

COMMENTARY

The fallacy of the average: on the ubiquity, utility and continuing novelty of Jensen's inequality

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ABSTRACT

Biologists often cope with variation in physiological, environmental and ecological processes by measuring how living systems perform under average conditions. However, performance at average conditions is seldom equal to average performance across a range of conditions. This basic property of nonlinear averaging – known as 'Jensen's inequality' or 'the fallacy of the average' – has important implications for all of biology. For instance, a burgeoning awareness of Jensen's inequality has improved our ability to predict how plants and animals will respond to a warmer and more variable future climate. But for many biologists, the fallacy of the average is still a novel concept. Here, I highlight the importance of Jensen's inequality, provide a simple graphical approach to understanding its effects, and explore its consequences at atomic, molecular, organismal and ecological levels.

KEY WORDS: Nonlinear averaging, Global change, Thermal performance curves, Geometric average, Bootstrap estimation, External fertilization, Intermediate disturbance

Introduction

Nature is variable. The position and orientation of atoms and molecules change as they are jostled by thermal agitation. Air temperature and sunlight fluctuate with the seasons and the weather. Physiological capacity varies from one individual to another, and ecological interactions shift from place to place and time to time. In large part, it is the combined effect of these and similar variations that makes biology such a complex and challenging field.

Often, biologists cope with variation by taking an average. For example, if substrate concentration varies through time in a cell, a biochemist might use the average concentration to calculate the average rate at which product is made. If prey density varies from place to place in the ocean, a marine ecologist might use mean density when calculating a predator's average foraging rate. A biomechanic might use the average velocity in a turbulent stream to calculate average drag on benthic algae. But therein lies a problem. Except under rare circumstances, the response of a system to average conditions is different from the system's average response to variable conditions, a conundrum known as 'Jensen's inequality', named for Danish mathematician Johan Jensen (Jensen, 1906). Also referred to as 'the fallacy of the average', Jensen's inequality is a basic tenet of nonlinear averaging. Put formally, it states that if $f(x)$ is a nonlinear function of x , the average of f , that is $f(\bar{x})$, is not equal to the function of average x , $f(\bar{x})$:

$$\overline{f(x)} \neq f(\bar{x}). \quad (1)$$

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Given that very few of nature's response functions are strictly linear, Jensen's inequality has near universal application in biology.

Some fields are well aware of Jensen's inequality and its consequences. For example, ecological physiologists and evolutionary biologists have innovatively incorporated the effects of Jensen's inequality into their efforts to model how plants and animals will respond to future changes in Earth's climate (e.g. Ruel and Ayres, 1999; Martin and Huey, 2008; Dillon et al., 2010; Williams et al., 2012; Vasseur et al., 2014; Colinet et al., 2015; Kingsolver et al., 2015; Dowd et al., 2015; Dillon and Woods, 2016; Koussoropolis et al., 2017). By contrast, biologists in other fields are often unaware of the quirks of nonlinear averaging. In an informal survey of colleagues and students over the years, I have found that fewer than half are aware of Jensen's inequality. Others remember encountering the concept in a statistics class, but have never found occasion to use it. The continued novelty of nonlinear averaging for many biologists is the impetus for this Commentary. My goals here are to explain the importance of Jensen's inequality, provide a simple graphical approach to understanding its consequences, and highlight its effects at atomic, molecular, organismal and ecological levels.

Basic concepts behind Jensen's inequality

The consequences of Jensen's inequality are best understood through examples. First, let us explore the simple case of a linear function. Oceanic phytoplankton are a major sink for the carbon dioxide that human activity is spilling into the atmosphere, and the rate at which these unicellular organisms absorb CO_2 from seawater is directly proportional to each cell's diameter, d (Fig. 1A) (Berg, 1983; Denny and Gaines, 2000). In a hypothetical population, half the cells are small ($d=10\ \mu\text{m}$) and half are large ($d=20\ \mu\text{m}$). As shown by the graph, each of the small cells absorbs CO_2 at a rate of $400\ \text{fmol s}^{-1}$, and each of the large cells at a rate of $800\ \text{fmol s}^{-1}$. Thus, the average rate of absorption is $600\ \text{fmol s}^{-1}$ per cell. But let's look at the question a different way. Average cell diameter in the population is $15\ \mu\text{m}$, and the function of absorption versus diameter tells us that a cell this size absorbs CO_2 at $\dots 600\ \text{fmol s}^{-1}$. In other words, for this linear function the average rate of absorption across cell sizes is equal to the rate of absorption by a cell of average size. Thus, one could use average cell size to accurately calculate the population's capacity to absorb society's waste CO_2 .

However, using the average in this fashion is problematic if the function in question is nonlinear. Consider, for instance, how metabolic rate changes with body temperature in ectotherms (Fig. 1B). In this hypothetical example, metabolic rate at any given temperature is three times that at a temperature 10°C lower (i.e. $Q_{10}=3$). Let's suppose that body temperature is constant at 20°C during the 12 h of daylight, and constant at 10°C at night, such that the average temperature is 15°C . What is the average metabolic rate? To find out, we graphically take the average of day and night rates by drawing a line between the two rates and locating its midpoint.

