Extraordinary intelligence and the care of infants

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We present evidence that pressures for early childcare may have been one of the driving factors of human evolution. We show through an evolutionary model that runaway selection for high intelligence may occur when (*i*) altricial neonates require intelligent parents, (*ii*) intelligent parents must have large brains, and (*iii*) large brains necessitate having even more altricial offspring. We test a prediction of this account by showing across primate genera that the helplessness of infants is a particularly strong predictor of the adults' intelligence. We discuss related implications, including this account's ability to explain why human-level intelligence evolved specifically in mammals. This theory complements prior hypotheses that link human intelligence to social reasoning and reproductive pressures and explains how human intelligence may have become so distinctive compared with our closest evolutionary relatives.

cognitive science | evolutionary dynamics | developmental modeling

The breadth and power of human cognition is qualitatively unlike that of even our closest evolutionary relatives. Although our mental abilities clearly aid survival and reproduction, our cognitive capacity also appears to go far beyond what is minimally required to live and reproduce, permitting us to engage in a remarkable breadth of cognitive and technical endeavors. The question of why human intelligence and brain size exhibits a drastic change over recent evolutionary history has not yet been resolved.

Numerous authors have theorized about possible factors that may have given rise to humans' powerful cognitive systems. These theorized factors include social learning and interaction (1–10), diet (11–13), relational/analogical abilities (14), language (15, 16), the rise of female food gathering (17), hunting (18, 19), a constellation of traits leading to improved causal reasoning (20), and general elaboration of abilities found in primates (21, 22). Although these theories often make testable predictions about the relationship between brain size and other factors, they have not yet explained why human intelligence so far exceeds that of other primates. They also do not explain why intelligence took so long to evolve in the history of life, nor do they provide mechanistic accounts of how proposed factors could concretely lead to the enormous increase in brain size and intelligence seen through hominid evolution (23, 24).

Here we show that extreme intelligence could have arisen through a positive evolutionary feedback loop: Humans must be born unusually early to accommodate larger brains, but this gives rise to particularly helpless neonates. Caring for these children, in turn, requires more intelligence—thus even larger brains. In this situation, brain size may be linked between parents and children in an unusual way. Increased brain size may help adults care for altricial neonates, yet also make such neonates less likely to survive childbirth due to physical constraints. We develop a formal model of this situation and show that it may result in self-reinforcing dynamics, eventually creating species that are much more intelligent than others. Populations can be pulled into a region of evolutionary phase space in which children come to be born even earlier and parents must have even bigger brains to care for them, similar to runaway dynamics observed in sexual selection.

After developing the model as a proof of principle for the dynamics of our account, we test its most basic assumption: Primate intelligence should be strongly dependent on pressures of childcare. As we show, weaning time—a measure of the helplessness of newborns—is a strong predictor of primate intelligence, over and above a variety of other measures. We conclude by discussing several other pieces of evidence in support of our account. In particular, the theory explains why human-level intelligence occurred in mammals and not in other lineages that had millions of years more time to evolve highly intelligent species. Under our account, the requisite dynamics only become possible through linking large brains and live birth, characteristic features of higher mammals.

The Evolutionary Model

The model presented here is meant to provide a demonstration that runaway selection for unusually large brains and high intelligence can occur from nothing more than the demands of caring for children who must be born early to accommodate their own large brains and who must have large brains to care for their own children. Our formalization is meant to illustrate the key mechanisms that may have been at play but necessarily simplifies a complex evolutionary history. As such, the model is in line with other work in biology aimed at capturing large-scale properties and dynamics from general principles (25–27).

The model contains three parameters that are assumed to be subject to selective pressures: an adult head/brain size R, a birth age T (i.e., period of intrauterine development), and a quantification of an individual's intelligence I. These variables are assumed to relate to survival in the way described above: Large brains R require earlier birth ages T but are also associated with higher I. Because the true form of many of these linkages is not known, we focus on providing an existence proof that plausible assumptions can give rise to a fitness landscape mode favoring altricial newborns and highly intelligent parents.

Model Implementation Assumptions. First, we assume a Gompertz growth curve—a standard in embryo development (28)—characterizes

Significance

One mystery of human evolution is why our cognition differs qualitatively from our closest evolutionary relatives. Here we show how natural selection for large brains may lead to premature newborns, which themselves require more intelligence to raise, and thus may select for even larger brains. As we show, these dynamics can be self-reinforcing and lead to runaway selection for extremely high intelligence and helpless newborns. We test a prediction of this account: the helplessness of a primate's newborns should strongly predict their intelligence. We show that this is so and relate our account to theories of human uniqueness and the question of why human-level intelligence took so long to evolve in the history of life.

