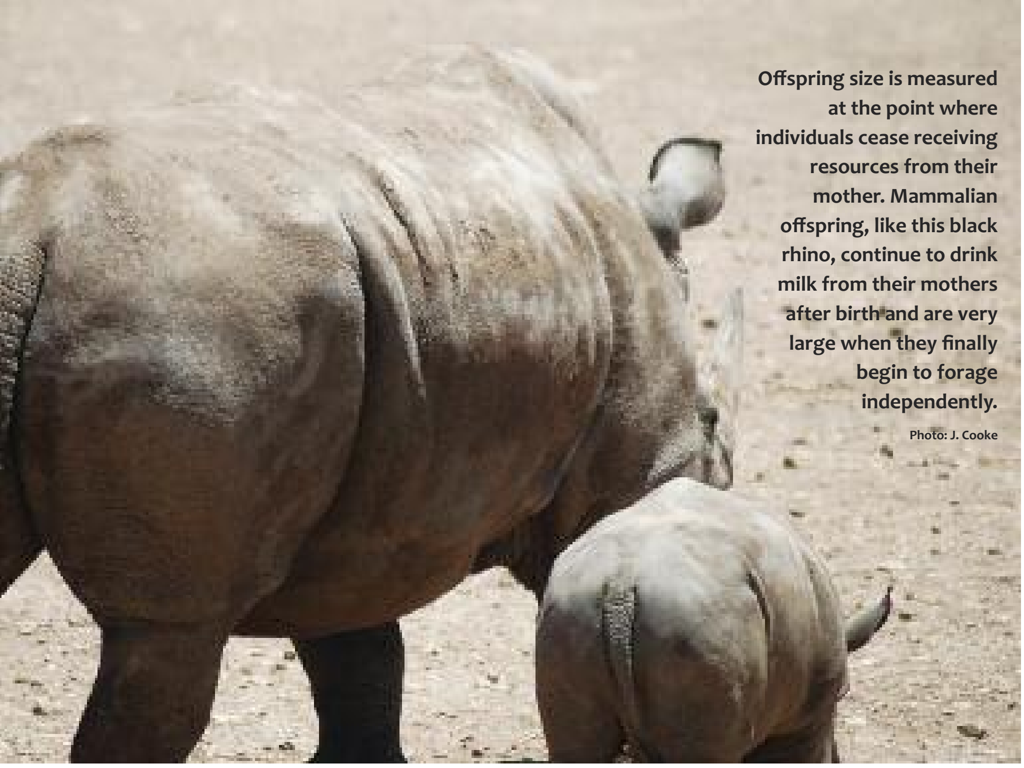

Offspring size is measured at the point where individuals cease receiving resources from their mother. Mammalian offspring, like this black rhino, continue to drink milk from their mothers after birth and are very large when they finally begin to forage independently.

Photo: J. Cooke

# Small Families and Big Babies

BY DANIEL FALSTER

**Why do humans have a few relatively big babies while fish and plant species have hundreds or even thousands of offspring?**

Offspring are the main currency of life. All animals and plants produce offspring to carry their genes into the future. Without offspring, populations would die out and species would become extinct.

If a mutation in a gene increases the number of surviving offspring, this demographic advantage allows the new gene to spread through the population. The gene is selected for. In contrast, bad mutations lead to fewer surviving offspring and the mutations are thus removed from the population. So evolution does its work by counting offspring.

If evolution works by counting offspring, then why do some species produce so few of them? Comparing many bird and mammal species to other groups like plants and fish that have hundreds or even thousands of offspring, you could be excused for wondering why mammals and birds have been so successful.

The simple answer as to why mammals produce so few offspring is that they invest more energy and resources into each one. Overall, an adult mammal devotes more energy towards reproduction than a fish or plant of similar size, but because they give so much energy to each offspring, mammals produce fewer of them.

The choice between making many small offspring versus few large offspring is called an evolutionary trade-off. Taking the amount of energy mothers have available for reproduction, and dividing by the energy invested per offspring, one can quickly calculate the maximum number of offspring of a given size that a mother could produce in any given year, or through her lifetime. Repeating the same calculation with many different offspring sizes gives a range of offspring size–number combinations that are possible for the mother. For any given species in the real world we see only one of these possible combinations.

