The many parallels between organismal growth and shows viewership

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I worked in mathematical biology and ecology for many years, and I have found that some mathematical and statistical tools that have been developed in mathematical biology could be used for better understanding and predicting the popularity of movies and TV shows.

Streaming services typically keep their data on viewership secret and no tests on data will be shown here. I will use the terms movies, shows, and content mostly interchangeably throughout the article.

Nobody knows anything

Studios with straight-to-theater business models and streaming services providing live or on-demand content, either subscription- (Hulu, Amazon Video, Apple, Disney, and others you know about) or advertisement-based (Tubi, Pluto TV), increase their revenues by increasing either the number of tickets that theaters sell, the number of paying members of the streaming service, or the money they can collect from advertisers, which we can assume is proportional to the number of viewers of shows. It is also well known that the probability of users paying recurrently for an on-demand streaming service increases with time spent watching its offerings. The same has been found across social media: the probability of churning (i.e., leaving the service) decreases with time spent on the platform.

For people involved in the show business, it has been historically challenging to make accurate predictions of the success of movies and TV shows. William Goldman – the author of the screenplays of "*Butch Cassidy and the Sundance Kid*", and of "*All the President's Men*" – wrote in his 1983 autobiography "*Adventures in the Screen Trade*":

- NOBODY KNOWS ANYTHING -

Not one person in the entire motion picture field knows for a certainty what's going to work. Every time out it's a guess and, if you're lucky, an educated one. They don't know when the movie is finished: B. J. Thomas's people, after the first sneak of Butch, were upset about their client's getting involved with the song "Raindrops Keep Fallin' on My Head." One of them was heard to say, more than once, "B. J. really hurt himself with this one."

The initial preview of Star! was such a success that Richard Zanuck cancelled any further previews and sent a wire to his father, Darryl, that said, "We're home. Better than Sound of Music. "The Sound of Music was then the most popular movie in history, and Star! went on to become the Edsel of 20th CenturyFox: No matter how they readvertised it or changed the logo or the title, no one came. And Richard Zanuck has as keen a mind about commercial films as anyone.

They don't know when the movie is starting to shoot either.

David Brown, Zanuck's partner, has said, "We didn't know whether Jaws would work, but we didn't have any doubts about The Island. It had to be a smash. Everything worked. The screenplay worked. Every actor we sent it to said yes. I didn't know until a few days after we opened and I was in a bookstore and I ran into Lew Wasserman and said 'How're we doing? and he said, 'David, they don't want to see the picture.' "

They don't want to see the picture – maybe the most chilling phrase in the industry.

With the invention and adoption of new statistical and machine learning algorithms and models, and the availability of much more computational power and data that anyone twenty years ago would have thought possible to use or collect, things have changed, and we now know much more about the determinants or early indicators of success of movies and TV shows than we did in the past. For instance, it was found by many professionals working in the entertainment space that some intrinsic properties of the piece of content (director and production team, actors, producer, studio, and budget, among others), along some proxies of interest from the general public (e.g., the number of people talking about the movie on social media), could provide more accurate predictions of shows popularity than hunches of old-timers or asking focus groups whether the movie will succeed or bomb.

The development of an understanding and prediction of cinemagoers or subscribers' viewing patterns nowadays is, or should be, one of the crucial tasks of the studios and streaming services' science teams. It allows making better-informed early decisions on renewals, tailoring new content around the ever-evolving taste of users, and more effectively allocating marketing money.

Models of popularity and growth

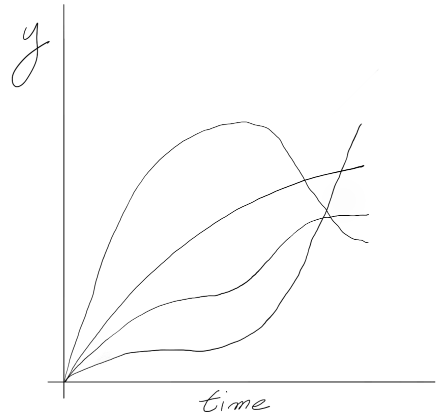
Models of show popularity predict how many people will watch those shows over some time horizon; usually, over the first weekend, first month, or over their entire lifetime. Some models make predictions far in advance of the movie or show's premiere (say, at the pre-production stage, after production has gotten the ok from the studio, or a few months before launch – where launch date is when the show comes up on the streaming service or in theaters), others start delivering predictions a few days after launch. Here, I will focus on models predicting the performance of the show after it has been launched in theaters or on streaming services (although most of the insights can be readily extended to predictions delivered at other stages of the show's lifetime).

