



# Why did sauropod dinosaurs grow so big? – A possible answer from the life history theory

Yuki Kanayama, Yoh Iwasa \*

Department of Bioscience, School of Science and Technology, Kwansei Gakuin University, 2-1 Gakuen, Sanda-shi, Hyogo 669-1337, Japan

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## ABSTRACT

Dinosaurs are known for their large body size. Sauropod dinosaurs (Sauropodomorpha) had an especially large body size; some species reached 30 m long and 50 tons. Many hypotheses have been proposed to explain this phenomenon. In this study we examined this question using the life history theory. We constructed a simple model of life history with the following assumptions: the body size of immature individuals increases following a logistic equation. A higher quality and availability of food plants make the initial growth rate faster and the final saturating size larger. The increase in body size stops once reproduction starts. Fertility increases with adult body size and food-plant quality. Mortality due to predation is mitigated by a larger body size. We calculated the optimal body size at maturity that would maximize the lifetime reproductive success or fitness. The analysis showed that adult body size increased with food-plant quality and availability but decreased with higher mortality due to predators and other factors. This conclusion is consistent with geological studies that suggest a high quality and availability of food plants in the Mesozoic era, efficient air-sac breathing, and the lightweight bones of sauropod dinosaurs, allowing rapid growth of small individuals.

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## 1. Introduction

Dinosaurs are a group that includes all species originating from a common ancestor of birds and triceratops (Seeley, 1887). They lived on Earth in the Mesozoic era, specifically from the late Triassic to the end of the Cretaceous period, a time-span of about 170 million years, lasting from about 243–233 million years ago to 66 million years ago. They suffered mass extinction when a giant meteorite hit the earth, an event that is confirmed by evidence at Chicxulub Crater in the Yucatan peninsula and shock quartz at the K/Pg boundary left in the strata (Hildebrand et al., 1991); however birds are considered to be dinosaurs that survived.

Many species of dinosaurs were much larger in body size than other reptiles and mammals and Sauropodomorpha species were much larger than other dinosaurs (Sander et al., 2011). They are descendants of the Saurischia and split from the Theropoda in the late Triassic period. The largest Sauropodomorpha species had a body length of more than 30 m and a body weight greater than 50 tons. However, an earlier species, the Panphagia dinosaur that lived in the late Triassic period, was not as large as later sauropodomorphs. It was omnivorous and bipedal, with a body length of 1.3 m (Martínez and Alcober, 2009). Dinosaurs include both

bipedal and quadrupedal sauropodomorphs. In the Jurassic period, the Sauropodomorpha developed very large body sizes (Wilson, 2002; Martínez and Alcober, 2009). These herbivorous dinosaurs were characterized by their long necks, and they collected food material from tall trees (Bates et al., 2016). They obtained nutrition by fermentation with the help of gut microbes (Wings and Martin, 2007; Gill et al., 2018).

Many hypotheses to explain the large body size of sauropod dinosaurs have been proposed. For example, they had air sac breathing, which allowed them to exchange oxygen in the lungs effectively, a trait found in birds, which are dinosaur descendants. Their pneumatized bones were hollow, and not only allowed the air sac breathing but also reduced the cost of locomotion (Wedel, 2003; Dumont, 2010). If this characteristic equipped them with efficient breathing, it would subsequently enhance the basal metabolic rate, resulting in rapid growth (Sander et al., 2011). Although the atmospheric oxygen concentration in the Mesozoic era was suspected to be lower than the level on contemporary Earth, a recent study concluded differently (Mills et al., 2016). Sauropod dinosaurs had long necks that allowed them to collect high-quality food plants, and they might have been able to forage more efficiently than their phytophagous competitors (Sander et al., 2011). Their ways of locomotion may also have contributed to this (Wilson and Carrano, 1999).

\* Corresponding author.

We might think that large bodied animals would be able to move (run, fly, or swim) faster than small-bodied animals. However, comparative studies have revealed that the largest animals cannot run at the fastest speeds (Hirt et al., 2017). Rather, the fastest movement speed is achieved by those that are somewhat smaller than the largest. The sauropod dinosaurs, with the large bodies, moved more slowly than predatory dinosaurs with a smaller body size. Hence, predator avoidance could be an important factor affecting the fitness of sauropod dinosaurs.

In this paper, we discuss factors, including the quality and food plants and the effect of predators, that had the strongest influence on the evolution of an extremely large body size in sauropod dinosaurs in the Mesozoic era. For animals and plants, the fitness or lifetime reproductive success depends on the timing of growth, reproduction, and mortality. Life history theory postulates that the phenotype attaining the maximum fitness is the one that is observed in the current ecosystem because it is the outcome of evolution. Analysis of observed patterns of growth and reproduction based on this idea has been very useful in clarifying key factors forming different life history traits, and is called “life history strategy” theory (Stearns, 1976, 1977). We constructed a very simple model for life history that included growth, mortality, and reproduction. The analysis of the model revealed that the most likely reason for the evolution of very large size would be the improved quality and availability of food plants in the Mesozoic era and morphological traits allowing fast juvenile growth. There are also additional benefits of predator avoidance. Considering these results, we discuss the climate and the atmospheric composition in the Mesozoic era.