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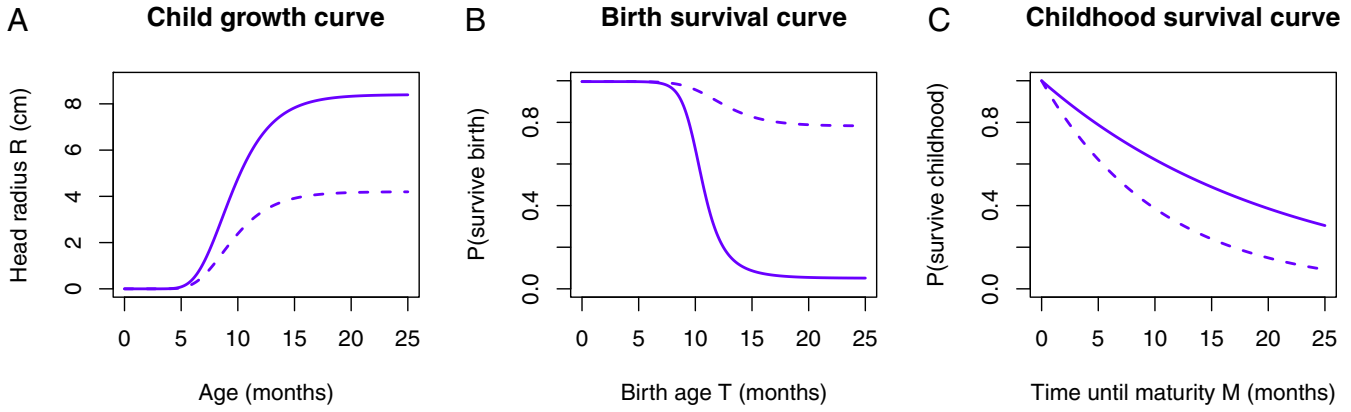

Fig. 1. The assumed relationships in Eqs. **1**–**3**, relating (*A*) age to head radius, (*B*) age to birth survival, and (*C*) age to childhood survival at $\gamma = 0.4$. The solid lines show the relationships for a typical adult human head $r = 8.4$ cm. The dotted lines show the curves for a head half as big.

children's head radius throughout gestation and neonatal development:

$$g(x,R) = Re^{-b \cdot e^{-c \cdot x}}, \qquad [1]$$

where x is the age and R is the adult (limiting) head size. There are two parameters here, b and c, controlling the y displacement at $x = 0$ and the growth rate, respectively. We fit $b = 37.1$ and $c = 0.42$ to head growth data from newborns from the World Health Organization (*Materials and Methods*).

Second, we assume that a characteristic size V constrains neonates' head size at birth. Children who are born with a head size larger than V will be assumed to be relatively unlikely to survive birth, matching the observation that our brains come with the cost of complex and dangerous childbirth (29–31), as well as the commonality of deaths due to cephalopelvic disproportion in humans and other primates (32–35). The shift to large infants has been argued to have occurred early in human evolution, with *Australopithecus* carrying neonates with nearly the same proportion of their body mass as modern humans, potentially an important driver of the development of alloparenting (36). In the model, if children are born at time T postconception, they will have a head size of $g(T,R)$ via Eq. **1**. We assume that the probability of surviving childbirth falls off sigmoidally once this size exceeds the fixed bound V:

$$P(\text{survive childbirth} \mid T,R) = \phi(V - g(T,R)), \qquad [2]$$

where ϕ is a standard logistic curve [$\phi(z) = 1/(1+e^{-z})$]. In general, one might consider the V to be subject to selective pressures. However, two prior accounts have critically argued for absolute physical constraints on children's size at birth. Under one theory, our ancestors faced a pressure for bipedalism (which constrained pelvis size) and also large brains (which pressured increasing pelvis size), resulting in the so-called "obstetric dilemma" (29, 31, 37, 38). Humans may have solved this dilemma by having young and incapable neonates and decreasing gestation time because pelvis size could not increase further. Alternatively, the metabolic costs of gestation may have constrained the maximum size child that mothers could support (39). Either case results in a maximum allowable size at birth. Consistent with these theories, we here fix $V = 5.48$ cm, a typical head radius for human newborns. Fig. S1 shows that the qualitative properties of the model do not depend strongly on the numerical value of V.