When we develop predictive models, we always face trade-offs between complexity of the model, interpretability of model parameters, ease of parameter estimation, and accuracy of predictions. For example, more complex models either in number of predictors, in how the predictors enter the model or in the algorithm used to estimate model parameters, may provide higher accuracy (here, accuracy is the ability of the model to both explains observed data and make correct predictions) at the expense of ease of parameter estimation, and interpretability of model predictors and model parameters (i.e., to what degree the model allows for understanding mechanisms and processes), or costs of maintaining data pipelines. To give an example of the feasibility of maintaining data pipelines or using certain predictors in models, production or marketing budgets might be highly predictive of viewership or box office revenue of shows and movies, but they might be available or reliably estimated only for some of them.

After the show is launched in movie theaters or on streaming services, content science teams know how many cinemagoers, subscribers or registered members have cumulatively watched the title since day one, i.e., the viewership of the show up to a certain day. In theory, trajectories of cumulative viewership over time might take on a variety of different forms, which also depend on the measure of viewership that is used. For instance, we could use straight numbers, which cannot go down over time, or fraction of total subscribers or registered users, whose trajectories can go down over time because subscribers and registered users can increase over time, while the cumulative number of viewers of the show can stall.

Therefore, the trajectories can be flat or almost flat (that is, showing little change over time), increase or decrease over time, and be linear or non-linear in shape. All the trajectories shown in the figure below are theoretically possible when using fraction of members as measure of viewership, although the trajectory monotonically increasing and then slowing down at later stages is what we empirically observe with shows and movies.

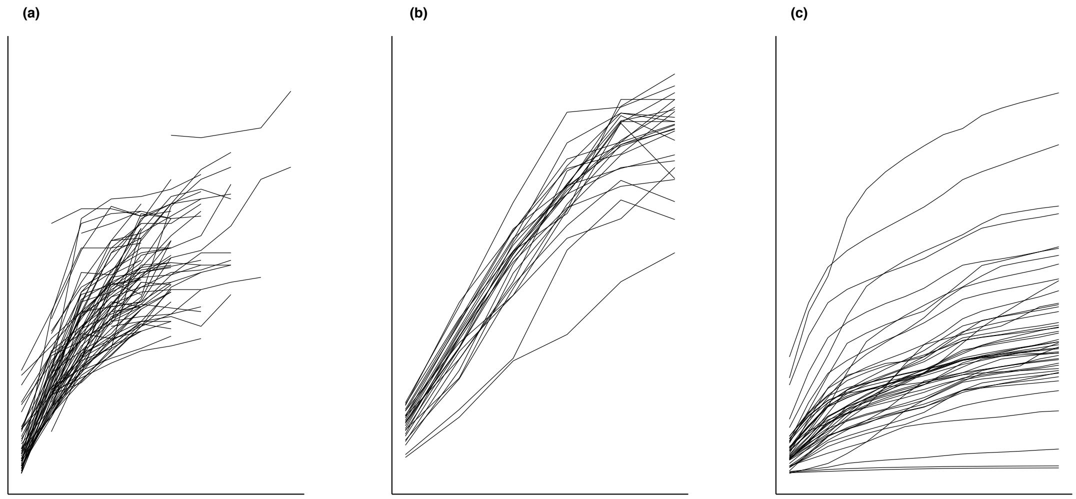
These trajectories of viewership over time take the name of time trends, growth curves or growth trajectories, or latent trajectories. I'll use the terms growth curves or growth trajectories throughout this article.



When problem solving, scientists often try to take advantage of models, solutions, and insights that may have originated in other fields or contexts. In particular, thinking in terms of similarities with more mature fields, where maturity is often synonymous with more mathematized — that is, theories are stated in mathematical terms —, can sharpen thinking and reasoning, and take advantage of frameworks, hypotheses, methods, theories, and software developed in those fields. Plus, hopefully, help not repeat the same mistakes that have been made long ago in those disciplines. At the same time, we need to be aware that it is possible to be side-tracked by forced analogies or by the use of tractable, but ultimately unrealistic, models.

Let's see how mathematical biology enters the equation when trying to predict shows viewership by having a look at the three-panel figure below.

Since time is on the x-axis and some dimension is on the y-axis, the lines are the empirical growth trajectories of some "entities" — let's call them individuals — that have been measured repeatedly over time.



The growth trajectories in the 3 panels are similar: the dimension on the y axis is almost always increasing for each individual and their growth tends to plateau toward the end of the curve; growth is heterogeneous among individuals, although the shapes of the individual trajectories are similar, that is they monotonically increase and then tend to plateau; then, who is on top at the beginning, tends to be on top at the end. What might be surprising is that (a) shows the growth in size (length) of freshwater fish (marble trout) living in a Slovenian stream throughout their lifetime (I studied marble trout for many years), (b) the growth in weight of Alaskan seabird chicks (black-legged kittiwake) before fledgling (I studied kittiwakes for some years), and (c) a random collection of normalized trajectories of tickets sold and movie viewership.