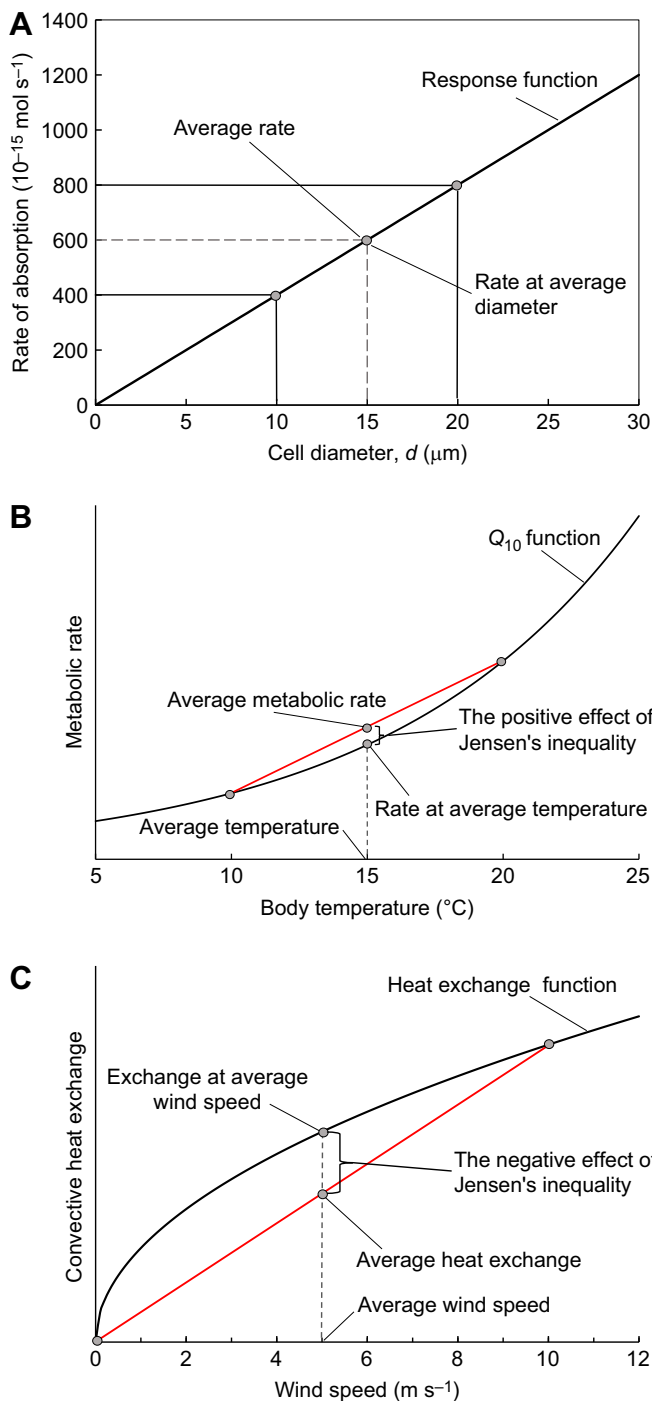


Fig. 1. Examples of response functions. (A) The rate of CO₂ absorption is a linear function of cell diameter. As a consequence, the average rate of absorption is equal to the rate at average cell size. (B) Metabolic rate is an accelerating, nonlinear function of temperature. When temperature varies (alternating between 10 and 20 $^{\circ}\text{C}$, for instance), average metabolic rate is greater than the rate at average temperature. (C) Convective heat exchange varies with wind speed as a decelerating, nonlinear function. If wind speed varies (alternating between zero and 10 m s^{-1} in this example), average heat exchange is less than the exchange at average wind speed.

(We use the midpoint because equal time is spent at the two temperatures. If more time were spent at one or the other, we would find the average by sliding the point proportionally along the red line.) But notice that the average metabolic rate is greater than the

metabolic rate at average temperature. That is, animals with variable body temperature use more energy per time than do animals with a constant body temperature, even when both have the same average temperature, a disparity that could have consequences for growth rate, reproductive output and foraging requirements.

Now consider a different example. The rate at which a leaf exchanges heat with the surrounding air depends on wind speed: convective heat loss increases approximately as the square root of speed (Denny, 2016), a relationship shown in Fig. 1C. The ability of leaves to stay cool in bright sunlight thus depends on the air flow around them. Let us suppose that two leaves experience the same average wind speed (5 m s^{-1}), but for one, speed is constant, and for the other, it alternates equally between 0 and 10 m s^{-1} , a rough approximation of turbulent flow. As we did for metabolic rate, we calculate average heat loss in the variable environment by drawing a line between values at the two alternating conditions and finding its midpoint. In this case, the average of the function is less than the function of the average. Leaves in turbulent flow might overheat while leaves in constant flow of the same average speed survive.

From these graphical examples, we can draw two conclusions. First, we see why Jensen's inequality is true: only if a function is linear does the average response equal the response at average conditions. Second, the disparity between the average of a function and the function of the average depends on the function's shape. If the function is concave upward (e.g. metabolic rate as a function of temperature), the average of the function is greater than the function of the average. Conversely, if the function is concave downward (e.g. heat loss as a function of wind speed), the average of the function is less than the function of the average.

Quantifying the disparity

If $\overline{f(x)} \neq f(\bar{x})$, then:

$$\overline{f(x)} = f(\bar{x}) + \text{something.} \quad (2)$$

What is this 'something' and how big is it? To answer this important question, consider Fig. 2, which shows two examples of thermal performance curves. To create curves of this sort, an organism's performance (e.g. metabolic rate, growth rate, fecundity) is typically measured at a series of constant temperatures, and a curve is fit to the data (Angilletta, 2009). At some critical low temperature (CT_{\min}) performance sinks to zero, as it does at some critical high temperature (CT_{\max}). In between, there is a temperature (T_{opt}) at which performance is maximized. First let us explore the curve in Fig. 2A. This species is a thermal generalist; it performs well over a broad range of temperature. Given this curve, we can predict performance at any particular average temperature (e.g. 30 $^{\circ}\text{C}$), and using our line-drawing method we can graphically calculate the average performance when temperature varies by $\pm 3^{\circ}\text{C}$, alternating between a constant 33 $^{\circ}\text{C}$ in the day and a constant 27 $^{\circ}\text{C}$ at night (the blue solid line). Because for temperatures near 30 $^{\circ}\text{C}$ the curve is concave downward, average performance in this variable environment is lower by 6% than performance at average temperature. Note what happens if the variation between day and night temperatures is increased to $\pm 4^{\circ}\text{C}$ (34 to 26 $^{\circ}\text{C}$; the red dashed line). The larger the variation, the greater the effect of Jensen's inequality; performance is now decreased by 11% relative to performance at the average temperature.

