy for age in allocating subsequent investment, from the perspective of the terminal investment hypothesis, either woman A would invest too much in the next offspring produced (prematurely exhausting her residual reproductive potential prior to menopause), woman B would invest too little (resulting in unexploited reproductive potential remaining at menopause), or both. Hence, while the optimality of adaptations is often constrained by a wide variety of factors, interindividual variation in the number of offspring borne by a given age has likely always been sufficiently high as to undermine to the point of failure any mechanism that used parity as a measure of the number of years remaining in a female's reproductive career. The human pattern wherein parity generally exercises a positive influence on birth weight while age does not is therefore not consistent with the predictions entailed by the terminal investment hypothesis.

EXAMINING THE TERMINAL INVESTMENT HYPOTHESIS IN *PAN TROGLODYTES*
Subjects and data description

In order to further explore the terminal investment hypothesis, we compiled birth records from the Yerkes National Primate Research Center (Atlanta, GA) and Alamogordo Primate Facility (Alamogordo, NM). This yielded an initial data set of 692 births by 175 females. Records included information on exact maternal age, parity, birth weight, sex of offspring, status of offspring at birth (living/dead), mode of delivery (stillbirth/miscarriage, vaginal delivery, or surgical delivery), presence of twins or triplets, and whether a delivery was premature. Our goal was to evaluate the effects of parity and maternal age on birth weight in normal, healthy infants. We therefore restricted consideration to full-term, live infants delivered vaginally. Examination revealed two births (each to a different female) recorded at implausibly late ages (60 and 67, respectively); suspecting that these records, dating to the 1920s, were erroneous, we discarded them.[4] Lastly, because twinning reduces birth weight, as was done in the human studies surveyed, we restricted our consideration to singletons.[5] This resulted in a data set of 436 offspring (44% male and 56% female) borne by 126 females ranging in age from 7.5–37.2 years (mean 17.1, SD = 5.6) at time of birth. Parity ranged from 1–15 offspring (mean = 4.5, SD = 3.3), and birth weight ranged from 0.67–3.3 kg (mean = 1.8, SD = 0.31).

Data analysis

In exploring the determinants of birth weight, we conducted a two-step, hierarchical regression. In the first step, we simultaneously examined the main effects of maternal age, parity, and sex of offspring on birth weight. We examined their interactions in the second step. Following the recommendations of Aiken and West (1991), continuous variables (maternal age, parity) were zero-centered, and the dichotomous variable (sex of offspring) was dummy-coded (1 and -1) before analysis. Nonsignificant interaction terms were removed from the model.

The first step of the regression revealed a significant main effect for parity, B = 0.02, $F(1, 433) = 4.66$, $P = 0.03$, $\beta = 0.17$. No effects were found for maternal age or for sex of offspring.[6]

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[4]So as to avoid biasing the analysis against the terminal investment hypothesis, we also conducted all analyses with the two suspect births included; inspection revealed that their exclusion did not change the results.

[5]A separate test revealed no relationship between maternal age and twinning, indicating that twinning is not an alternative strategy to the modulation of birth weight.

[6]It is interesting that neither we nor Gavan (1952) found chimpanzee birth weight to be sexually dimorphic, whereas this pattern is common in much of the human data, and also occurs in rhesus ma-

The second step of the regression revealed no significant main effect for sex, nor were interaction effects found between sex and the other predictors. As in the first step of the model, no main effect was found for maternal age, but a significant interaction was found between maternal age and parity, B = −0.002, F(1, 432) = 3.97, P = 0.05, β = −0.09. Controlling for these effects, the main effect of parity remained significant, B = 0.05, F(1, 432) = 9.24, P = 0.003, β = 0.24.

Because gestation length was shown to be importantly related to birth weight in the human literature (Andersson et al., 2000; Dhall and Bagga, 1995; Eriksson et al., 1997; Feleke and Enquoselassie, 1999; Karn and Penrose, 1952; McKeown and Gibson, 1951; Nyaruhucha and Msimbe, 1993; Petridou et al., 1996; Rogers et al., 1987; Yudkin et al., 1983), we explored its mediating effects by adding it to the model described above, using observations for which gestation length was recorded (N = 303). The analysis revealed a significant positive relationship between gestation length and birth weight when the effects of the other variables were statistically controlled, B = 0.01, F(1, 298) = 51.76, P < 0.0001, β = 0.35.[7] However, the other predictors were not significantly changed by the addition of gestation length to the model.