Since the growth trajectories of fish size, bird weight, and viewership are similar, it follows that similar mathematical models might be used to predict growth in size and weight of organisms or in viewership of movies, and to understand the causes of its variation among organisms or movies. That is, we might be able to describe and model the growth of viewership or movie tickets sold through the lens of models used in ecology and evolutionary biology, which are mature scientific fields with a long history of use of mathematics to express theories and state testable hypotheses.

Here, I will see how the use a hierarchical formulation of a growth function that has been very popular in the life sciences to describe the growth of organisms can provide accurate predictions of the growth of viewership and tickets sold over time, and help us better understand the dynamics of movie watching.

Parallels between modeling of growth of vertebrates and of movie viewership

Variation

Understanding the causes of within- and among-population variation in vital rates of organisms, such as their probability of survival, growth, and reproduction, life histories (that is, how vital rates vary together and the trade-offs among them), and population dynamics (how the number of individuals in a population changes over time) is a central topic in ecology and evolutionary biology.

Within populations, organisms often differ in the ability to acquire resources and in their life-history strategies. For example, speed of body growth and probability of survival are often negatively correlated, and organism may "decide" to grow faster or slower depending on the physical environment, food, and other biological and environmental constraints or opportunities. I wrote "decide" in quotes because those are not the conscious decisions that we associate with "human choice", but physiological responses that are induced by environmental cues.

Most importantly, organisms vastly differ in their contributions to the next generation: across many species, it is common that only a small fraction of potential parents will have offspring, and some parents will have many. We can easily find a parallel with entertainment here by noticing that only some tv shows have subsequent seasons, and a few of those have many subsequent seasons.

In the natural world, variation is everywhere. Some organisms grow faster, some have more offspring, some live a much longer life than others. In entertainment, on-the-surface very similar shows can reach vastly different popularity. Finding out which traits are strongly associated with "winners" is bound to be a never-ending open question in ecology and evolutionary biology, as well as in entertainment.

Models of growth

Mathematical models have been prominent in the disciplines of ecology and evolutionary biology for many decades. Among vital rates, body growth is probably the one that has historically received the most attention from ecologists, in part because it tends to rapidly adapt to environmental conditions and can be an early indicator of a change in the environment

Body growth is not a single trait but the outcome of a complex suite of behavioral, morphological, and physiological processes. In general, we may say that growth is a process and size-at-age, weight-at-age, and cumulative-viewership-at-day or cumulative-tickets-sold-at-day are the realizations of the growth process.

For studying the growth of organisms and of viewership, the identification of a functional form that can reasonably approximate the empirical trajectories is a crucial first step in the development of a useful growth model. As we have seen before in the three-panel figure, the similarity of growth trajectories suggests that we might use similar models to understand and predict the growth of organisms, and of cumulative viewership and theater tickets sold after launch.

Several functions have been used to model the growth trajectories of organisms whose size or weight first rapidly increases and then tends to plateau: historically, for vertebrates the most widely used have been the Logistic, the Gompertz, and the von Bertalanffy growth functions. In ecology and fishery (the field that investigates the environmental and biological factors affecting catch and stock sustainability) studies, the von Bertalanffy growth function has been by far the most popular growth function.

The von Bertalanffy growth function

*If you are not mathematically inclined, you can skip the more mathematically formal section below and move to the "**Biological insights can inform the analysis of shows performance**" section.*

Ludwig von Bertalanffy, the formidable scientist and philosopher whose seminal contributions to the General Theory of Systems have motivated much research in biology, sociology, psychology and many other fields, hypothesized (the first related publication is of the 1930s) that the growth of an organism results from a dynamic balance between anabolic and catabolic processes.

If $W(t)$ denotes mass at time t, the von Bertalanffy assumption is that anabolic factors are proportional to surface area, which scales as $W(t)^{\frac{2}{3}}$, and that catabolic factors are proportional to mass. If a and b denote these scaling parameters for anabolism and catabolism, the rate of change of mass is:

$$\frac{dW}{dt} = aW(t)^{\frac{2}{3}} - bW(t)$$

If we then assume that mass and size, $L(t)$, are related by $W(t) = \rho L(t)^3$ with ρ corresponding to density (although the exponent can take values different from 3 – its value can be taken as the estimate of the slope of weight-length regression in the log-log space), then calculus shows that:

$$\frac{dL}{dt} = q - kL$$

where $q = \frac{a}{3\rho}$ and $k = \frac{b}{3\rho}$. Setting $L = \frac{q}{k}$ to be the asymptotic size L_∞ (that is, the size obtained in the limit of infinite time), the most popular form of the solution for size/length is:

$$L(t) = L_\infty\left(1 - e^{-k(t-t_0)}\right) + \varepsilon_L$$

where t_0 is the hypothetical age at which size is equal to 0 (the parameter t_0 rarely has a biological meaning — it is more to be intended as a curve-fitting parameter) and ε_L is the error (which, in other formulations, is assumed to be log-normal). For weight W at time t, we have:

$$W(t) = (W_\infty(1 - e^{-k(t-t_0)}))^3 + \varepsilon_W$$

with a definition of parameters similar to the above[note1].

In the vast majority of applications of growth models in the life sciences, parameters are estimated at the population level, and interpreted as those of an average individual in the population. In fish biology, von Bertalanffy growth function's k and L_∞ (estimated on data often assumed to be cross-sectional) and adult mortality rates are commonly used synthetic descriptors of the life-history strategies of fish populations.

However, the approach of pooling together all data to estimate the average growth curve using standard non-linear regression methods provides biased parameter estimates, and does not take into account the large variation in growth often observed in organisms living in the same population. This greatly limits the breadth and scope of applications of the "average" growth functions in ecology, evolutionary biology, and fishery science. After all, many have seen fish living in the same population and of similar age with very different — sometimes hugely different! — sizes[note2]. And for most investigations, we are interested in each individual — and not population-average — growth trajectory.

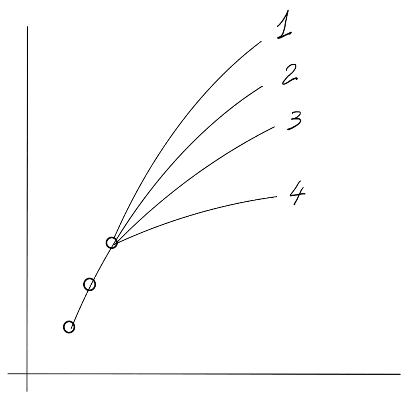
Individual variation in growth can arise from a variety of processes. Individuals within a population vary in their metabolic rates, aggressiveness, territoriality, and life-history strategies (i.e., partition of energy to competing functions, such as growth, storage, reproduction and maintenance), which largely determine their foraging dynamics and access to resources. Then, especially for territorial species, the occupation of more profitable space provides the opportunity to access higher-quality and more abundant resources.

The estimation of individual or group variation in growth requires longitudinal data, that is multiple observations over time coming from the same organism (or from the same piece of screen content in the case of entertainment), advanced statistical modeling, and can be computationally difficult because parameters typically enter growth models non-linearly. The collection of longitudinal data is challenging when studying species, but easier when studying the performance of shows: especially for long-lived and elusive organisms (e.g., fish), the collection of longitudinal data can take many years and much effort (individuals are usually tagged with a unique ID identifier), when at all possible. As marine scientist John Sheperd said: "Managing fisheries is hard: it's like managing a forest, in which the trees are invisible and keep moving around", but longitudinal data of movies and shows viewership are always available for their producers, creators or distributors.

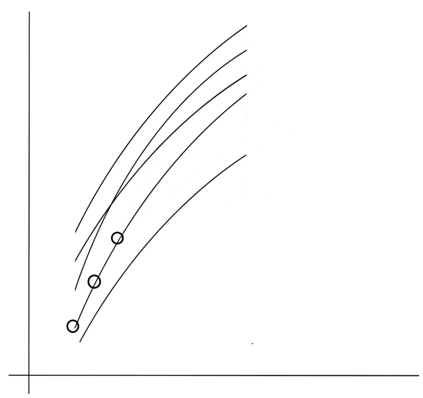
Hierarchical models

For model development and model fitting, data for a particular individual (fish, bird, show) whose trajectory is incomplete are unlikely to be adequate for the estimation of parameters of the growth model for that data-poor individual. Additional information may be needed, such as data of other individuals thought to be similar (i.e., the concept of ''borrowing strength''). Models in which all members in a group influence the estimate of each effect are alternatively called hierarchical, random-effects, multi-level, or mixed-effects models.

Random effects are assumed to be realizations of a stochastic process. The assumption of common statistical distribution induces a dependence, which means that the estimate of the random effect pertaining to an individual is influenced by the estimates of random effects for all other individuals relating to the same factor or group (say, for an organism year-of-birth, sex, location, or it can be more simply the whole population). This limits the over-interpretation of processes that may be the result of small sample size, as those realizations will be pulled toward the mean of the group ("shrinkage"), and the realizations that are strongly supported by data contribute more information to the statistical distribution of the effects. Modeling and estimating random effects also address the lack of independence between repeated measurements of the same individuals.