We can apply the same procedures to the thermal performance curve in Fig. 2B. Everything is the same except that this curve is for a thermal specialist; the animal can perform only over a narrow

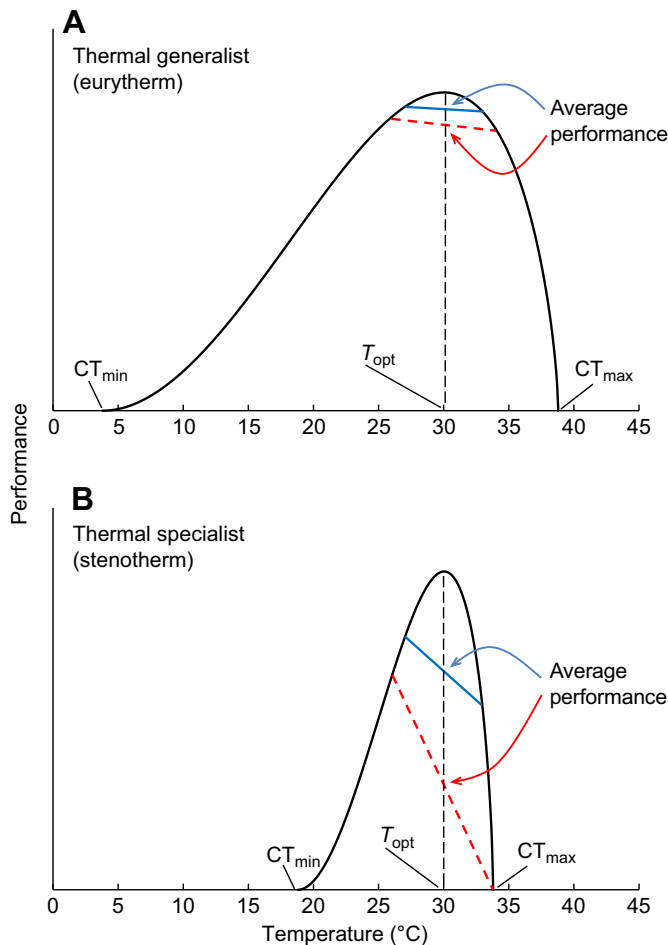


Fig. 2. Illustrating Jensen's inequality using thermal performance curves. (A) The curve for a thermal generalist (a eurytherm). Near an average temperature of 30°C, the performance curve is concave downward, so average performance when temperature varies is less than performance at average temperature. Increasing the range of temperature variation (the dashed red line versus the solid blue line) increases the effect of Jensen's inequality, but only slightly. (B) The performance curve for a thermal specialist (a stenotherm). Because the curve near 30°C is more strongly concave, increasing the range of temperature variation drastically increases the effect of Jensen's inequality.

range of temperatures, and as a result the concavity of the curve is more pronounced. Because of this change in shape, the effect of Jensen's inequality is magnified. For temperatures varying by $\pm 3^\circ\text{C}$, average performance relative to performance at average temperature is reduced by 30% rather than 6%; for a variation of $\pm 4^\circ\text{C}$, performance is reduced by 66% rather than 11%.

From these examples we see that the 'something' in Eqn 2 depends on both the amount of variation and the shape of the curve. (This holds true even when x has a distribution of values rather than just the two in this simple example; for instance, in reality there is a continuous distribution of air temperatures as the environment cycles between day and night.) Mathematical analysis helps to quantify these conclusions. It can be shown (e.g. Chesson et al., 2005; Denny, 2016) that:

$$\overline{f(x)} \approx f(\bar{x}) + S\sigma_x^2. \quad (3)$$

In other words, the magnitude of the effect of Jensen's inequality – the 'something' – is set by S , a descriptor of the shape of the function, and by σ_x^2 , the variance of the input variable x .

As you might expect from Fig. 2, the shape factor S depends on the local 'curvature' of f :

$$S = \frac{1}{2} f''(\bar{x}), \quad (4)$$

where $f''(\bar{x})$ is the second derivative of f evaluated at mean x . (Strictly speaking, the second derivative is an accurate measure of curvature only when the first derivative is zero, but a looser definition serves our purposes here.) Note that for a curve that is concave upward, f'' is positive, while for a curve that is concave downward, f'' is negative. Thus, the sign of S accounts for the qualitative effects we noticed in Fig. 1B,C: if the curve is concave up, S is positive and $\overline{f(x)} > f(\bar{x})$; if the curve is concave down, S is negative and $\overline{f(x)} < f(\bar{x})$. For a straight line, the second derivative is zero, and $\overline{f(x)} = f(\bar{x})$. Eqn 3 also tells us that the effect of Jensen's inequality scales in proportion to σ_x^2 . The more variable the driver of a nonlinear system, the greater the disparity between $\overline{f(x)}$ and $f(\bar{x})$.

It is important to note that, in all but a few situations, Eqn 3 is an approximation. Only if f is a quadratic equation (fitting the form $y = ax^2 + bx + c$) is Eqn 3 exact. In all other cases, this relationship provides an estimate of $\overline{f(x)}$, but the estimate's accuracy can be less than one would desire, especially if σ_x , the standard deviation of x , is a large fraction of the relevant range of x (e.g. the range between CT_{\min} and CT_{\max}). To calculate $\overline{f(x)}$ with reliable accuracy, one needs to substitute the brute force of a computer for the elegance of Eqn 3. Suppose you want to calculate $\overline{f(x)}$ for a given mean value of x . First you must specify how x varies around that mean. In an ideal case, you would have a large number of empirical data that define the distribution of x . Barring that, you might suppose that x is normally distributed with a mean of \bar{x} and a specified σ_x . In either case, you would write a program that randomly chooses a value of x from the x distribution; this x can then be used to calculate $f(x)$ for this specific case. Iterating this procedure hundreds to thousands of times provides a large random sample of how performance would play out given the known (or assumed) variation in x , and one can then average these individual values to provide a reliable estimate of $\overline{f(x)}$. For example, Benedetti-Cecchi (2005) used this bootstrap procedure to show that spatial variation in species richness reduces primary productivity.