## 2. A simple model of life history

Here, we consider a simple model for the growth of body size, reproduction, and mortality. The scheme of the model is illustrated in Fig. 1, and the symbols are listed in Table 1. We begin with the growth of body size for an herbivorous dinosaur. Individuals that are able to acquire more, better quality food should be able to grow faster and reach a larger size. Let  $x$  be the body size, measured in terms of the weight. It is a function of age  $a$ . The higher quality

**Table 1**

Symbols adopted in this paper.

$x(a)$	body size of juveniles as a function of age $a$
$a$	age
$P$	exponential growth rate of small immature individuals (which is mostly strongly affected by the quality of food plants)
$h$	effect of growth saturation
$a^*$	age at the onset of reproduction (age at maturity)
$x(a^*)$	adult body size
$m(a)$	fertility as a function of age $a$
$m_0$	coefficient of fertility of mature animals
$k$	dependence of fertility on the body size
$s$	dependence of fertility on $P$ (or food-plant quality)
$l(a)$	survivorship until age $a$
$u_0$	mortality due to processes other than predators
$C$	mortality due to predators
$g$	suppression effect of large body size on predation risk
$\phi$	fitness (or the lifetime reproductive success)

of food plants should make the growth rate faster. Here, we assume that body size  $x(a)$  follows a logistic equation given as follows:

$$\frac{dx}{da} = Px - hx^2. \quad (1)$$

$P$  is an exponential growth rate for small individuals, and it also affects the final size, which is  $x(\infty) = P/h$ . We believe that the most important factor enhancing  $P$  is the quality and availability of food plants. However,  $P$  may also be affected by many other factors, including the length of the season in which the animals can grow within a year and the anatomical structures that allow them to grow faster, among others.

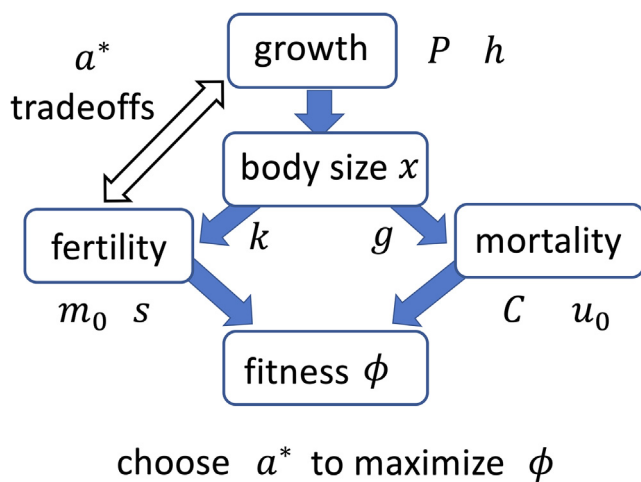
Eq. (1) indicates the growth of an individual before the onset of reproduction. At a certain age, the individual starts reproduction. It will then allocate resources to reproductive activities and the growth rate should slow down. A key idea of life history theory is tradeoff concept. If an individual starts reproduction earlier (i.e., when it is in a smaller size), the growth rate would be slower than if it starts reproduction later. In this case, the reduced growth rate represents the cost of reproduction, or the tradeoffs between growth and reproduction. Here, for simplicity, we assume that the body size of the individual stops increasing and all the resources obtained from the food, minus maintenance costs, would be used for reproduction. This pattern is the simplest representation of the tradeoffs between growth and reproduction, and it is observed in theoretical studies of the optimal growth schedule (e.g., Iwasa and Cohen, 1989).

Fertility is the number of offspring produced per year. Let  $a^*$  be the age at the onset of reproduction. Then, the fertility should be greater for an individual with a larger body size under better food conditions. Here we assume as follows:

$$m(a) = \begin{cases} 0, & 0 < a < a^* \\ m_0 x(a^*)^k P^s, & a > a^*, \end{cases} \quad (2)$$

$x(a^*)$  is the body size in the reproductive stage. The number of offspring increases in proportion to the power function of the body size (proportional to  $x(a^*)^k$  with  $0 < k < 1$ ). We adopted  $k = 1/2$  as the standard case. In addition, even if the body size of the parent is the same, more offspring should be produced if food quality is better, which indicates a power function of food-plant quality  $P^s$  (with  $s > 0$ ).

We assume that the annual mortality is the sum of the mortality caused by predators and that caused by processes other than predation, for example, accidents, infectious and noninfectious diseases, famine, and severe climate. We assume that the mortality due to predators can be reduced for individuals with larger body size, which we assume is  $C/(1 + gx(a))$ . We adopt the following formula for the instantaneous mortality:



**Fig. 1.** Processes considered in this model. There is a tradeoff between growth and fertility. No reproduction is made in the growing phase, and no growth is made in the reproductive phase. The onset of reproduction occurs at age  $a^*$ . Body size affects both fertility and mortality. The fitness  $\phi$ , or the lifetime reproductive success, is calculated from integration of these two processes. The value  $a^*$  should evolve to the one that maximizes the fitness  $\phi$ . The optimal life history may depend on parameters, such as  $P, h, m_0, s, k, u_0, C$ , and  $g$ . However, the sensitivity analysis shows that only a small number of parameters have significantly large effects (see the text).

$$u(a) = u_0 + \frac{C}{1 + gx(a)} \quad (3)$$

The first term on the right-hand side of Eq. (3) is the mortality other than predators. Here we assume that this is independent of body size  $u_0$ .