Early in a female chimpanzee's reproductive career, a tradeoff exists between growth and reproduction, and so advancing age should initially be positively correlated with birth weight, followed by a decrease in the correlation as maturation slows and ends.[8] Conversely, late in a female's reproductive career, senescence may progressively limit the maximal investment in reproduction possible, leading to a negative correlation between advancing age and birth weight (cf. Broussard et al., 2003; Weladji et al., 2002). In light of these possibilities, so as to ensure that the absence of a correlation between age and birth weight which we found was not due to a concave function, we graphically analyzed the data for such a trend, but did not observe such effects.

Life-history theory suggests that females may differ with regard to the timing of reproduction and, consequently, the allocation of investment therein. Specifically, if individuals who initially allocate greater resources to growth and maturation delay the onset of reproduction, and if, as the above results suggest, parity exercises an influence on birth

weight, then the presence of late maturers in the sample could skew the pooled results against the pattern predicted by the terminal investment hypothesis. To address this possible confound, we constructed a fixed-effects regression model in which the intercepts of each subject are allowed to vary, but the slopes are predicted to be patterned in a specified direction. This is conceptually equivalent to running separate within-subjects regression analyses, and then testing whether the aggregate pattern of slopes is different from a slope of zero. The coefficient in this model describes the within-unit relationship between the predictors and the dependent variable (Hox, 1995).

Subjects with only one offspring were dropped from the analysis, as within-subject assessments of the relationships among the variables of interest are not possible with fewer than two data points. This left us with data on 397 births for 89 subjects with a mean maternal age at parturition of 15.8 years (SD = 4.4).

The variables of maternal age, parity, and their interaction term were entered simultaneously into the model. The results of the fixed-effects regression revealed a marginal within-subjects effect for parity in the expected direction, β = 0.44, F(1, 305) = 2.71, P = 0.10; however, no significant effects for either maternal age or the age/parity interaction were found.[9] Hence, although this mode of analysis somewhat reduces the significance of the effect of parity on birth weight, the fact that it does not at the same time enhance the effect of age indicates that the patterns observed in the sample as a whole are not attributable to between-female differences in life-history trajectories.

Discussion

In our sample of 436 births by 126 captive female common chimpanzees, maternal age exercises no effect on birth weight. In contrast, parity is positively correlated with birth weight, and interacts antagonistically, rather than synergistically, with the effects of age: increasing age reduces the positive influence of parity on birth weight, suggesting that age effects in chimpanzees should be interpreted primarily in terms of the constraining role of senes-

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caques (Broadhurst and Jinks, 1965; Silk et al., 1993; Valerio, 1969) and savanna baboons (McMahan et al., 1976), but not in tufted capuchins (Fragaszy and Adams-Curtis, 1998).

[7]Although Silk et al. (1993) reported a negative correlation between maternal age and gestation length in rhesus macaques, we found no such pattern in our chimpanzee data.

[8]Data supplied by Nishida et al. (2003) and Goodall (1986, p. 81) indicate that first birth typically occurs during late adolescence in wild females.

[9]Ideally, within-class analyses should employ cases in which the number of observations within each class is sufficiently high as to ensure that homogeneity of error variance assumptions are not violated within classes (Hox, 1995). However, because the number of subjects in our dataset with many recorded births is small, limiting our analysis to such cases would force us to discard the majority of our data, a step that would increase the probability that the sample of live births analyzed would be unrepresentative. Nevertheless, despite this limitation, so as to reassure ourselves that our initial result was not an artifact of a small number of observations within each class, we conducted six additional fixed-effect analyses, focusing on subjects for whom the minimum number of offspring in the dataset was, respectively, 5, 6, 7, 8, 9, and 10. In none of these additional analyses did we find a significant effect for maternal age, thus confirming our initial result.

cence (cf. Weladji et al., 2002), a pattern consistent with some of the human data (Bardham, 1966; Karn and Penrose, 1952; Loeb, 1965; MacLeod and Kiely, 1988; Namboodiri and Balakrishnan, 1959; Selvin and Janerich, 1971; Shami and Khan, 1980).