With standard non-linear methods of parameter estimation, parameter estimates and prediction of unobserved data would be based only on data collected for that individual. With only a few data points, both parameter estimates and the prediction of unobserved data are uncertain.



By using a hierarchical model, parameter estimates and prediction of unobserved data depend on data collected for the specific individual and on the trajectories of similar individuals that were included in the data set.

Although parameter estimation in hierarchical models can still require considerable work, the many — in some cases groundbreaking — advances in theories, algorithms, and software of the last few years have made the development of hierarchical models and the estimation of their parameters much easier than they used to be.

Hierarchical formulations of the von Bertalanffy growth function allow taking into account heterogeneity in growth, addressing the lack of independence between repeated measurements of the same individuals and of individuals in homogeneous groups, and modeling individual trajectories. For instance, in a hierarchical formulation of the von Bertalanffy growth function, asymptotic size L_∞ for individual i in group j (e.g., for sexually dimorphic species sex can be one of such groups — think elephant seals, in which males are much bigger than females) can be modeled as:

$$L_{\infty,i,j} = \alpha + \beta_j j + \gamma z + \sigma_v v_{ij} + \varepsilon_{L,i,j}$$

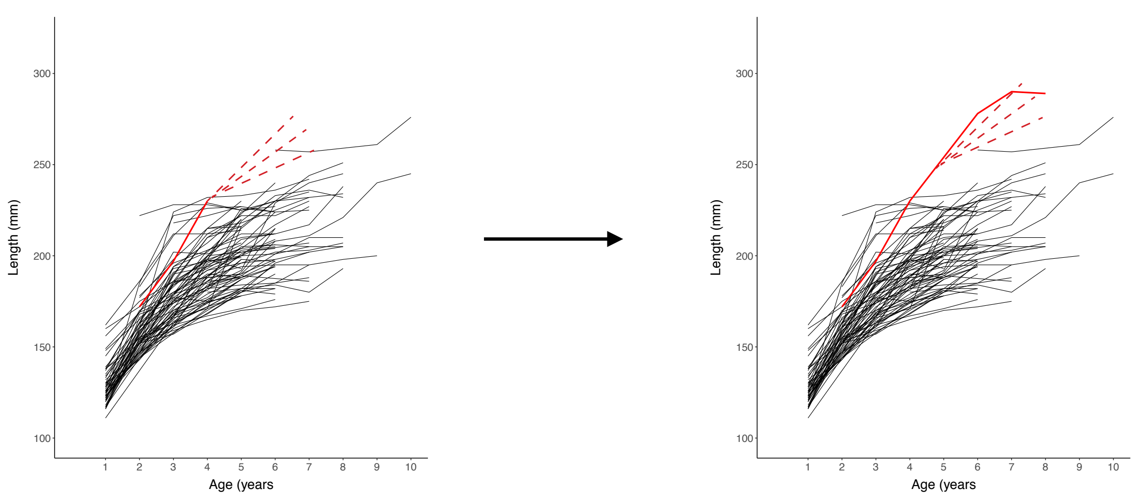
where β is a regressor coefficient for the (i.e., categorical) fixed effect, γ is the regressor coefficient for a continuous effect (e.g., population density, some measure of food quality or quantity), σ_v is the standard deviation of the (common) statistical distribution of the random effect, and $v_{ij}$is the random effect for individual i in group j. Intuitively, the random effect constitutes a deviation from the expected behavior of the individual in group j and subject to condition z. Theoretically, any of those predictors can enter the equation non-linearly and more predictors and more random effects can be used, although we need to keep in mind, as usual, the trade-off between model complexity and the interpretability of the model and its parameters.

Similarly, k can be modeled as:

$$k_{i,j} = \alpha + \beta_j j + \gamma z + \sigma_u u_{ij} + \varepsilon_{k,i,j}$$

External validation and other measures of model accuracy can help us select the most appropriate model formulation.

When using a reasonably appropriate growth model, the variation in growth and size that characterizes organisms can almost always be modeled retrospectively. However, in the natural sciences, there have been limited attempts at predicting missing size observations or unobserved growth trajectories. The lack of attempts can be mostly ascribed to the challenges of fitting hierarchical models for growth and the often-intrinsic unpredictability of the growth curves of some organisms, for which it may be impossible to accurately predict later portions of the growth trajectory when only a few observations early in life are available.



A note on why I cannot show model fit on real data

Shows viewership and ticket-sold data are proprietary, and while I was able to use them to fit models on my laptop, I cannot show the data in public. But I can say that the hierarchical von Bertalanffy growth model provides excellent predictions of short- and long-term performance of shows, and I provide a note as well on how to estimate parameters using modern tools[note3].