Then the probability of a new born individual to survive until age  $a$  is given as follows:

$$l(a) = \exp\left(-\int_0^a u(a')da'\right), \quad (4)$$

where the annual mortality  $u(a)$  is given by Eq. (3).

### 2.1. Fitness

In the evolution, natural selection would help to realize the phenotype that achieves the greatest fitness, or the greatest lifetime reproductive success in stationary populations. One type that had a larger number of offspring than others would increase its fraction in subsequent generations and, after many generations, the population would become composed only of the type with the greatest fitness. In the following, we search for the phenotype achieving the maximum fitness and examine the possible effects of different environmental factors in realizing the evolution of a large body size.

In the following we calculate the fitness of a phenotype with different life history traits. In particular, we note the size at the maturity  $x(a^*)$ . In our model this corresponds to the body size observed in the fossil records. We then examine what are the factors that make this larger.

The lifetime reproductive success is the fertility,  $m(a)$ , multiplied by the survivorship until age  $a$ ,  $l(a)$  and then integrated over different ages (from  $a = 0$  to  $a = \infty$ ). It is given as follows:

$$\phi = \int_0^\infty m(a)l(a)da. \quad (5)$$

Fertility  $m(a)$  and survivorship  $l(a)$  can be calculated from Eqs. (2) and (4), respectively. For simplicity, we consider asexual species in which each mother produces daughters of the same phenotype.

### 2.2. Adaptive life history

Starting reproduction very early is not very profitable because an individual starting reproduction at a young age would have a small body size at maturity, which causes relatively low fertility because the fertility increases with the body size, as indicated by Eq. (2). In contrast, starting reproduction at an old age is not profitable either, because the body size would be saturated, as indicated by Eq. (1), and the mortality is given by Eq. (3). Hence, there exists an intermediate optimal age for the onset of reproduction.

Fig. 2A illustrates the fitness for different ages for maturity  $a^*$ , the latter being in the horizontal axis. The optimal age of reproduction is indicated by the peak of the curve, which is marked by a solid circle. Three curves indicate the fitness for different values of the food-plant quality  $P$ . We can see that for each value of  $P$ , there is an optimal age of the onset of reproduction  $a^*$ . As indicated by the solid circle, the optimal age for the onset of reproduction is younger for higher  $P$ , which implies that, in an environment in which the availability of good-quality food plants is high, the dinosaur finds it better to start reproduction younger. The size at maturity  $x(a^*)$  is larger for higher  $P$  (see the caption to Fig. 2A).

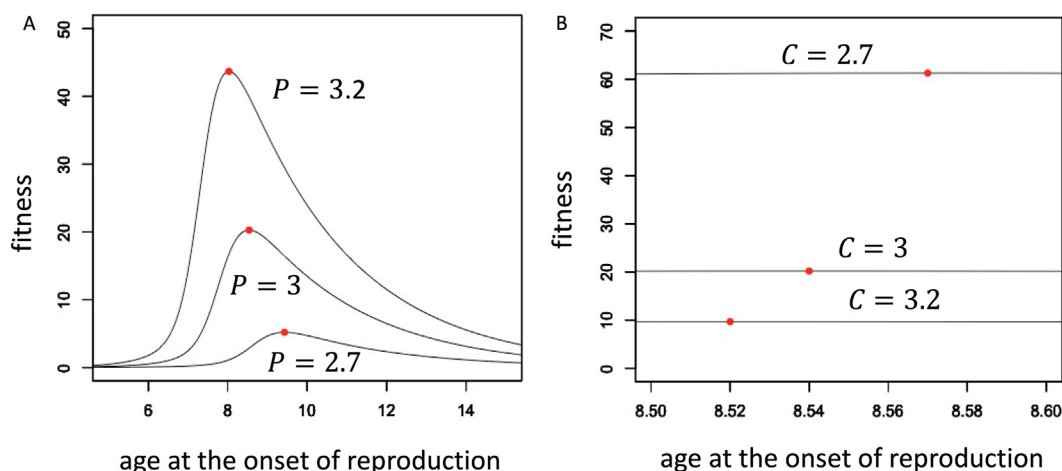
Fig. 2B illustrates that how the curve changes with  $C$ , the magnitude of mortality due to predation. We can see that the optimal age of reproduction becomes younger as  $C$  increases.

These are the results of a direct search for the optimal parameters. In this model, we can derive a mathematical equation that is satisfied by the optimal size for the onset of reproduction, as discussed in the next section. This is a more efficient way to calculate the optimal body size.

### 3. Analysis of optimal size of maturity

In this model, we can derive an equation satisfied by the optimal size at maturity.