In Fig. 3, I have used a bootstrap to estimate how a standard deviation of 5°C affects average performance given the nominal curve of Fig. 2A. As we expect, where the nominal performance curve is concave downward, average performance is lower. Furthermore, T_{opt} for average performance is lower than that of the nominal curve. In other words, realized performance in a variable thermal environment is predicted to be generally lower than in a constant environment, and is likely to reach its peak at a lower temperature. This effect has been observed in a variety of organisms (Martin and Huey, 2008; Dowd et al., 2015), and it affects how one predicts the consequences of climate change (e.g. Vasseur et al., 2014). Note, however, that where the nominal curve is concave upward (near CT_{\min}), average performance is higher than nominal performance.

The bootstrap procedure outlined above provides a convenient means to accurately estimate the effect of Jensen's inequality for any function. It is crucial to realize, however, that bootstrapping is accurate only in a mathematical sense. Biology (and, in particular, physiology) can throw a spanner into the works. Consider, for instance, the average thermal performance curve of Fig. 3. When calculating this curve, I implicitly assumed that, for each random

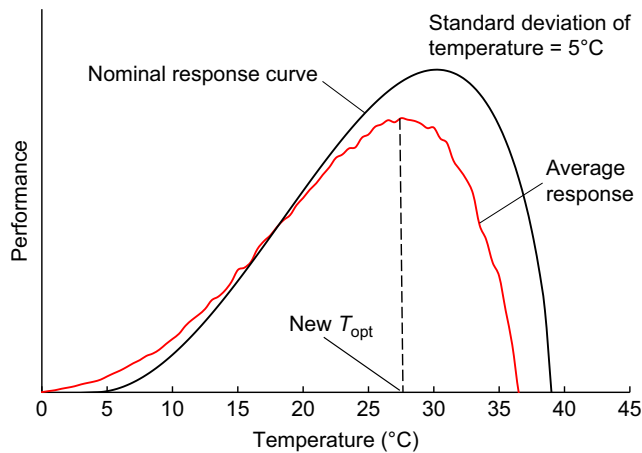


Fig. 3. Average performance under variable conditions (the red curve) differs from that under constant conditions (the nominal response). In general, performance when temperature varies is lower than when temperature is constant, and peak performance occurs at a lower temperature. Note, however, that, for low temperatures near CT_{min} , the nominal performance curve is concave upward, so performance when temperature varies is higher than when temperature is constant. In calculating the effect of Jensen's inequality, I assumed a normal distribution of x with a standard deviation of $5^{\circ}C$, and allowed $f(x)$ to be less than 0 for values below CT_{min} and above CT_{max} .

choice of temperature in the bootstrap, the performance of the organism is not affected by thermal history. That is, I assumed that as an organism moves through a particular body temperature, it has the same performance it would have if it were held at that temperature for an extended period (i.e. the conditions under which the nominal curve was measured). In reality, the organism's past temperature is likely to affect its current physiology such that its actual performance is different from that predicted by the nominal performance curve measured for a fully acclimatized organism. For example, previous short-term exposure to a high temperature could lead to 'stress-hardening', a physiological adjustment that allows the organism subsequently to perform better than predicted by the pure mathematics of nonlinear averaging. Conversely, previous exposure might incur damage, causing the organism to perform worse than suggested by Eqn 3. In short, physiology (and other time-sensitive processes) has the potential to modify the predictions of Jensen's inequality. For temperature-dependent performance, this time sensitivity has the potential to undermine the utility of nominal performance curves measured under constant conditions (Kingsolver and Woods, 2016). For many other aspects of performance, the complex interactions between environmental variability and physiology have not been characterized.

Jensen's inequality is important at all levels of organization

Despite the caveats described above, Jensen's inequality provides invaluable insight into how nature works. A few pertinent examples help to illustrate the ubiquity and importance of nonlinear averaging for atoms, molecules, organisms and ecological communities.

Van der Waals forces

Jensen's inequality plays a key role in explaining the properties of matter. For instance, the London dispersion force – a consequence of nonlinear averaging at the atomic level – is one important component of the suite of dipole interactions (known as van der Waals forces) that help hold materials together. Consider, for instance, water. Although the London dispersion force is weaker than the hydrogen bonds between water molecules (another sort of

dipole–dipole interaction), they account for a substantial fraction of the force binding water molecules to each other (Israelachvili, 2011). Without these dispersion forces, water would evaporate more readily and, as a consequence, terrestrial life could be much different. Van der Waals attractions are also important in maintaining the secondary and tertiary structure of proteins (Creighton, 1984), a critical contributor to the catalytic capability of enzymes, and some animals (such as geckos and some insects and spiders) use van der Waals forces to climb vertical walls and even hang from the ceiling (Autumn, 2006).

How does Jensen's inequality lead to atomic attraction? Atoms consist of a positively charged nucleus surrounded by a cloud of negatively charged electrons; in an electrically neutral atom, the number of positive charges equals the number of negative charges. Because opposite charges attract, electrons are attracted to the nucleus, and it is this attraction that holds the atom together. Conversely, one would expect two neutral atoms to repel each other; brought into close proximity, the symmetrical, negatively charged electron cloud of one atom should repel the cloud of the other. But, in reality, neutral atoms are attracted to their neighbors. The details of the mechanism behind this attraction are complex, but a simplified explanation provides the information we need (de Podesta, 2002).