After childbirth, children must survive to a reproductive age. Under the theory, the probability of surviving should increase with their parent's intelligence, denoted I_p, but will depend on the amount of time until the child reaches maturity. We make the very simple assumption that children have a constant hazard rate of death until their time of maturity. We assume that the rate is inversely proportional to parental intelligence I_p, giving rise to an exponential failure distribution,

$$P(\text{survive to adulthood} \mid M, I_p) = e^{-M(\gamma/I_p)}. \qquad [3]$$

Here γ is a free parameter capturing the rate of mortality, and M is the amount of time it takes to reach maturity. Thus, doubling intelligence will have the effect of halving the rate at which deaths occur. Halving the time-till-maturity will give the newborn half as much time to fail. We computed time-till-maturity M as the time after birth at which Eq. **1** reaches 99% of R [i.e., as $x - T$, where x solves $g(x,R) = 0.99 \cdot R$].

Finally, we assume that head size R and intelligence I are inherently linked (see Fig. S2). There are many forms this linkage could take: intelligence could be a function of brain size, both could be a function of a third inherited variable, or mutations could tend to increase and decrease both together. While all three of these can give rise to runaway selection, in our exploration, only the latter appears to make it possible for time-to-maturity to correlate better with intelligence than brain size does, a finding in our empirical section below. We therefore focus here on the case where mutations to R are highly (90%) correlated with mutations to I. This assumption is plausible given evidence for overall enlargement of the brain throughout mammalian evolution, rather than selection of particular subsystems (40–42), dynamics which have been argued to occur from simple genetic mechanisms (21).

To visualize the assumed relationships between variables, Fig. 1 plots Eqs. **1**–**3** at $r = 8.4$, a typical adult head radius (solid), and $r = 4.2$, a radius half as big (dotted). These show three simple relationships. First, the smaller radius asymptotes at the smaller value under the Gompertz growth function (Fig. 1*A*). Second, birth survival at any birth age is increased for the smaller radius but approaches 1 as the birth age (and thus head size at birth) decreases (Fig. 1*B*). Third, smaller-brained species have a lower chance of surviving childhood due to decreased intelligence (Fig. 1*C*), but survival for both decreases as time-till-maturity increases. In the model, the probability of surviving until adulthood is the product of Eqs. **2** and **3**, treating the survival of birth and childhood as statistically independent events, given T, R, and I.

Childcare Demands Can Yield Self-Reinforcing Dynamics. Fig. 2*A* shows the probability of surviving to a reproductive age (i.e., Eq. **2** multiplied by Eq. **3**) for values of children's birth age T (x axis)