We note that  $m(a) = 0$  for  $0 < a < a^*$ ,  $m(a) = m_0 x(a^*)^k P^s$  for  $a \geq a^*$ . Then the integrand of Eq. (5) is 0 for  $0 < a < a^*$ , and is positive for  $a \geq a^*$ . The latter is,



**Fig. 2.** Fitness for different ages for the onset of reproduction. (A) Different curves are for different values of  $P$ , the exponential growth rate for small individuals. We interpreted  $P$  as the quality and availability of food plants. The optimal age at the onset of reproduction is indicated by a solid circle for each curve. The optimal onset of reproduction becomes younger as  $P$  increases. The body size increases with  $P$  ( $x(a^*) = 1.241 \times 10^4$ ,  $a^* = 8.78$ , for  $P = 2.7$ ;  $x(a^*) = 1.402 \times 10^4$ ,  $a^* = 8.54$ , for  $P = 3$ ;  $x(a^*) = 1.506 \times 10^4$ ,  $a^* = 7.58$ , for  $P = 3.2$ ). (B) Different curves are for different values of  $C$ , the risk of mortality due to predators. As  $C$  increases the optimal onset of reproduction becomes younger. The body size decreases with  $C$  ( $x(a^*) = 1.409 \times 10^4$ ,  $a^* = 8.57$ , for  $C = 2.7$ ;  $x(a^*) = 1.401 \times 10^4$ ,  $a^* = 8.54$ , for  $C = 3$ ;  $x(a^*) = 1.395 \times 10^4$ ,  $a^* = 8.52$ , for  $C = 3.2$ ). Parameters are:  $m_0 = 300$ ,  $u_0 = 0.033$ ,  $g = 8 \times 10^{-5}$ ,  $C = 3$ ,  $P = 3$ ,  $h = 2 \times 10^{-4}$ ,  $k = 0.4$ ,  $x_0 = 1 \times 10^{-4}$ , unless specified otherwise.

$$m_0 x(a^*)^k P^s \exp\left(-\int_0^{a^*} \left(u_0 + \frac{C}{1+gx(a')}\right) da'\right) \\ \times \exp\left(-\int_{a^*}^a \left(u_0 + \frac{C}{1+gx(a')}\right) da'\right),$$

Now we note that the body size is a constant for  $a \geq a^*$ , and the integrand of the last factor of the above quantity is independent of  $a'$ . By integrating the above quantity with respect to  $a$  from  $a^*$  to infinity, we have the following equation:

$$\phi(x(a^*), a^*) = \frac{m_0 x(a^*)^k P^s}{u_0 + \frac{C}{1+gx(a^*)}} \exp\left(-\int_0^{a^*} \left(u_0 + \frac{C}{1+gx(a')}\right) da'\right). \quad (6)$$

Here, we note that  $x = x(a^*)$  is a function of the onset of reproduction  $a^*$ . Its dependence can be obtained from the logistic equation given by Eq. (1), if we replace  $a$  by  $a^*$ . The fitness Eq. (6) depends on  $a^*$  in two ways: directly on  $a^*$ , and indirectly via  $x = x(a^*)$ . As we search for the optimum  $a^*$  that achieves the maximum fitness  $\phi$ , we calculate  $d\phi/da^* = 0$ . Hence

$$\frac{d\phi}{da^*} = \frac{\partial\phi}{\partial a^*} + \frac{\partial\phi}{\partial x} \frac{dx}{da^*} = 0. \quad (7)$$

After some calculations, as explained in Appendix A, we can derive the following results: We define the following function of  $x$  for  $x > 0$ .

$$\psi(x) = (P - hx) \left\{ k + \frac{Cgx}{\left(u_0 + \frac{C}{1+gx}\right)(1+gx)^2} \right\} - \left(u_0 + \frac{C}{1+gx}\right). \quad (8)$$

The solution of  $\psi(x) = 0$  is the optimal body size  $x(a^*)$  that maximizes fitness.

Note that Eq. (8) contains  $x = x(a^*)$ , but not  $a^*$  explicitly. Hence, we can calculate the optimal body size at maturity once we specify other parameters. For the purpose of testing the theory, this is very convenient because from fossils we can tell the adult size much more easily than the age at the start of reproduction.

Note that Eq. (8) is independent of  $m_0$ , implying that the optimal adult body size does not change when fertility is multiplied by a constant that is independent of the size. Eq. (8) is also independent of parameter  $s$ , which is the power of fertility as a function of plant quality  $P$ . In contrast, it depends on  $k$ , which is the power of fertility as a function of body size  $x(a^*)$ .

Eq. (8) holds exactly. To obtain the solution, however, we need a numerical analysis.

### 3.1. Simple cases

In a few cases with some very large or very small parameters, we can derive an explicit solution of the optimal body size of the reproductive adults.

#### (i) When predation mortality is small

Considering the situation in which the fraction of mortality due to predation is much smaller than the mortality due to processes other than predation, we have  $u_0 \gg C/(1+gx)$ , which makes Eq. (8) to  $k(P - hx) = u_0$  approximately. Hence, we have the following results:

$$x = \frac{1}{h} \left(P - \frac{u_0}{k}\right), \text{ if } u_0 \gg \frac{C}{1+gx} \quad (9)$$

This implies that when predation is much smaller than other mortality factors, the size increases with juvenile growth rate  $P$  but decreases with  $u_0$  mortality factors other than predation. Other parameters related to predator abundance or predator avoidance do not affect body size at maturity.