Averaged over time, an atom's electron cloud is spherically symmetrical (Fig. 4A). However, on the scale of 10^{-16} s, quantum uncertainty allows electrons to bunch together on one side of the atom, momentarily giving that side a net negative charge and the opposite side a net positive charge. In other words, for a brief period the atom is an electrical dipole. As dipoles are wont to do, the asymmetrically arranged electrons of one atom induce a dipole of opposite sense in a neighboring atom, such that the local negative charge of one atom is adjacent to the local positive charge of its neighbor. For that instant, the atoms attract each other. An instant later, the electrons rearrange, bunching up in another area, but again the dipole effect leads to net attraction. In short, although atoms with an average disposition of electrons would repel each other, because of quantum variation in electron position there is, on average, a net attraction.

External fertilization

Many, if not most, benthic marine organisms reproduce sexually by broadcasting eggs and sperm into the surrounding water. Because the motility of gametes is limited (Vogel et al., 1982), successful fertilization often relies on turbulent water motion to bring together gametes from distant parents (Denny and Shibata, 1989). The random swirl and mix from turbulent eddies does indeed transport gametes, but at the same time, like any diffusive process, turbulence tends to disperse particles, thereby reducing their concentration. Because the likelihood of an egg meeting a sperm depends on their co-occurring concentration, the very water motion required for fertilization can compromise the process by promoting dilution. This fact led to a long-standing paradox. Calculations based on time-averaged concentrations of gametes suggested that external fertilization should be dangerously inefficient (Denny and Shibata, 1989). Nonetheless, external fertilization has been retained by many species.

The solution to this paradox is provided by an extension of Eqn 3. Within a turbulent eddy, F , the rate of external fertilization (no. $m^{-3} s^{-1}$) is set by the manner in which swimming sperm find essentially immobile eggs (Vogel et al., 1982). Imagine that you are a sperm swimming in a random direction. The more eggs there are in that direction (that is, the greater the concentration e of eggs,