Biological insights can inform the analysis of shows performance

The von Bertalanffy growth function is able to well describe a variety of shows viewership or tickets-sold growth trajectories, but other functions with similar flexibility and similar resulting shapes of trajectories are likely to be comparably accurate in describing empirical growth trajectories (e.g., Logistic, Gompertz, and Richards growth functions). The crucial question is how the von Bertalanffy growth function and other similar growth functions are able to approximate both growth of fish in size or seabird chicks in weight, and viewership or tickets sold for screen entertainment, and which biological insights that have been facilitated by the use of the model in the life sciences can help get insights on the performance of shows.

For many organisms with indeterminate growth for which the von Bertalanffy growth function has been used, most growth occurs in the earlier stages in life (i.e., before sexual maturity), since after sexual maturity more energy is allocated to reproductive functions at the expense of growth, maintenance, and repair. Likewise, it is not unusual to observe 30-50% of total viewership or tickets sold over the lifetime of the show to be realized in the first one or two weekends after launch (the early stages of life for the show), which shows that title viewing, especially early on, is rarely opportunistic and mostly planned.

Most shows are now launched in theaters and on streaming services on Fridays. Especially for the more popular shows, we can assume that subscribers, members, and people who want to spend a few hours at the movie theater with their significant other, friends, or are bold enough to go alone, are waiting for the title to be out, and weekend days allow more time for leisure than other days of the week. After this planned-in-advance viewing phase, watching is likely to become more opportunistic, and growth of viewership or tickets-sold slows down, especially after the second or third weekend of showing. At that point, the attention of people is directed to other shows.

This viewing preference (planned and robust early on, then more opportunistic and sparser) also explains why viewership growth trajectories rarely cross. Parallelly, the maintenance of size hierarchies (that is, if you are bigger than another individual early on in life, you are also likely to be bigger later in life) throughout the lifetime is often observed in many species; although catch-up growth can occur (growth speeds up after an initial phase of slow growth), what happens in the first stages of life (e.g., of which early growth is a proxy) strongly influences what will happen throughout the organisms' lifetime (e.g., maximum size).

One major difference between the growth trajectories of organisms and of movie viewership is their variation, which is represented in the "width" of the collection of growth trajectories. If we take a random collection of shows and of fish and birds living in the same population, the variation in viewership-at-day after launch is much larger than variation in size-at-age of fish and weight-at-age of birds. Although there are fish populations that include both normal-growing and stunted individuals, and whose size-at-age distribution is thus expected to be bimodal, the allowed variation in size-at-age is constrained by what makes life in that environment possible or the organisms sufficiently competitive. Similarly, for seabirds, slow-growing chicks can be – and often are – abandoned by their parents because less likely to survive than chicks growing faster. Since shows are not taken out when they fail to reach a viewership threshold or tickets sold, the variation in growth of viewership or tickets sold is allowed to be much larger than the variation in growth among fish or birds living in the same population[note4].

Another topic to be investigated is whether the parameters of the growth function can be interpreted as description of processes (i.e., mechanisms) that govern the growth of the organism or growth of viewers, but that's material for another article (for entertainment, for biology see note1).

Models developed for the life sciences can help studying other problems in the entertainment space

We'll now have a look at how shows congestion, the international success of shows initially produced specifically for certain countries or regions, and marketing can be seen under the light of theories and ideas showing up in ecology and evolutionary biology.

The problems and concepts I am going to describe are not new, and the life sciences are far from being the exclusive source of models and insights to be applied to problems of competition or optimization. For instance, one of the crucial tasks of supply chain engineering is avoiding congestion, economics deals with competition and optimal allocation of resources, and both engineering and design routinely deal with trade-offs among competing functions.

Exploitative vs interference competition for movies congestion

Competition among organisms of the same species or of different species can generally take two forms: exploitative competition, in which individuals compete for a resource that is shared fairly equally among them, and interference competition, in which some individuals (e.g., larger) reduce the access of other individuals (e.g., smaller) to the resource they are competing for (most often space, food, and access to mates). For instance, in some fish populations, higher population densities, smaller variation in growth, and weaker maintenance of size hierarchies may suggest that exploitative competition is operating, while the opposite would be true in the case of interference competition, which is a winner-take-all (or take-most) situation.