#### (ii) When predation risk dominates the mortality

Next, we consider the opposite situation, in which the effect of predators is dominant:  $u_0 \ll C/(1+gx)$ . Then

$$\psi(x) = (P - hx) \left(k + \frac{gx}{1+gx}\right) - \frac{C}{1+gx}.$$

If, we further assume  $gx \ll 1$ , we have  $\psi(x) = (P - hx)k - C$ , which leads to

$$x = \frac{P}{h} - \frac{C}{k}. \quad (10)$$

In contrast, if we consider  $gx \gg 1$ , the effect of large size suppressing the predator risk is strong. Then we have

$$\psi(x) = (P - hx)(k + 1) - \frac{C}{gx}.$$

Then, the local maximum of the fitness is obtained from  $\psi(x) = 0$ , which becomes

$$x = \frac{1}{2h} \left( P + \sqrt{P^2 - 4hc/g(k+1)} \right) = \frac{P}{h} - \frac{C}{P(k+1)g}. \quad (11)$$

Both in Eqs. (10) and (11), the abundance of predators  $C$  has a negative effect on the optimal body size at maturity. In contrast,  $P$ , has a positive effect on the ESS body size at maturity.

### 3.2. Regression analysis of parameter dependence

Note that Eq. (8) holds exactly at the ESS value of  $x$ . In general, we need to solve Eq. (8) numerically. In this section, we report the results of the numerical sensitivity analysis.

If we knew for sure what would be a plausible range of values for all the parameters in the model, we could generate parameter values by random numbers within their plausible range, and then apply the statistical analysis to know the dependence of the key quantity of the model on parameters, and examine the sensitivity by applying multivariate analysis.

However, in modeling biological systems, we often face the situation in which we do not know what are the plausible range of parameters, but we still would like to know the general dependence of the model on a number of parameters – whether the focal quantity increases or decreases with a given parameter, or which parameter is likely to have a stronger effect than others. If we adopt the sensitivity analysis using a range of parameter values, the outcome may depend on the choice of the range of parameters we examine.

One method to overcome this problem is to choose multiple sets of standard parameter sets, and for each parameter set, we perform sensitivity analysis using multivariate analysis of the model with small deviations around the standard parameter set. By comparing the sensitivity analysis at different choices of standard parameter sets, we can know whether the sensitivity on the same parameter is positive everywhere, or it is positive for some range but can be negative in others. The sensitivity can be consistently positive or it can change the sign of sensitivity depending on the choice of the standard parameter sets. Such information (rather than exact quantitative values of the sensitivity) is important for understanding the model. An examples of the use of this method is Kurosawa and Iwasa (2005) in which the sensitivity of the period of oscillation was analyzed in a circadian oscillation model in order to study the mechanisms for temperature compensation of circadian clock. Another example is Uriu et al. (2009) in which the gradient of the period of oscillation of a segmentation clock gene *her* was analyzed to know the mechanisms for its travelling wave in the presomitic mesoderm of zebrafish embryo.



We first chose a set of standard parameter values and generated a number of parameter combinations that were close to but slightly different from the standard values. For each combination of parameters, we calculated the ESS size at maturity. Then, we performed a multivariate analysis of the data and extracted the tendency of how the size at maturity changes depending on each parameter.

The results of the regression analysis may depend on the choice of the standard set of parameters. According to the discussion in the previous section, there are different formulas that differ in the relative magnitude of the mortality due to predators and the mortality due to processes other than predators. In the following, we chose four cases in which the standard values of the parameters were selected to be deliberately different.

#### Case 1 Two mortalities are similar in magnitude

We chose the following set of parameters:

$$m_0 = 1, u_0 = 0.03333, g = 6 \times 10^{-3}, C = 1, P = 2, \\ h = 2 \times 10^{-4}, k = 0.5$$

The largest body size of an animal that never reproduces is  $P/h = 1 \times 10^4$  kg, which is 10 tons. Suppose that the individual starts reproduction when it reaches the maximum size. Then, it has a size at maturity of 5 tons. We can see that the mortality due to processes other than predators is  $u_0 = 0.03333$ , and mortality due to predators for this adult individual is  $C/(1 + gx) = 0.03226$ , so the two values are similar in magnitude. The mean longevity of adults is approximately 15 years.

Using this choice of standard parameter values, we examined the ESS size of maturity with the parameters multiplied by factors 0.8, 0.9, 1.0, 1.1, and 1.2 for each of the following five parameters:  $m_0$ ,  $u_0$ ,  $g$ ,  $C$ , and  $P$ . We fixed  $k = 0.5$  and  $h = 2 \times 10^{-4}$ . Based on these  $5^5 = 3125$  cases, we have the following regression formula:

$$\ln x = 8.379 + 1.035 \ln P - 0.028 \ln u_0 - 0.002 \ln C + 0.003 \ln g. \quad (12)$$

It was derived using the software in R language software.

This implies that the size at maturity is most strongly affected by  $P$ , juvenile growth rate (which strongly reflects the food-plant quality), and is also negatively affected by  $u_0$  the mortality due to other than predators. The regression coefficient of  $\ln m_0$  was zero, in this case and in all the regression analyses below.

#### Case 2 The mortality due to predators is small.

We examined the situation in which the mortality due to predators was much weaker than the other mortality factors. We chose the standard parameter sets where  $g = 2 \times 10^{-2}$ ,  $C = 0.2$ , but others were the same as in Case 1. Then  $C/(1 + gx) = 0.00392$ , which is much smaller than  $u_0 = 0.03333$ . Using the same methods for Case 1, we have the following result of the regression analysis:

$$\ln x = 8.341 + 1.034 \ln P - 0.034 \ln u_0 - 0.001 \ln C + 0.001 \ln g. \quad (13)$$

The dependence on each parameter is similar to that in case 1.