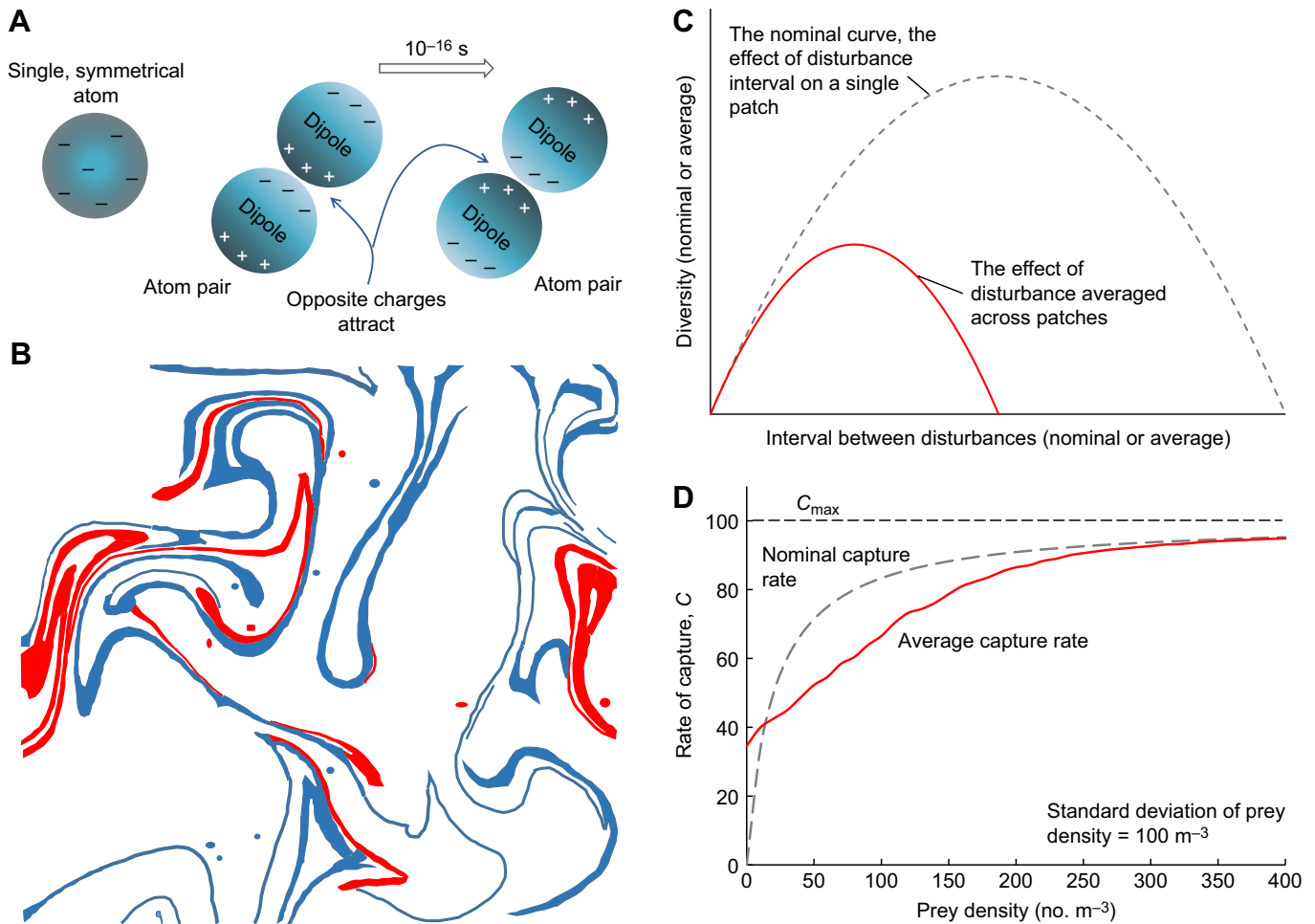


Fig. 4. Applications of Jensen's inequality in nature. (A) The London dispersion force. In the solitary atom on the left, electrons are symmetrically distributed. However, when two atoms are close together, chance asymmetry in one atom's electron cloud produces an electrical dipole, which in turn induces a complimentary dipole in the other atom. Even as these dipoles shift through time, there is a net electromagnetic attraction. (B) External fertilization. In this heuristic slice through turbulent flow, tendrils of eggs (red) and sperm (blue) intertwine. As a result, the local co-occurring concentration of gametes can be high, even though the average concentration measured over a larger volume can be low, i.e. there is more gamete-free water (white) than there is water containing gametes. Redrawn from Crimaldi (2012). (C) The intermediate disturbance hypothesis. For a given patch of organisms within a community, diversity varies with the time allowed for succession, with maximum diversity at an intermediate time (the gray dashed line). However, if each of the many patches in the community has a fixed probability of disturbance and is disturbed independently of the others, the interval between disturbances varies randomly among patches. Using Jensen's inequality to take this variation into account, we find that the average diversity across the community (the red solid line) is less than that expected within a single patch. Modified from Denny (2016). (D) The Holling type II functional response. Because the nominal curve (gray dashed line) is concave down, the rate of prey capture when prey density varies is lower than when prey density is constant. See the 'External fertilization' section for an explanation of the exception at very low prey density.

no. m^{-3}) and the larger the 'target' each egg presents (the projected area of each egg, A , m^2), the more likely you are to contact an egg. Likewise, the greater your speed (u , m^2), the sooner you are likely to hit your target. This is for one sperm; obviously, the more sperm there are in a given volume (i.e. the greater the concentration s of sperm, no. m^{-3}), the more eggs that will be fertilized in a given period.

The overall rate of fertilization depends on the product of these four factors (A , u , e and s). Traditionally, A and u are multiplied to form a single coefficient, k , the encounter rate kernel ($m^3 s^{-1}$; Kiørboe, 2008), leaving us with the following model for the rate of external fertilization:

$$F = kse. \tag{5}$$

Thus, F is a linear function of the product se , implying that:

$$\overline{F(se)} = F(\overline{se}). \tag{6}$$

However, F can nonetheless be nonlinear, because the product of s and e depends on how one varies with respect to the other. For example, if s always equals e , $F = ks^2$, which is clearly nonlinear. More generally, if, when the concentration of sperm is high, the concentration of eggs also tends to be high (that is, if s and e positively co-vary), their average product can be high. Conversely, if when s is high e tends to be low and vice versa (that is, if they negatively co-vary), their product is small. As a result, one cannot reliably use the average concentrations of sperm and eggs to calculate their average product:

$$F(\overline{se}) \neq F(\overline{s}\overline{e}). \tag{7}$$

How, then, can we calculate the average rate of fertilization? Again mathematical analysis comes to our aid. The average product of s and e is equal to the product of average s and e plus their

covariance, $Cov(s, e)$ (Chesson et al., 2005; Denny, 2016):

$$\overline{se} = \bar{s} \bar{e} + Cov(s, e). \quad (8)$$

Thus:

$$F(\overline{se}) = F(\bar{s} \bar{e} + Cov(s, e)). \quad (9)$$

In short, even if the average concentrations of eggs and sperm are low (such that the product $\bar{s} \bar{e}$ is small), if the concentrations of eggs and sperm positively covary, $Cov(s, e)$ can be large, and the average rate of fertilization can therefore be high.

In an elegant series of experiments, John Crimaldi and his colleagues have shown that when eggs and sperm are shed into turbulent flow, the gamete streams are initially stretched into slender tendrils that can be intertwined by eddies (Fig. 4B) (Crimaldi et al., 2008). Because of this short-term behavior, even when the average concentrations of gametes are low, their local concentrations tend to be high and positively correlated. As a result, actual rates of fertilization can be two, even three, orders of magnitude higher than those estimated using average gamete concentrations, helping to explain why external fertilization is so widely found in nature.

Species diversity

In a seminal paper in 1978, Joe Connell proposed what has become known as the ‘intermediate disturbance hypothesis’. The logic goes like this. Through time, species can recruit to an initially barren habitat. As a result, species diversity initially increases. However, at some point, species begin to compete for resources, so, as succession progresses, competitively inferior species lose out to competitively more dominant species and diversity decreases. But this temporal pattern can be disrupted by disturbance. If the community is disturbed often, succession is likely to be halted in its early stages, and diversity is low. If the interval between disturbance events is long, competition has time to run its course, and diversity is similarly low. There is, however, an intermediate disturbance interval at which diversity is maximal; thus the name of the hypothesis. The relationship between disturbance interval and diversity is shown as the dashed line in Fig. 4C.

In this explanation, I have tacitly assumed that each disturbance event affects the community as a whole. In a more realistic scenario, individual patches within the community can be disturbed independently of others. In that case, one might want to predict the average diversity measured across all the patches that comprise the community. Suppose that in a given year, each patch has the low probability p of being disturbed, and that patches are disturbed independently. Given this more realistic scenario, what is the average species diversity of the community?

Because the probability of disturbance is low and equal among patches, the process described here conforms to the Poisson interval distribution (Berg, 1983; Denny and Gaines, 2000), with two relevant aspects coming into play. First, for any given patch, the average time between disturbance events is:

$$\bar{t} = \frac{1}{p}; \quad (10)$$

i.e. the lower the probability of disturbance, the longer the average time between disturbances. Second, the variance of the interval between disturbances is equal to the square of the average interval:

$$\sigma_t^2 = \bar{t}^2. \quad (11)$$

This is important because we know that the greater the variance of an input variable (in this case inter-event interval), the larger the

effect of Jensen’s inequality on average performance. One can use these two relationships to calculate how diversity (an index of community ‘performance’) varies, not as a function of a given interval between disturbance events, but rather as a function of the average interval for the community as a whole (Denny, 2016). This is the solid red curve in Fig. 4C. Because the nominal curve is concave downward, the random variation in inter-event interval decreases average diversity. And, because in this case the variance in interval length increases as the square of the average interval, the effect is unusually drastic. In essence, except when the probability of disturbance is very high (i.e. when average inter-event interval is short), the negative effects of rare, long intervals more than offset the positive effects of the relatively common intermediate-length intervals. As a result, because of Jensen’s inequality, average diversity measured over a community made up of independently disturbed patches is predicted to be much lower than one would expect if single disturbance events were to periodically impact the entire community.