In the only other published study of the determinants of chimpanzee birth weight, examining captive animals, Gavan (1952) reported that maternal age is significantly negatively correlated with birth weight, while parity is not significantly associated with birth weight either alone or after controlling for maternal age. These results should be interpreted with caution, however, as Gavan's sample size (1952) was quite small (N = 42), and first-borns were very underrepresented, factors that may have skewed the results (Broadhurst and Jinks, 1965). Given that our findings are likely to be substantially more reliable, the same issue that emerged in the human case is therefore present in the chimpanzee, namely the contrast between the absence of a positive age effect and the presence of positive parity effect. Because female chimpanzees exhibit considerable variation in age at sexual maturity, age at first birth, and lifetime fertility (Nishida et al., 2003; Pusey et al., 1997), as in the human case, it is unlikely that natural selection would have substituted parity for age as an index of time-limited reproductive potential.[10]

Limitations

The terminal investment hypothesis is premised on the insight that the level of current investment should be calibrated with respect to probable future reproductive opportunities. While menopause in humans and senescence in chimpanzees create finite endpoints to female reproductive careers, these are not the only hard constraints on future reproduction, as premature death can truncate the reproductive career in advance of these endpoints. It is therefore reasonable to presume that evolved mechanisms governing the allocation of maternal investment should be sensitive to the probability of dying at various ages. Specifically, investment in offspring produced early in a female's reproductive career can be expected to increase to the extent that age-specific mortality rates climb prior to the cessation of reproduction due to menopause or senescence.

The above proposition suggests that assessments of the allocation of reproductive investment over time should take age-specific mortality rates into consideration. Examining published findings for some of the societies represented in the 31 publications reviewed above, it is clear that, while age-specific female mortality is nearly constant through the reproductive years in many developed nations (United Nations Department of Economic and Social Affairs, 1999, p. 448, 455, 459, 476), the same is not true with regard to a number of the developing nations examined, with sometimes steep increases in female age-specific mortality with age (Central Statistical Authority (Ethiopia) and ORC Macro, 2001, p. 109–110; National Statistical Office (Malawi) and ORC Macro, 2001, p. 179–181; International Institute for Population Sciences and ORC Macro, 2000).

Unfortunately, because the 31 publications employed do not provide raw data, it is not feasible to reassess published results in light of the impact of age-specific mortality rates. Although this necessarily limits the evidentiary power of the findings reported, it is nonetheless noteworthy that, while the slope of the change in age-specific mortality rates with age varies dramatically across populations, this variation is not mirrored in the pattern of results described earlier. For example, Malawi has the steepest slope in this regard (National Statistical Office (Malawi) and ORC Macro, 2001, p. 179–181), yet evinces the same pattern of maternal determinants of birth weight as found in developed nations having nearly flat age-specific mortality rates during the reproductive years. This suggests that re-evaluation of the findings presented above in light of age-specific mortality rates would likely not fundamentally change the overarching pattern evident therein, namely that parity generally exercises a positive influence on birth weight in humans, while age has little or no effect in this regard.

Turning to the chimpanzee data, among captive females, age-specific mortality is low and essentially constant from ages 5–25; the probability of death increases only slightly (from 0.02 to 0.03) between ages 25–30, with an equivalently small rise (to 0.04) between ages 30–35 (Hill et al., 2001). Because the majority of mothers in our sample are under age 25, with very few individuals over age 30 (compare with Caro et al., 1995), it is reasonable to presume that, if they exist, evolved mechanisms that calibrate reproductive investment as a function of current age-specific mortality rates should exercise little or no influence over birth weights in our sample. However, since little is known about the factors at issue, we cannot rule out the possibility that the captive environment creates evolutionary disequilibrium, as such evolved mechanisms could be canalized in this regard, in which case they would not be responsive to the reduced risk of death present in the captive environment. While substantial differences in mortality rates between extant wild chimpanzee populations (Hill et al., 2001) suggest that such canalization is unlikely to have occurred, even if the

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[10]With regard to other nonhuman primates, to our knowledge only two other studies on the effects of age on birth weight have been conducted to date. Silk et (1993) found that, in captive rhesus macaques, age exercises a positive influence on birth weight; the authors reported that parity has no effect on gestation length, but it is difficult to interpret this with regard to birth weight, as they also documented that older mothers have both heavier infants and shorter gestations than younger mothers. In the same species (but using a substantially smaller sample), Broadhurst and Jinks (1965) found that, while maternal age does make a contribution to birth weight, the effect is much smaller than that of parity. Of additional interest, examining captive long-tailed macaques, Dang et al. (1992) found that birth weight increased through parity 4, and then plateaued; the authors did not, however, assess the impact of maternal age.

mechanisms were canalized, this would be unlikely to significantly impact our results, as the risk of death in wild females is both relatively low and essentially constant between ages 10–25 (Hill et al., 2001), the period encompassing the majority of births in our sample. We therefore conclude that, for both humans and chimpanzees, consideration of the potential impact of age-specific mortality does not suffice to reconcile our findings with the predictions of the terminal investment hypothesis.