#### Case 3 Mortality due to predators is dominant.

We then examined the situation in which the mortality due to predators is greater in magnitude than the mortality due to processes other than predation. We chose

$g = 2 \times 10^{-3}$ ,  $C = 3$ , which makes  $C/(1 + gx) = 0.2727$ , which is 8.2 times greater than  $u_0$ . Then the regression line is

$$\ln x = 8.695 + 1.139 \ln P - 0.022 \ln u_0 - 0.057 \ln C + 0.058 \ln g. \quad (14)$$

This also has a similar tendency, but there are some effects of predator-related parameters. Note that a higher risk of predation

tends to reduce the size at maturity rather than increase it. Again, the effect of juvenile growth rate  $P$  was the strongest.

#### Case 4

We note from the formula Eq. (9) in the last section, which suggests that  $\ln x$  might have a larger regression coefficient on  $\ln P$  if  $u_0/k$  is as large as  $P$ . We chose  $u_0 = 0.1$ , and  $k = 0.1$ . The other parameters are the same as those in Case 1. Then we have the following regression:

$$\ln x = 8.452 + 1.026 \ln P - 0.013 \ln u_0 - 0.006 \ln C + 0.006 \ln g. \quad (15)$$

We can see that the mature body size is most strongly dependent on the parameter  $P$ , although it may also depend on mortalities (i.e.,  $C$  and  $u_0$ ) in a negative manner.

In all four cases, the regression lines were similar: the adult body size  $x(a^*)$  depended most strongly on  $P$ , but weakly on mortality parameters.

## 4. Discussion

The question of why the sauropod dinosaurs in the Mesozoic era evolved very large body sizes has been studied extensively in paleobiology using diverse methods, including bone anatomy, tooth morphology, foraging behavior, mode of digestion, food availability, parental care, and other social interactions (Sander et al., 2011). In this paper, we attempted to answer the same question in the light of life history theory. The key assumption of the theory is a tradeoff between growth and reproduction (Stearns, 1988). Once the reproduction starts, the individual allocates fewer resources to growth, and its size increases more slowly than if reproduction had started later. In the current study, we simplified this tradeoff and assumed that, after the onset of reproduction, body size growth stops and the adult body size remains the same afterwards. We assumed a simple model for fertility and mortality, and asked what life history phenotype would evolve. This is a typical model in life history theory (Stearns, 1976, 1977).

In this study we adopted  $\phi$ , given by Eq. (5), as a criterion for evolutionary stability. It is the lifetime reproductive success of a newborn individual. The use of this criterion is justified by the population genetics theory as follows. In a population with overlapping generations, the invasibility of a rare allele modifying life history traits can be judged in terms of its Malthusian parameter (see Charlesworth, 1973), which concludes that the phenotype that achieves the maximum Malthusian parameter would be the ESS. This criterion is mathematically equivalent to the maximization of reproductive value for a newborn individual, which is the same as  $\phi$ , except that the reproductive success made in old age needs to be discounted (Taylor et al., 1974; León, 1976). Since we search for the ESS life history for a species in the stationary state (rather than an exponentially growing population), this justifies the use of  $\phi$  as the criterion for the evolutionarily stable phenotype.

Life history theory has explained the evolution of diverse phenotypes of growth, reproduction, and other life history traits. It succeeded in clarifying the conditions for annual versus perennial life forms to evolve (Gadgil and Bossert, 1970; Iwasa and Cohen, 1989), the shoot/root balance of a growing plant (Iwasa and Roughgarden, 1984), and the males of very small size (dwarf males) of marine invertebrates (Yamaguchi et al., 2013). In the present study we adopted it to determine the size at the onset of reproduction for sauropod dinosaurs.

### 4.1. Processes affecting adult body size

The mathematical analysis of the model in the present study revealed that the optimal body size for adults  $x(a^*)$  is given by

the solution of Eq. (8). Sensitivity analysis revealed that parameter  $P$  always has a strongly positive effect on adult body size.  $P$  is defined as the speed of exponential growth of the body size for young animals. We interpreted this as the quality of food plants available in the environment. However, any other processes or factors that improve the speed of size growth would contribute to  $P$  (for possible anatomical or morphological traits, see below).

We note that it is not obvious that increasing the growing speed (higher  $P$ ) results in the evolution of a larger body size at maturity to evolve. We might think that the enhanced  $P$  should always increase the size at maturity in the optimal life history. This is not the case, as demonstrated in the following counter example. Suppose fertility rate is a step function of the body size:  $m = m_0 H_+[x - x_m] P^s$ , where  $H_+[\cdot]$  is Heaviside function ( $H_+[x] = 1$ , if  $x \geq 0$ ; but  $H_+[x] = 0$ , if  $x < 0$ ). Then, the optimal size for maturity is fixed ( $x(a^*) = x_m$ ), independent of  $P$ . If there is a fixed size for maturity, a fast-growing animal (with a large  $P$ ) could reproduce at a younger age than a slow-growing one (with a small  $P$ ) in order to avoid mortality before maturity, but the optimal strategy is to make the maturity size independent of the speed of juvenile growth. Alternatively, in a different setting, the age of maturity could remain unchanged and the enhanced growth speed  $P$  could result in a larger adult body size, because fertility increases with body size as indicated in Eq. (2), if  $k$  is positive.