Predator–prey interactions and enzyme kinetics

In 1959, Buzz Holling explored the theory of how predators interact with their prey. His basic idea was that predation involves two steps: searching for prey and handling prey once they have been found. The more concentrated prey are, the more prey a predator can catch per unit time, so as prey density increases from zero, the rate of capture initially increases linearly. However, as a predator catches prey more often, handling time begins to interfere with its ability to further increase the rate of capture, and eventually an asymptote is reached. Based on these ideas, Holling derived an equation (the Holling type II functional response) describing the rate of prey capture (C , number per time) as a function of prey density (ρ , number per area or volume) (Fig. 4D, dashed gray line):

$$C = \frac{\alpha \rho}{1 + \alpha \rho / C_{\max}}. \quad (12)$$

Here, α is a coefficient describing the initial slope of the function and C_{\max} is the maximum possible capture rate. Our understanding of nonlinear averaging immediately allows us to draw an important conclusion. Because the Holling type II process is concave downward, Jensen’s inequality tells us that any temporal or spatial variation in prey density reduces the rate of prey capture (Fig. 4D, solid red line). The only exception is at very low prey densities. Because capture rate cannot be negative, when prey density is near zero, the increase in capture rate accompanying positive deviations in density is not offset by any decrease in rate when deviations are negative. As a result, when ρ is small, average capture rate can exceed nominal capture rate.

Similar kinetics apply at a much smaller scale. The rate at which an enzyme can convert substrate to product depends on how often the enzyme encounters a substrate molecule – a rate proportional to substrate concentration – and how quickly the substrate can be handled by the enzyme’s active site. Thus, enzyme activity is directly analogous to predator–prey interactions, and the Michaelis–Menten equation used by biochemists to model and describe enzyme kinetics is mathematically identical to Eqn 12. Because of Jensen’s inequality, any variation in substrate concentration reduces the average rate of enzyme activity.

Geometric versus arithmetic averaging

There are different ways to calculate an average, and these can affect the consequences of Jensen’s inequality. In all the examples

discussed above, the average referred to is the arithmetic average:

$$\bar{x}_{\text{arith}} = \frac{1}{n} \sum_{i=1}^n x_i, \quad (13)$$

where x_i is an individual measurement of performance and n is the total number of measurements. The arithmetic average is appropriate when cumulative performance depends on the sum of performance across time, e.g. growth. There are processes, however, for which cumulative performance instead depends on the product of performance across time, and in this case the geometric average should be used:

$$\bar{x}_{\text{geom}} = (\prod_{i=1}^n x_i)^{1/n}. \quad (14)$$

Consider, for instance, a population of individuals that reproduce once per year and then die. If each individual produces r young, population size in year $i+1$ is r times population size in year i . Growth of the population through time is thus a multiplicative process. As a consequence, if reproduction is zero in any year, the population dies out regardless of what happens in other years, and this sensitivity to individual years can affect overall performance. Fig. 5 shows how geometric averaging affects the results of Jensen's inequality for the thermal performance curve shown in Fig. 3. Predicted reproductive performance is lower when using geometric averaging than when using arithmetic averaging, and the temperature of maximum performance is shifted to even lower temperatures. Note also that at low temperatures, the effects of geometric averaging are opposite to those of arithmetic averaging; relative to the nominal curve, arithmetically averaged performance is increased but geometrically averaged performance is decreased. Note that these specific conclusions apply only to this particular thermal performance curve. More generally, the effect of using geometric – rather than arithmetic – averaging will vary depending on the nature of each specific response function.

Conclusions

Because nature is variable and biological response functions are typically nonlinear, it is dangerous to assume that average performance is equal to the performance under average conditions. Ecological physiologists and evolutionary biologists have heeded this warning in their attempt to predict the effects of the

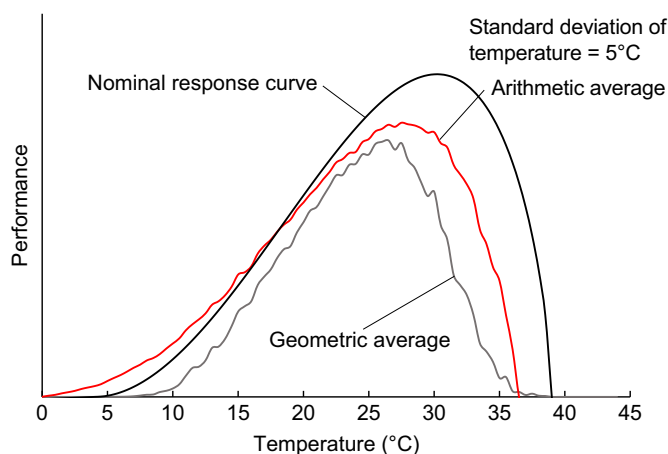


Fig. 5. The effect of geometric averaging on average performance. When the geometric (rather than arithmetic) average is used to calculate average performance, performance is reduced. Here, the geometric average was calculated for 20 reproductive cycles with a standard deviation of 5°C among cycles.

looming shifts in Earth's climate. For example, Vasseur (2014) found that as Earth warms, the increased variance in temperature is likely to have greater impact than the increase in average temperature. But the importance of Jensen's inequality extends far beyond the study of thermal biology. Indeed, the consequences of nonlinear averaging are so pervasive and important that the basic concepts should be a prominent part of every undergraduate biology curriculum, although this is seldom the case.