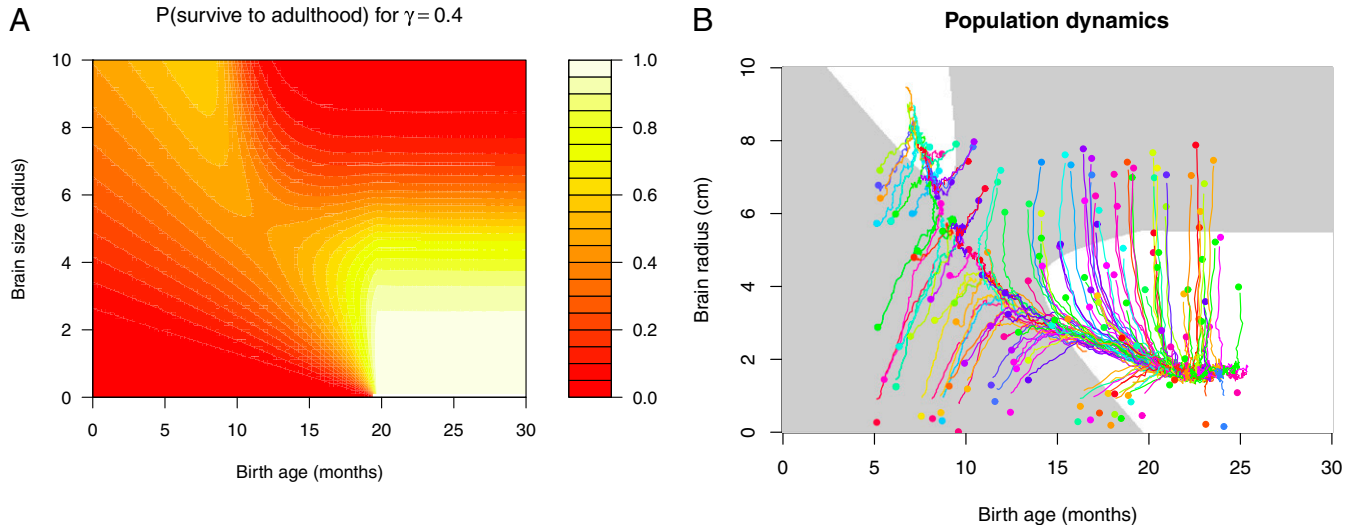

Fig. 2. (*A*) The fitness landscape implied by Eqs. **1**–**3**, giving a child's probability of surviving as a function of head size and birth age. This shows a shape in which an avenue for underdeveloped neonates and intelligent parents (to the upper left) opens up only after birth age has been pushed sufficiently low. (*B*) Each color represents the mean of a population over time, starting from the specified circle. The background has been thresholded at 50% survival. Populations with high birth ages tend to decrease in brain size and increase in birth age. Populations with sufficiently low birth ages and large brains will be swept away to the upper left, with self-reinforcing dynamics.

and head size R (y axis). To create Fig. 2*A*, we have assumed that I_p, the parent's intelligence, is equal to the child's brain size at the limit of growth. This approximation holds in populations in which there are only small changes across generations.

The shape in Fig. 2*A* illustrates the key features of our account. First, the fitness landscape is relatively flat for late-born species with small brains (lower right). However, if species are born early enough and with large enough brains, a new avenue opens of up having bigger brains and consequently earlier births, as shown by the leg of high survival probability that goes to the upper left. Critically, survival probability at the far edge of this leg (big head size and low birth age) is higher than for more moderate values of these variables, meaning that populations can get pulled to the upper left simply by the dynamics of Eqs. **1**–**3**. The diagonal lean of this leg means that low birth ages and big brains can exhibit self-reinforcing dynamics, in which big-brained populations are pressured toward lower birth ages and populations with lower birth ages are pressured toward bigger brains.

Fig. 2*B* shows the dynamics of the full evolutionary model. Without this simulation, it is perhaps not intuitively clear that runaway dynamics could realistically exist in the mixed evolutionary situation in which larger brain size in the parent increases survival in childhood, but larger brain size in the child decreases survival during childbirth. In Fig. 2*B*, a population size of $N = 1{,}000$ is simulated for 100 generations from a variety of starting locations (circles). In the model, random parents are chosen from the population; their respective T, R, and I values are averaged; and they produce a child whose T, R, and I values are subject to Gaussian additive noise (mutations) with an SD of 1.0. If the child survives birth (via Eq. **2**) and childhood (via Eq. **3**), the child replaces a random member of the population. The population trajectory depends strongly on the starting position: Only sufficiently early-born big-brained species will be pulled to the upper left region in a self-reinforcing cycle. This demonstrates that the dynamics of Eqs. **2** and **3** can give rise to species with unusual levels of intelligence and neonate altriciality. Critically, the model shows that this is possible even when no forces other than childbirth and childcare are present. We note that as should be expected, the fitness landscape and corresponding dynamics are sensitive to the parameters.

Altriciality and Intelligence in Primates

The basic ecological prediction of the model is that species should exist only in the high-survival regions of Fig. 2*A*. Species with well-developed neonates can have a variety of brain sizes, but as altriciality increases, species must have large brains and high intelligence. To test for this trend of increasing intelligence with greater altriciality, we combined data on weaning times (43) as a proxy for altriciality, with a measure of general intelligence from a Bayesian metaanalysis of primate cognition tasks (44) and brain size measures (45) (*Materials and Methods*).

Altriciality Covaries with Intelligence Across Genera. Fig. 3 shows the correlation between weaning age and intelligence across the primate species for which these species were available. The correlation is statistically significant (Kendall's $\tau = 0.62$, $p < 0.001$). We note that the model above also qualitatively captures this relationship. In the simulation used for Fig. 2 (*Materials and Methods*), the weaning times were highly correlated ($R^2 = 0.96$) with intelligence.