Under the assumptions we adopted in this paper, the evolutionary adaptation for a large  $P$  results in a larger maturity size as well as an earlier onset of reproduction (see Fig. 2A). This is not a direct outcome of increasing  $P$ , but it is the result of the optimal choice of the onset of reproduction, and was revealed by analysis of the model.

In the main text, we analyzed the model by changing  $P$  with  $h$  fixed. We also analyzed the case in which both  $P$  and  $h$  increase with their ratio fixed, implying that the growth rate of small individuals becomes faster but the asymptotic value of the body size if they would stay immature is fixed. The results showed that the optimal size of the onset of reproduction again increased with  $P$  with the sensitivity larger than the values on other parameters.

A counter-intuitive result of the sensitivity analysis was that the mortality due to predators  $C$  was not effective in enhancing the adult body size. We hypothesized that a strong mortality due to predators would favor a larger body size at maturity because a larger body size might allow the animal to escape predation risk. However, the results were sometimes opposite – a stronger predation risk reduced the optimal adult body size (see Fig. 2B). This is because there is an alternative effect: whatever the process causing it, enhanced mortality tends to make an early maturation more profitable, and the presence of a higher mortality tends to encourage an early onset of reproduction. Size-independent mortality,  $u_0$ , certainly had an effect on reducing the reproductive size in the ESS, and the size-dependent mortality factor (due to predators) also had a similar effect. The predator risk showed both of these two tendencies, which worked in an opposite way to each other. According to our analysis, the effect of reducing the mature size turned out to be stronger than the opposite effect.

From these results, we conclude that the growth rate for small animals  $P$  is the most likely factor that explains the large body size at maturity.

#### 4.2. Fast growth rate of juveniles for sauropods in the Mesozoic

There is supporting evidence that the growth rate for small individuals is strongly correlated with the size at maturity in paleontology (Erickson et al., 2001). Importantly, some sauropod dinosaurs became smaller in size on islands, where the growth rate in the small individuals slowed down (Sander et al., 2006), which

suggests that a downward change in adult body size  $x(a^*)$  occurs when the growth rate  $P$  is reduced.

The most plausible explanation for the increase of  $P$  in the Mesozoic era is the improved availability of good quality food plants because sauropod dinosaurs are herbivorous (Sander et al., 2011). An evidence supporting that they ate soft plant tissue is provided by *Nigersaurus taqueti*, the early Cretaceous dinosaur. Morphological analysis of skull bones, the fragile bones, tooth replacement patterns, and light skull construction indicate that *Nigersaurus* was a ground-level herbivore that gathered and sliced soft vegetation, the culmination of a low-browsing strategy (Sereno et al., 2007).

In addition to the higher quality of the food plant, a longer season per year in which food plants were available might contribute to an increase in  $P$ . Air sac breathing and other physiological mechanisms allowing more efficient use of energy might also contribute to improvement in  $P$ .

Based on the distribution of distinctive sediments, fossils and oxygen isotope data, the climate of the Mesozoic world was appreciably more equitable than that of today with no polar ice caps (Hallam, 1985). Green-house effects are an obvious cause of the high temperature. In fact, some studies estimate that the  $\text{CO}_2$  level in the Mesozoic era was much higher than that in the contemporary world (Hay, 2011; Hay and Floegel, 2012). At the Triassic-Jurassic boundary, many species went extinct. This has attracted much research, which concluded that strong volcanic activity quadrupled atmospheric  $\text{CO}_2$  level, resulting in an air temperature enhanced by 3 to 6°C (McElwain et al., 1999; Huynh and Poulsen, 2005; Mander et al., 2010). In the Cretaceous period, the temperature was high and the world was covered with grasses. Based on the reports of forest fires, the oxygen concentration was also high (Bond and Scott, 2010). Although previous literature had suggested that atmospheric oxygen level was lower in the Mesozoic era than on the present-day Earth, recent analysis with additional data and computation of the climate model has concluded that the atmospheric oxygen concentration was also higher than or similar to the present level (Mills et al., 2016). These estimates seem to support the possibility of greater food availability and improved food-plant quality in the Mesozoic era, although there are many unknown factors and potential errors associated with the estimates. This argument may also be supported by the presence of giant herbivorous birds in genus *Gastornis* in the Early Tertiary (after the extinction of dinosaurs), in which the climate was warm (Angst et al., 2014). However, these giant birds went extinct in the latter half of the Cenozoic era, when the climate became colder.

On the other hand, there are morphological, anatomical, and behavioral factors relating to sauropod dinosaurs that might also contribute to the enhancement of growth rate  $P$ . For example, the long neck of sauropods would help them perform more efficient and selective foraging of good-quality food (Sander et al., 2011). In addition, air-sac breathing, common to bird species, allows for more efficient use of energy and higher activity than mammals and other reptiles (Sander et al., 2011), as long as atmospheric oxygen concentration is not much lower than on the earth today (Mills et al., 2016).

We would like to emphasize that the life history theory tells us that whatever factors helped to enhance  $P$  were likely to contribute to the evolution of the gigantic body size of sauropod dinosaurs.

Finally, we would like to note that neither the approach nor the model in this paper is specific to sauropod dinosaurs. The argument is based on a general theory of life history evolution, applied to the question of why the sauropod dinosaurs become very big in the adult size. The question has not been asked before using the explicit mathematical theory of life-history strategy. We believe that an analysis applied to a biological phenomenon using the gen-

eral well-established theoretical framework is an important contribution to the science, because it has never been done before.