The challenge for evolutionary biologists is then to figure out why evolution settled on the particular combinations of size and number that it did. So to understand why the small families of birds and mammals make evolutionary sense, we need to ask why these species invest so heavily in each offspring.

The usual approach to a question like this is to construct a mathematical model describing the life cycle of a species. This model can then be used to conduct virtual experiments, most of which would be impossible to do with real organisms. For example, we could let elephants have many small babies instead of few large ones and then ask whether this alters the dynamics of the population.

Similarly we can test alternative theories about different factors that might be causing the evolution of offspring size. Each alternative theory is translated into equations, and then our model species are allowed to evolve. The model predicts what offspring size will yield the greatest evolutionary success under different circumstances, and this prediction is then compared with the characteristics of real organisms in the wild. If the predicted offspring size is close to what is observed in nature then that suggests we have probably incorporated into the model the most important influences on the evolution of offspring size.

Using mathematical models, my colleagues and I recently tested several ideas about the evolution of offspring size. We were interested in two questions in particular. First, why do some taxa such as plants and fish make their offspring so much smaller than others, such as mammals and birds? Second, why is it that species with larger-bodied adults tend to have larger offspring, even within a group such a mammals or plants.

Previously, many researchers thought that survival during the earliest stages of life would be important in determining how large offspring are. Our model indicated that survival early during life was indeed important, but only indirectly. The likeliest factor driving evolutionary increases in offspring size was competition for resources among rival offspring as they approached adulthood. Survival during early life influenced the predicted offspring size indirectly by varying the strength of the competitive effect.

Once an offspring becomes independent of its mother, it needs to acquire energy so that it can grow to maturity. Different species obtain their energy in many different ways – plants use the Sun's energy to photosynthesise, some animals eat plants and other animals eat animals – but all share the common challenge of gathering enough resources to grow. Sometimes there's not enough food to go around and someone misses out. More often than not it's the littlest or weakest ones that are left hungry because the bigger individuals use their size to ensure they get a feed. Missing dinner several times inevitably leads to death for smaller individuals, while the larger ones continue to flourish. So, because of competition for resources, larger individuals have a better chance of reaching maturity.

Notice that we now have two trade-offs, each pushing evolution in different directions. Smaller offspring sizes are favoured because these allow a mother to produce more offspring. At the same time, larger offspring sizes are favoured because this gives each offspring a better chance of surviving long enough to produce offspring themselves.

It turns out that it's not the number of offspring that are born which matters to evolution, but the number that survive long enough to produce offspring themselves because that will lead to the greatest number of the mother's genes being copied into subsequent generations. In the end, evolution will favour the offspring size that gives the best combination of these two trade-offs: number of offspring produced and fraction surviving.

So the deeper answer as to why mammals have such small families is that strong competition among rival offspring favours larger offspring. Exactly how large depends on the severity of competition among offspring for a particular species. The factors that influence how much competition there is include the amount of energy invested in reproduction by the parents, how long the parents live, and how safe the environment is (i.e. what proportion of juveniles are eaten by predators or are unable to locate a good territory to grow).

With this background behind us we're now in a position to look at why offspring size varies so greatly across species.

## Predictions Across Different Species and Environments

Using the model we developed, we were able to predict offspring and family sizes across hundreds of animal and plant species and determine the causes for the differences between species. In mammals, offspring size after the mother has stopped investing ranges from 1 gram for some species of shrew to several hundred kilograms for a baby rhinoceros or elephant. In plants, offspring size varies from 0.0001 gram to around 100 grams.

The single biggest influence on these enormous differences between species is the parent's size. Within many different groups – mammals, reptiles, plants, birds and even butterflies – you see the same pattern: the larger the parent, the larger the baby. It might seem obvious that larger parents have larger offspring, but there's no physiological reason why this has to be the case.

Blue-footed booby with chick. Like mammals, most bird species have large offspring, each receiving a lot of resources from their mother.