A simple bootstrapping procedure allows one to estimate the effects of input variation on performance, although these strictly mathematical predictions must be viewed with caution, especially when dealing with physiological performance. However, even without the math, an understanding of the basic concepts of nonlinear averaging allows one to qualitatively estimate the effects of Jensen's inequality for any response function, and I urge all biologists to exercise this ability when viewing both the literature and the wider world.

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Competing interests

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References

- Angilletta, M. J., Jr. (2009). *Thermal Adaptation: A Theoretical and Empirical Synthesis*. New York: Oxford University Press Inc.
- Autumn, K. (2006). Properties, principles, and parameters of the gecko adhesive system. In *Biological Adhesives* (ed. A. M. Smith and J. A. Callow), pp. 225–256. Berlin: Springer-Verlag.
- Benedetti-Cecchi, L. (2005). Unanticipated impacts of spatial variance of biodiversity on plant productivity. *Ecol. Lett.* **8**, 791–799.
- Berg, H. (1983). *Random Walks in Biology*. Princeton, NJ: Princeton University Press.
- Chesson, P., Donahue, M. J., Melbourne, B. and Sears, A. L. (2005). Scale transition theory for understanding mechanisms in metacommunities. In *Metacommunities: Spatial Dynamics and Ecological Communities* (ed. M. Holyoak, M. A. Leibold and R. D. Holt), pp. 279–306. Chicago, IL: University of Chicago Press.
- Colinet, H., Sinclair, B. J., Vernon, P. and Renault, D. (2015). Insects in fluctuating thermal environments. *Annu. Rev. Entomol.* **60**, 123–140.
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302–1310.
- Creighton, T. E. (1984). *Proteins: Structures and Molecular Properties*. New York: W. H. Freeman.
- Crimaldi, J. P. (2012). The role of structured stirring and mixing on gamete dispersal and aggregation in broadcast spawning. *J. Exp. Biol.* **215**, 1031–1039.
- Crimaldi, J. P., Cadwell, J. R. and Weiss, J. P. (2008). Reaction enhancement of isolated scalars due to vortex mixing. *Phys. Rev. E* **74**, 016307.
- Denny, M. W. (2016). *Ecological Mechanics: Principles of Life's Physical Interactions*. Princeton, NJ: Princeton University Press.
- Denny, M. W. and Gaines, S. (2000). *Chance in Biology*. Princeton, NJ: Princeton University Press.
- Denny, M. W. and Shibata, M. F. (1989). Consequences of surf-zone turbulence for settlement and external fertilization. *Am. Nat.* **134**, 859–889.
- de Podesta, M. (2002). *Understanding the Physical Properties of Matter*, 2nd edn. London: Taylor and Francis.
- Dillon, M. E. and Woods, H. A. (2016). Introduction to the symposium: beyond the mean: biological impacts of changing patterns of temperature variation. *Integr. Comp. Biol.* **56**, 11–13.
- Dillon, M. E., Wang, G. and Huey, R. B. (2010). Global metabolic impacts of recent climate warming. *Nature* **467**, 704–706.

- Dowd, W. W., King, F. A. and Denny, M. W.** (2015). Thermal variation, thermal extremes and the physiological performance of individuals. *J. Exp. Biol.* **218**, 1956-1967.
- Holling, C. S.** (1959). Some characteristics of simple types of predation and parasitism. *Can. Entomol.* **91**, 385-398.
- Israelachvili, J.** (2011). *Intermolecular and Surface Forces*, 3rd ed. New York: Academic Press.
- Jensen, J. L. W. V.** (1906). Sur les fonctions convexes et les inégalités entre les valeurs moyennes. *Acta Math.* **30**, 175-193.
- Kingsolver, J. G. and Woods, H. A.** (2016). Beyond thermal performance curves: modeling time-dependent effects of thermal stress on ectotherm growth rates. *Am. Nat.* **187**, 283-294.
- Kingsolver, J. G., Higgins, J. K. and Augustine, K. E.** (2015). Fluctuating temperatures and ectotherm growth: distinguishing non-linear and time-dependent effects. *J. Exp. Biol.* **218**, 2218-2225.
- Kjørboe, T.** (2008). *A Mechanistic Approach to Plankton Ecology*. Princeton, NJ: Princeton University Press.
- Koussoropolis, A.-M., Pincebourde, S., Wacker, A.** (2017). Understanding and predicting physiological performance of organisms in fluctuating and multifactorial environments. *Ecol. Monogr.* (in press).
- Martin, T. L. and Huey, R. B.** (2008). Why "suboptimal" is optimal: Jensen's inequality and ectotherm thermal preferences. *Am. Nat.* **171**, E102-E118.
- Ruel, J. J. and Ayres, M. P.** (1999). Jensen's inequality predicts effects of environmental variation. *Trends Ecol. Evol.* **14**, 361-366.
- Vasseur, D. A., DeLong, J. P., Gilbert, B., Greig, H. S., Harley, C. D. G., McCann, K. S., Savage, V., Tunney, T. D. and O'Connor, M. I.** (2014). Increased temperature variation poses a greater risk to species than climate warming. *Proc. R. Soc. B Biol. Sci.* **281**, 20132612.
- Vogel, H., Czihak, G., Chang, P. and Wolf, W.** (1982). Fertilization kinetics of sea urchin eggs. *Math. Biosci.* **58**, 189-216.
- Williams, C. M., Marshall, K. E., MacMillan, H. A., Dzurisin, J. D. K., Hellmann, J. J. and Sinclair, B. J.** (2012). Thermal variability increases the impact of autumnal warming and drives metabolic depression in an overwintering butterfly. *PLoS ONE* **7**, e34470.