### CRedit authorship contribution statement

**Yuki Kanayama:** Investigation, Software, Validation, Visualization. **Yoh Iwasa:** Conceptualization, Formal analysis, Investigation, Methodology, Project administration, Software, Supervision, Validation, Writing.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Appendix A

On the derivation formulae

We start from the formula for the fitness given by Eq. (6), which is written as

$$\phi(x, a^*) = \frac{m_0 x^k P^s}{u_0 + \frac{C}{1+gx}} \exp\left(-\int_0^{a^*} \left(u_0 + \frac{C}{1+gx(a')}\right) da'\right). \quad (\text{A.1})$$

We replaced  $x(a^*)$  by  $x$ . It is the size at maturity. Thanks to the simplifying assumption we adopted, the adult body size remains unchanged after the onset of reproduction. Note that the integral within the exponential term contains quantity  $x(a')$ , which should be regarded as a function of age  $a'$  given by Eq. (1). These two should be distinguished. The fitness is a function of two variables:  $x$  and  $a^*$ .

We attempt to search for the optimal age of the onset of reproduction  $a^*$ . We note that the fitness given by Eq. (A.1) depends both directly on  $a^*$ , through the range of integral included in the exponential term and also indirectly via changing  $x(a^*)$ . If  $a^*$  becomes larger, the juvenile period becomes longer and the body size of adults larger. This effect can be given by Eq. (1). On the other hand, a larger  $a^*$  enhances the fraction of individuals killed before the onset of reproduction. These two are represented by the indirect and the direct dependence on  $a^*$ . We can calculate this by

$$\frac{d}{da^*} \phi(x, a^*) = \frac{\partial}{\partial a^*} \phi(x, a^*) + \frac{\partial}{\partial x} \phi(x, a^*) \cdot \frac{dx(a^*)}{da^*}, \quad (\text{A.2})$$

where the first term and the second term indicate the direct and indirect effects, respectively. From Eq. (A.1), we calculate Eq. (A.2) as follows

$$\begin{aligned} & \frac{m_0 x^k P^s}{u_0 + \frac{C}{1+gx}} \frac{\partial}{\partial a^*} \left\{ \exp\left(-\int_0^{a^*} \left(u_0 + \frac{C}{1+gx(a')}\right) da'\right) \right\} \\ & + \frac{\partial}{\partial x} \left\{ \frac{m_0 x^k P^s}{u_0 + \frac{C}{1+gx}} \exp\left(-\int_0^{a^*} \left(u_0 + \frac{C}{1+gx(a')}\right) da'\right) \right\} \frac{dx}{da^*} = 0. \end{aligned} \quad (\text{A.3})$$

On the other hand, from Eq. (1), we have

$$\frac{dx(a^*)}{da^*} = Px - hx^2. \quad (\text{A.4})$$

Hence, Eq. (A.3) becomes:

$$\frac{m_0 x^k P^s}{u_0 + \frac{C}{1+gx}} (-1) \left(u_0 + \frac{C}{1+gx(a^*)}\right) \exp\left(-\int_0^{a^*} \left(u_0 + \frac{C}{1+gx(a')}\right) da'\right)$$

$$+ \frac{\partial}{\partial x} \left\{ \frac{m_0 x^k P^s}{u_0 + \frac{C}{1+gx}} \right\} \exp\left(-\int_0^{a^*} \left(u_0 + \frac{C}{1+gx(a')}\right) da'\right) \cdot (Px - hx^2) = 0$$

which can be rewritten as

$$\left(u_0 + \frac{C}{1+gx(a^*)}\right) = \frac{\partial}{\partial x} \ln \left\{ \frac{m_0 x^k P^s}{u_0 + \frac{C}{1+gx}} \right\} \cdot (Px - hx^2). \quad (\text{A.5})$$

The first factor in the right hand side of Eq. (A.5) can be rewritten as

$$\begin{aligned} \frac{\partial}{\partial x} \ln \left\{ \frac{m_0 x^k P^s}{u_0 + \frac{C}{1+gx}} \right\} &= \frac{\partial}{\partial x} \ln \{x^k\} - \frac{\partial}{\partial x} \ln \left\{ u_0 + \frac{C}{1+gx} \right\} \\ &= \frac{k}{x} - \frac{1}{u_0 + \frac{C}{1+gx}} \frac{(-1)gC}{(1+gx)^2} \end{aligned}$$

Hence, Eq. (A.5) becomes

$$\left(u_0 + \frac{C}{1+gx}\right) = \left(k + \frac{1}{u_0 + \frac{C}{1+gx}} \frac{gCx}{(1+gx)^2}\right) \cdot (P - hx). \quad (\text{A.6})$$

We define the following function as  $\psi(x)$ :

$$\begin{aligned} \psi(x) &= (P - hx) \left\{ k + \frac{Cgx}{\left(u_0 + \frac{C}{1+gx}\right)(1+gx)^2} \right\} \\ &\quad - \left(u_0 + \frac{C}{1+gx}\right). \end{aligned} \quad (\text{A.7})$$

Then the solution of  $\psi(x) = 0$  is equivalent to the solution of  $x = x(a^*)$ . Eq. (A.7) is the same as Eq. (8) in the text.

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