Country, time of the year, other shows or movies launched at the same time, constitute the habitat for shows and, as it happens for organisms, the performance of shows is also a function of the habitat in which they happen to live. Shows compete with each other for members, subscribers, and moviegoers' watching time, and too many shows available at the same time can lead to "congestion". Although the overall time dedicated by "users" (i.e., people) to watching can increase, we all agree there is a limit somewhere (i.e., 24 hours a day if we skip working, sleeping, and taking care of ourselves and others) and often the first 3 to 10 days determine the fate of the show. That is, a TV show launched in a heavily trafficked window may underperform because of viewers watching other shows in the first days after launch, and never recover after that.

Looking at the problem through the lens of exploitative (shows competing with each other all have lower performances than when not competing) and interference (some shows do not get any negative effects from the competition with other shows, others perform much worse than when not competing) competition, and using mathematical tools and insights from ecological research may help set up strategies and tactics that can mitigate the loss of viewership for shows that are launched when there is risk of "congestion".

Adaptation for shows targeting a specific country or region

Adaptation is a central topic in evolutionary biology. Although adaptation is more a property of species or populations than of individuals, a parallel can be made between populations that are strongly adapted to some habitats and ill-suited to others, and shows that are successful in certain countries and bomb in others.

The show might be "too adapted" to their target countries – in terms of topic, storyline, language, cast – when it does not have the necessary variation (which, for species, would be genetic and phenotypic variation) to thrive in another environment. How much a show that has been produced specifically for certain countries is watched in regions that are not its primary has parallels with how vital rates and risk of extinction change when a population faces a new environment. Studying how evolutionary biologist have modeled how genetic and phenotypic variation determine those changes can help sharpen our thinking on the determinants of the global success of "regional" shows.

Food supplementation as marketing

Supplementation of food to wild animals is often applied as a conservation tool, as it can yield an immediate increase in productivity and vital rates related to fitness. In general, an organism can grow bigger by either acquiring more resources and allocate the same proportion of resources to growth or use the same resources and allocate more of them to growth. Or be one of those size winners and make the energy pie bigger and also give more slices of the pie to growth. Although shows, of course, do not possess any biological machinery and their viewership or tickets they sell is not coming from any physiological process, greater exposure through marketing can help shows get more of the resources they thrive upon, that is the attention and time of members, subscribers, and cinemagoers.

However, in animal species long-term carry-over effects of food supplementation can be negative for both the food-supplemented individual and for the overall population. One hypothesis, or potential outcome, is that food supplementation early in life has a silver spoon effect by permanently increasing the quality of the individuals that have been food-supplemented. In this case, food supplementation would have long-term positive effects on the fitness of food-supplemented individuals.

Another hypothesis is that the positive effects on fitness of food supplementation may only be short-term and might have delayed negative consequences, for instance by only temporarily increasing the survival chances of poor-quality individuals, with higher than expected mortality – in some cases of all supplemented individuals due to increased competition – after the food supplementation stops.

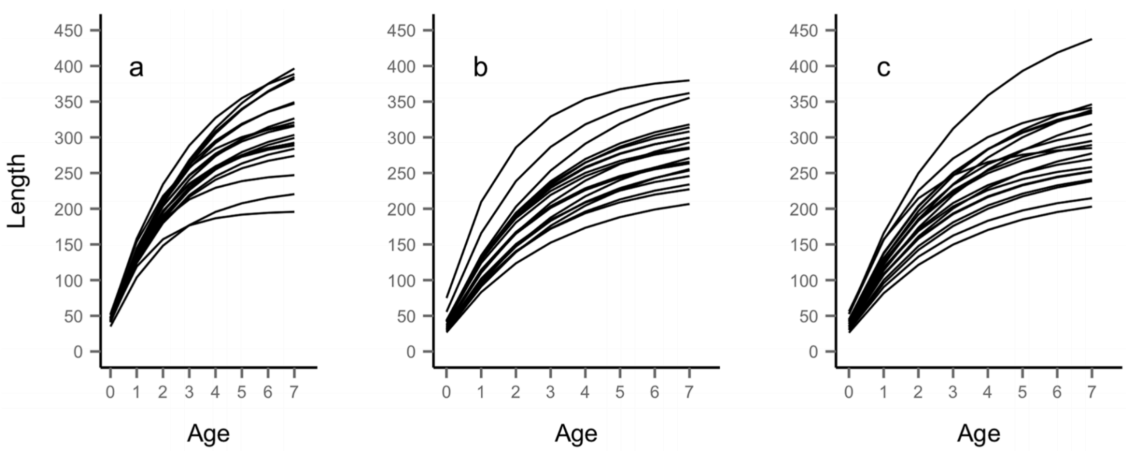
Likewise, leaving aside the problem of optimal allocation of a semi-finite resource (that is, dollars to be spent on marketing), strong marketing of high-quality shows can increase their success by making them more visible and appealing. On the other hand, strong marketing of poor-quality shows may only temporarily increase their viewership, which can then reach viewerships at the end of their lifetime that are lower than what could have been reached with softer marketing, for example by causing negative word-of-mouth from viewers whose expectations in terms of shows quality were not met, and then getting a hard pass from potential viewers.