Our tests of the terminal investment hypothesis are premised on the assumption that incremental increases in birth weight occur at the expense of residual reproductive potential. As noted earlier, evidence of long-lasting maternal depletion in humans is mixed, while only indirect inference is presently possible in the case of chimpanzees. Although even temporary depletion can impact residual reproductive potential by either 1) creating a trade-off between the length of the interbirth interval and the extent to which depleted stores are replenished, or 2) increasing morbidity and mortality during the period of replenishment, given both a priori theoretical grounds and considerable evidence (Khan et al., 1998; King, 2003; Winkvist et al., 1998) suggesting that the extent of depletion is profoundly contingent on maternal dietary adequacy, it follows that these consequences may be markedly attenuated in well-nourished populations. With regard to the human data, although the 31 publications surveyed encompass societies of widely varying degrees of prosperity, few of the authors included information on dietary adequacy, making it difficult to directly assess the extent to which this factor may contribute to the pattern of results observed. Nonetheless, several observations are noteworthy. First, even in wealthy developed Western nations, holding stature constant, maternal weight independently affects birth weight (Kirchengast et al., 1998; Kirchengast and Hartmann, 1998), suggesting that an environment of abundance does not wholly swamp mechanisms responsible for the allocation of maternal investment. Second, in one sample from a developing nation (India) that contained substantial variation with regard to maternal nutritional adequacy, controlling for stature, maternal weight and parity independently contributed to birth weight, but age had no effect (Malik et al., 1997), indicating that it is unlikely that the overarching patterns we report simply reflect pervasive dietary abundance. With regard to our chimpanzee data, although dietary information is not available for individual animals, in general, captive populations of primates have larger fat reserves, and are more buffered against the costs of pregnancy and lactation, than is true of wild populations (Dufour and Sauther, 2002). As a consequence, while the aforementioned human findings suggest that this is unlikely, we cannot rule out the possibility that investment in birth weight constitutes a trivial cost for captive chimpanzee females and, as a result, was freed from adaptive modulation in the individuals studied.

Compared to our analysis of the pooled chimpanzee data, our within-subjects test did not improve the performance of maternal age as a predictor of birth weight, thus further failing to support the predictions of the terminal investment hypothesis. However, it should be noted that the within-subjects test transformed the previously highly significant impact of parity on birth weight into a marginal effect, suggesting that individual differences do substantially influence reproductive performance. This observation both 1) begs the question of the origins of such differences (an issue beyond the scope of this paper), and 2) underlines the difficulties which phenotypic correlation can pose in investigations employing within-species variation to examine questions of ultimate causation (cf. Sear et al., 2003).

CONCLUSIONS

Although a minority of the 31 studies of the determinants of human birth weight that we examined revealed a positive influence of age, the vast majority did not. In contrast, many of these studies documented a positive influence of parity on birth weight. The disparity between these two factors is pronounced in our study of maternal determinants of chimpanzee birth weight, as parity exercises a positive effect, whereas the only influence of age is to constrain the contributions of parity with advancing age. It is not possible to reconcile these findings with the interpretation that the absence of a positive effect of age on birth weight may be congruent with the terminal investment hypothesis, as the presence of increases in absolute investment with advancing parity underlines the capacities of female humans and female chimpanzees to tangibly enhance the fitness prospects of successive offspring. On the basis of this preliminary evidence we therefore conclude that, at least in humans and our closest relatives, the common chimpanzee, the terminal investment hypothesis of Williams (1966) is not supported. Should the patterns which we reported be replicated in future investigations, it will be necessary to formulate a new explanation of the determinants of reproductive investment. Given the breadth, cogency, and simplicity of the terminal investment hypothesis, this may turn out to be a substantial theoretical challenge indeed.

ACKNOWLEDGMENTS

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