The relationship between weaning and intelligence is also statistically significant when controlling for phylogenetic relatedness. Using a phylogenetic generalized least squares linear regression that respects the nonindependence of the sampled genera and phylogenetic data provided by ref. 46, weaning time is a significant predictor of intelligence (standardized $\beta = 0.78$, $t = 3.32$, $p < 0.01$). As these make clear, weaning time is strongly related to behavioral measures of intelligence.

Altriciality Predicts Intelligence Beyond Other Factors. It is important to establish that the linkage between altriciality and intelligence is not due to confounding variables. In principle, it is easy to imagine a history of life in which altriciality is correlated with intelligence, yet has no direct causal influence. For instance, a selective pressure for intelligence (due to, e.g., environmental factors) might increase brain size and thus through physical constraints lower the birth age. To test this, we can perform a more detailed analysis looking for effects of weaning time over and above other predictors. If altriciality effects were determined by another variable, the effects should disappear once the other variable is controlled.

In fact, weaning time has a strong relationship to intelligence controlling for other variables, and most control predictors have

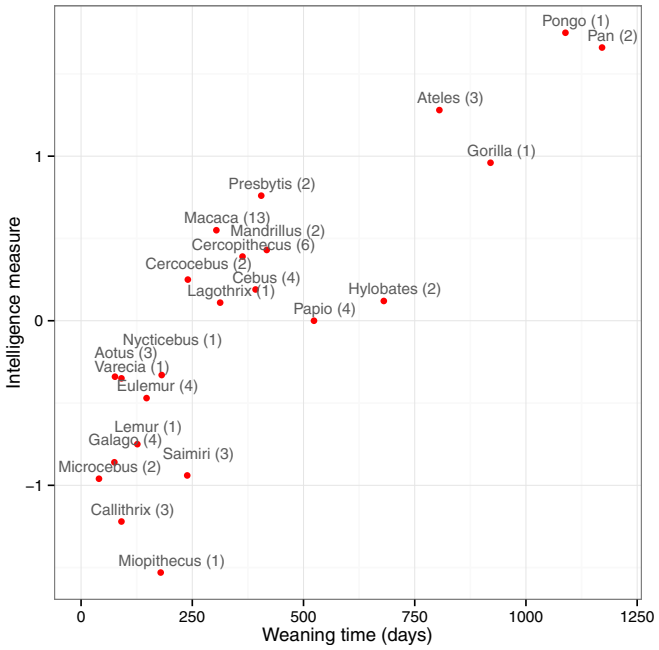

Fig. 3. Relationship between weaning time and intelligence (Kendall's $\tau = 0.62$) across all primate genera for which these data were available ($N = 23$). Numbers give the count of species in each weaning estimate (x axis).

zero effect once weaning time is controlled. Table 1 shows a separate phylogenetic least squares regression in each row, with coefficients for weaning age (first three columns) and a variety of other predictors (last three columns) using all genera for which these measures were available. These results demonstrate our predicted positive effects of weaning age on intelligence controlling for each covariate, reaching statistical significance in all but two cases and marginal significance in those. Moreover, controlling for weaning time, only one of the other covariates is statistically significant, and weaning time is still a significant predictor in that regression. The significance may be an artifact of using brain volume divided by body mass (see Table S1 for a more detailed analysis). Table S2 shows similar, although quantitatively stronger, effects using standard nonphylogenetically controlled regressions. Table S1 shows similar effects with multiple brain and body size predictors. These results are strongly suggestive that our a priori prediction of the importance of weaning both holds and the pattern is unlikely to be the result of these other variables.

The evolutionary model can also exhibit a stronger relationship between time-till-maturity and intelligence than brain size and intelligence. Because intelligence and brain size are correlated but not deterministically related, either one may come to determine survival, controlled in large part by γ. In the model runs for Fig. 2 above which used $\gamma = 0.4$, weaning time was always a significant predictor of intelligence once brain size was controlled, but brain size was often (15%) not a significant predictor once weaning time was controlled.

Discussion

The dynamics of the model explain how extreme levels of intelligence may evolve without requiring additional outside pressures. Once a population has moved into the appropriate region of the space, trends for growing brain sizes and lowering birth ages will mutually reinforce each other. This can lead to runaway selection for premature infants and big brains, relative to the other present physical and ecological constraints. One must still explain why human populations happened to move into parts of space that would lead to these runaway dynamics. It is possible that environmental factors—perhaps those already proposed to play a pivotal role in human evolution—helped to move our species to this region of dynamical space. We emphasize that the theory should be viewed tentatively. Our results show strong effects of altriciality on primate intelligence, and our model demonstrates that runaway selection is logically possible, but further work is needed to test this relationship and the model's assumptions.