Notes

Note1: There is a long-standing debate among biologists on whether the parameters of the von Bertalanffy growth function to model the growth of organisms are to be considered curve-fitting parameters with no biological interpretation (i.e., providing just a phenomenological description of growth) or parameters that describe how anabolic and catabolic processes govern the growth of the organism (i.e., providing a mechanistic description of the growth process). In the original mechanistic formulation of the von Bertalanffy growth function, asymptotic size results from the interplay between environmental conditions and behavioral traits, and the growth coefficient is closely related to metabolic rates and behavioral traits (i.e., the same physiological processes affect both growth and asymptotic size). However, in most studies asymptotic size and growth rate are commonly treated as independent parameters with no connection to physiological functions, thus offering only a phenomenological description of growth. In addition, two of the parameters of the von Bertalanffy growth function often lie well beyond the observational data (t_0 and L_∞).

The estimates of L_∞, k, and t_0 tend to be highly correlated. This correlation does not offer any biological insights, since it occurs because different combinations of L_∞ and k can basically provide the same fit to the data, in particular when the range of ages in the data set is limited. In other words, by slightly increasing or decreasing L_∞ and k in opposite directions, the same likelihood is obtained.

With the hierarchical formulation, L_∞, k, and t_0 can be positively or negatively correlated (or show no correlation); their correlation gives us biological and ecological insights on the processes leading to growth variation among individuals (Vincenzi et al., 2014). Other model formulations attempt to more closely connect von Bertalanffy growth function parameters to measurable biological processes (Vincenzi et al., 2016). In the figure below, from left to right, a simulated collection of von Bertalanffy growth trajectories with negative, positive, and no correlation between L_∞ and k.



Note2: Birds and mammals are usually considered to display determinate growth, that is growth in size stops at the end of their development – long bones and vertebrae no longer grow, although mass can grow, as we all become very aware after the holidays. On the other hand, fish show indeterminate growth – the growth of the organism likely occurs throughout its life, although it slows down after sexual maturity. More time for growth can lead to more time and opportunity for bigger size differences among organisms, even when living in the same population at the same time. See for example the two marble trout below, of similar age and quite different size.

Note3: Several modeling tools to fit hierarchical models are now available, such as platform-independent JAGS, BUGS, STAN, and, among many others, the *nlme*, *lme4*, and *brms* packages and associated functions in R or *PyMC3* in Python. Another tool that has been recently developed for fitting hierarchical models is Template Model Builder (TMB). TMB is a general random effect tool integrated in R that was inspired by ADMB (Automatic Differentiation Model Builder), an open source statistical software package for fitting non-linear statistical models, whose development was motivated by high p-low N problems in fishery. Although this fact may not be well known outside of ecology and fishery science, terrific advancements in statistics and applied math were motivated by fishery problems (for an early look at those problems see for example Beverton, RJH and Holt, S (1957) On the Dynamics of Exploited Fish Population; for a more recent look on the topic, see Mangel, M (2006) The Theoretical Ecologist's Toolbox). TMB can be used to fit generic random-effects models and is very flexible in model formulation.

Note4: Multiple, non-exclusive processes can explain the maintenance of size hierarchy in fish populations, two of which are (a) among-fish differences in genetic growth potential and (ii) habitat heterogeneity. While the former process is intuitive and can be interpreted in the entertainment context as the quality of the shows (show's quality is conceptually similar to the genetic growth potential of organisms, although it is a circular, ill-defined concept, because quality is largely defined by how many members have watched the show), for the latter it can be shown analytically and with computer simulations that a patchy distribution of resources with some portions of the habitat that are more profitable than others can lead to the maintenance of size ranks throughout fish lifetime. For example, bigger fish living in streams are often found in the uppermost part of the stream, where a larger portion of stream drift is available since no fish are living upstream.

A third mechanism – that of early imprinting or predictive response – can also explain the persistence of size differences throughout the lifetime of organisms of the same species. Across taxa, the environmental conditions experienced during the first stages of life have the potential to influence their vital rates, morphological and behavioral traits, and life histories throughout their lifetime. For example, harsh environmental conditions early in life tends to accelerate the processes leading to sexual maturity because the signal the organism gets is "it's now or never", but more benign environmental conditions can signal that there is time to more fully develop before reproducing. The physiological adaptations are thus set early in life and are predictive responses – the individual is "making bets" on how the future is going to be – that are mostly set after an early window of opportunity.

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