Photo: J. Cooke

Competition provides the answer. The larger an animal or plant is, the more energy it has to invest in reproduction and the longer it lives. Consequently, if these large parents were to produce small offspring they would produce a lot of them. This would intensify competition, and there would be a big advantage for offspring that were effective competitors, shifting the mother's best evolutionary strategy toward larger but fewer offspring.

There are also interesting differences between groups. For a similar-sized mother, mammals have babies that are 1000 times bigger than a fish and 10,000 times bigger than a plant.

Our model helps us identify two important differences between the groups to explain the differences. First, at a given size, mammals are able to invest about 50 times more energy into reproduction than plants. Most of this difference is because of our higher metabolic rates.

Second, the environment in which a species lives plays an important role in determining the amount of competition. When baby plants, corals or fish are born, the offspring are dispersed around the landscape. To survive the offspring need to land in a good spot (e.g. a sunny gap in the forest or a nice empty spot on a reef). Most offspring miss, so there is a very high mortality for offspring during this recruitment process.

In contrast, mammal and bird offspring can find a territory relatively quickly. Combined, the higher metabolic rates and higher initial survival of mammal offspring means there are potential more offspring to compete with, and this competition selects for larger offspring sizes.

## Can Evolution Put the Survival of the Species at Risk?

Most people think of evolution as being good for a species over the long-term. This is most probably true for adaptations relating to the physical environment, like the ability to survive a drought. But it may not be the case for adaptations that are driven by competition.

The evolution of offspring size within a species can be likened to an "arms race" between countries, where different parents are the countries, and their babies the weapons. What matters in an arms race is not the total size of your armaments but how big they are relative to your competitors. The same holds true in biological competitions.

And like an arms race, there is a tendency for different individuals in a species to produce ever-larger weapons (babies) provided they can afford them. As we all know, an escalating arms race at best wastes a lot of resources that could be better directed elsewhere. At worst it leads to disaster.

With the evolution of large offspring and small families, disaster comes in the form of hunting, fishing, disease outbreaks or any other event that dramatically increases the mortality of adults. With their small families it is difficult for mammal and bird populations to cope with these losses because a small family size translates into slower recovery times for the population. Consequently if harvesting, predation or disease persists, such species may become extinct.

**Compared with animals, plants have many, small offspring (seeds). Some species have offspring as small as 0.0001 g, allowing mothers to produce thousands of them. The seed shown here is relatively large for a plant, but is still considerably smaller than any mammal or bird offspring.** Photo: D. Falster

## Parental Care, Language and the Demographic Transition

Competition may also have played an important role in the evolution of communication. Mammalian parents continue to support their offspring beyond birth by giving milk, food and shelter. Offspring might also benefit from the transfer of skills from the mother, which represents a further energetic investment in an offspring's future success. So, rather than size at birth, the size of an offspring when it leaves its mother is a better measure of the total investment, even if still a little rough.

On average, mammalian babies are about six times heavier at weaning than they are at birth. Our model suggests that the long periods of parental care needed to achieve this size gain are due to competition. Long periods of parental care and close family groups were also likely prerequisites for the evolution of communication within family groups.

Theory for the evolution of offspring investment may shed light on one other aspect of human behaviour, which is the tendency for societies to have fewer and fewer offspring as we become richer, live longer and live in safer environments. This pattern can be seen by comparing countries of differing economic success, or in the historical changes experienced by individual countries. This is known as the demographic transition.

At first the demographic transition seems to be an evolutionary puzzle: our potential to raise children grows but we have fewer of them. But this pattern is consistent with the predictions from our model, and with the broad patterns of investment observed across species.

For their size, human parents gather resources in far greater quantities than parents in other plant and animal species. Correspondingly, they invest a large amount into few offspring, each very well resourced. By the time they leave home at 18 years of age or more, our offspring have absorbed a lot of expensive goods, all of which might be considered investments in their future success. These include food, medicines, clothes, schooling, maybe music lessons, a car or even a home deposit. All of these would be spread more thinly if there were more offspring to be supported, and in this key sense they are like the energy distributed by (say) plants into seeds.

As you could guess, modelling humans, with their complicated societies, may be a little more complicated than other organisms but, if correct, our work suggests that our big expensive babies, and our small families, might also make evolutionary sense.

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