If the runaway dynamics demonstrated here did play a pivotal role in human evolution, it would mean that many of the rich cognitive abilities observed in humans may be epiphenomenal of selection for neonatal care. In general, this is difficult to assess because nearly every human ability could be construed as useful

Table 1. Analyses predicting the behavioral intelligence measure from weaning age and a control covariate using a phylogenetic least squares regression

Weaning age			Control variable (standardized)				
Coefficient	SE	P value	Predictor	Coefficient	SE	P value	$\hat{R}^2$
0.96	0.35	0.01	scale(neocortex)	−0.13	0.38	0.37	0.71
0.76	0.40	0.04	scale(total brain volume$^{1/3}$)	0.20	0.47	0.33	0.72
0.89	0.38	0.02	scale(total brain volume$^{2/3}$)	−0.01	0.42	0.49	0.71
0.95	0.35	0.01	scale(total brain volume)	−0.11	0.37	0.38	0.71
0.86	0.37	0.02	scale(neocortex/total brain volume)	0.09	0.72	0.45	0.72
0.99	0.28	0.00	scale(EQ)	−0.30	0.25	0.12	0.66
0.89	0.28	0.00	scale(adult body mass)	−0.04	0.20	0.42	0.71
0.62	0.25	0.01	scale(total brain volume/adult body mass)	−0.52	0.20	0.01	0.75
0.83	0.32	0.01	scale(neonate body mass)	0.13	0.35	0.36	0.71
0.65	0.30	0.02	scale(neonate body mass/adult body mass)	−0.35	0.23	0.07	0.71
0.68	0.37	0.05	scale(log(neocortex))	0.41	0.51	0.21	0.73
0.67	0.37	0.04	scale(log(total brain volume))	0.41	0.48	0.20	0.73
0.86	0.35	0.01	scale(log(neocortex/total brain volume))	0.09	0.72	0.45	0.72
0.98	0.28	0.00	scale(log(EQ))	−0.28	0.29	0.17	0.66
0.66	0.33	0.03	scale(log(adult body mass))	0.44	0.38	0.13	0.74
0.77	0.28	0.01	scale(log(total brain volume/adult body mass))	−0.29	0.22	0.10	0.73
0.56	0.33	0.06	scale(log(neonate body mass))	0.78	0.48	0.07	0.71
0.84	0.30	0.01	scale(log(neonate body mass/adult body mass))	−0.09	0.24	0.36	0.71

Other variables have little effect once weaning is controlled, pointing to the importance of altriciality over and above these other factors in determining intelligence. All P values are one-tailed. $\hat{R}^2$ gives the raw correlation between fit and observed values.

for childcare in some way. However, the account complements several prior theories of human distinctiveness, notably theories based in social interaction (2, 3, 7, 10, 47), as well as reproduction and childrearing (48–51). Altricial neonates require substantial parental attention. Sophisticated means of reading social intentions may have evolved specifically to care for young children who cannot address their own needs. Such demands might also give rise to social systems of cooperative breeding for childrearing—systems that could efficiently organized or share time and material resources and which have been suggested as pivotal in human evolution (50, 51). This fits well with the view that human reproductive behavior—including monogamous pair bonding, parenting, and social relationships—may have been a driving factor throughout human evolution (48, 49).

Our theory also addresses the question of why extraordinary intelligence evolved in humans and not in other species. Why did insects, reptiles, or fish—each of which has been around far longer than mammals—not develop such cognition first? If our intelligence has been driven by environmental or social challenges, why did species that lived in harsh environments or social groups long before humans not develop human-like intelligence? The answer provided by our account lies in the model's inherent linking of intelligence and the timing of childbirth. The runaway dynamics of the model only become possible in viviparous species. This is because in oviparous animals, the skull can form after eggs are laid so there is no inherent linkage between the maturity of offspring at birth and the animal's brain size or intelligence. However, in live birth, animals must traverse the birth canal with a mostly formed skeletal structure, meaning that birth age and maturity must be set inherently to accommodate brain size. As Fig. 2*B* illustrates, the runaway dynamics are only possible when brains become large enough to permit runaway dynamics. Because one of the defining features of mammals is a neocortex, our account explains why extraordinary intelligence evolved in viviparous mammals, namely, the clade *eutheria*.

At the same time, if the demands of childcare are an important factor, we should see links between altriciality and intelligence without runaway selection in other species. This has been noticed previously, where altricial bird species have larger brains in adulthood relative to body size (52). Corvids and parrots, for instance, are unusually intelligent; they also have an extended development before the young are independent from their parents' nutritional support (53).

Our account also predicts a particularly strong coupling between mothers' intelligence and rates of infant mortality. In the Serbian Roma, there are significant effects of IQ on infant mortality ($R = -0.26$) after controlling for parental education and age (54). However, more commonly, education effects on infant mortality have been quantified. Mothers with 13 or more years of education have approximately half the rates of infant mortality than those with 0 to 11 years among California parents (55). Decreases in child mortality in the developing world have been attributed to improving healthcare as well as education even over and above effects of economics (56–58), with a decline of approximately 8% in under-5 mortality for every year of maternal education. Studies of the developing world also show that child mortality also exhibits patterns consistent with our model's assumptions, with a mode of deaths near birth (≤1 mo) and another in early childhood (9–24 mo). This matches the model, in which children's survival depends on two separable factors: surviving birth and surviving childhood. This literature highlights the importance of parental care, as well as the inherent difficulty of raising human children.

Conclusion

It is very hard to imagine an adult of any other species raising a human infant. In the literature on feral children, there are no clear cases of children adopted in infancy. It has even been suggested that purportedly feral children were instead autistic and it was only conjecture that they were raised by animals (59). This observation raises an evolutionary puzzle: How could it be the case that humans have evolved to the point that so much intelligence is required to raise our own children? This motivates the search for mechanisms that could solve such a paradoxical thinkin'-and-egg problem.

Our modeling has shown that the evolutionary dynamics of caring for neonates may select for intelligence, which in turn requires even more brainpower, pushing infants to be born even earlier to accommodate their larger brains. The model is not intended as a full account but rather as a piece of a much more complex evolutionary and reproductive history in which multiple traits are interrelated (49). Our work has intentionally focused on a simplified model to understand if the requisite dynamics are possible from basic assumptions. As the account predicted, the helplessness of a species' neonates is a particularly good predictor of parental intelligence, over and above other factors. Finally, this theory can explain why such intelligence evolved in mammals rather than other lineages that had more time to evolve human-level intelligence, yet failed to do so.

Materials and Methods

Gompertz Fitting. The Gompertz equation (Eq. **1**) was fit to male child growth standards provided by the World Health Organization. These standards consist of head circumference measurements from children 0–13 wk after birth or, in our analysis, 38–52 wk postconception. We fit these parameters using least-squares fitting via R's *stats* library's optim function (60), including one single additional data point for 0 head size at $t = 0$ months postconception.

Model Methods. To generate Fig. 2 and the reported model correlations, a population was started randomly at a birth age between 5 and 25 and a brain size between 0 and 8. The model was run on population sizes of 1,000 individuals for 100 generations. The correlations (e.g., between weaning age and intelligence) were computed by dividing 1,000 runs into life histories of 25 species and computing the average correlation within histories. Because Fig. 3 and associated statistics excludes humans, the model correlations excluded the very large-brained ($R > 6$) and high-birth age ($T > 8$) species. We note that the dynamics and correlations are sensitive to a number of implementational choices, including the number of generations, distribution of starting positions, correlation between intelligence and brain size mutations, and the point at which individuals are considered to be mature. Parameters were explored using a grid search. Code is provided for the model by S.T.P.

Weaning Age Estimate. Weaning ages were retrieved from ref. 43. To find the average level in each genus, we used the median of the reported times. Missing weaning ages for *Presbytis* and *Cercocebus* were added using ref. 61. Weaning times used were raw, not transformed allometrically.

Brain Size Estimates. Brain size estimates were taken from ref. 45, using both neocortex and total brain size measures from Table 1. Note that in this table there appeared to be an error on the total brain size of *Miopithecus*. We used the value 37,760 mm^3.

Phylogenetic Generalized Least Squares Regression. A phylogenetic tree for primate genera was shared by the authors of a recent molecular phylogeny (46). We performed a phylogenetic generalized least squares regression using the ape package in R (62), assuming a Brownian motion model and using the *gls* function from nlme.

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