Jensen's inequality predicts effects of environmental variation

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Many biologists now recognize that environmental variance can exert important effects on patterns and processes in nature that are independent of average conditions. Jensen's inequality is a mathematical proof that is seldom mentioned in the ecological literature but which provides a powerful tool for predicting some direct effects of environmental variance in biological systems. Qualitative predictions can be derived from the form of the relevant response functions (accelerating versus decelerating). Knowledge of the frequency distribution (especially the variance) of the driving variables allows quantitative estimates of the effects. Jensen's inequality has relevance in every field of biology that includes nonlinear processes.

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Historically, ecologists have emphasized the importance of average environmental conditions. The concept of environmental variance is almost completely absent from the 40 foundation papers (published from 1887–1971) identified by Real and Brown[1]. Through the 1960s, the word 'variance' appeared in the abstract of only about ten papers per thousand published by the Ecological Society of America (Fig. 1). However, the number of such papers has increased since then to about 50 per thousand during the 1990s. This suggests a growing recognition among ecologists that an explicit consideration of variance is essential to explain many of the important patterns and processes in nature. Jensen's inequality provides a fundamental tool for understanding and predicting consequences of variance, but it is only just beginning to be explicitly acknowledged in the primary literature[2–5], and we can find no mention of Jensen's inequality in any biology or biometry textbook.

Jensen's inequality is a mathematical property of nonlinear functions. Credited to the mathematician J.L. Jensen (1859–1925), it was first described at the end of the 19th century[6,7]. The inequality states that for a nonlinear function, $f(x)$, and a set of x values with a mean of $\bar{x}$ (and a variance greater than zero), the average result of $f(x)$, $\overline{f(x)}$, does not equal the result of the average x, $f(\bar{x})$. When $f(x)$ is accelerating (2nd derivative is positive), $\overline{f(x)}$ is greater than $f(\bar{x})$. When $f(x)$ is decelerating (2nd derivative is negative), $\overline{f(x)}$ is less than $f(\bar{x})$. The sign of the difference between $\overline{f(x)}$ and $f(\bar{x})$

depends only on the form of the function (accelerating versus decelerating).

Jensen's inequality has relevance to any area of biology that includes nonlinear functions (Box 1). Here, we develop examples from physiological ecology (photosynthesis as a function of irradiance and metabolic rate as a function of temperature) and plant–herbivore interactions, but it seems that examples could be drawn just as easily from biochemistry,

ecosystem science or any biological discipline in between. At any scale, Jensen's inequality implies that environmental variance can have important and predictable biological consequences that cannot be inferred from average environmental conditions. For any nonlinear response function, environmental variance will consistently elevate or depress the response depending on the form of the function. Therefore, whenever biological systems involve nonlinear responses, the description and interpretation of environmental data should include an explicit consideration of the variance.

Variance in light regimes depresses primary production

Although photosynthetic organisms are taxonomically diverse, the biochemistry of photosynthesis is relatively highly conserved. Carbon assimilation as a function of irradiance is almost always a decelerating saturation function (e.g. Fig. 2a, D.S. Canny *et al.*, unpublished). Furthermore, the light regime of every habitat is inherently variable because of seasonal cycles, diurnal cycles and shading from clouds and other organisms. Jensen's inequality predicts that, because the assimilation function is decelerating, this variance at temporal and spatial scales should depress net primary production compared with the expectation based upon average irradiance.

The understory light environment of closed canopy forests is particularly variable with long periods of low-level diffuse light punctuated by short periods
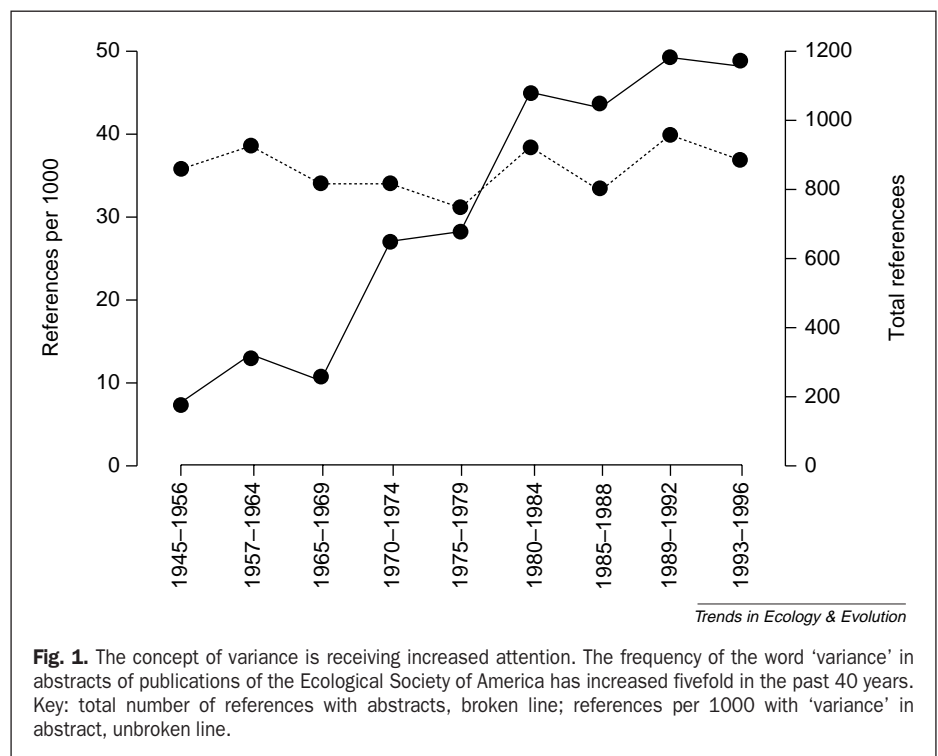

Fig. 1. The concept of variance is receiving increased attention. The frequency of the word 'variance' in abstracts of publications of the Ecological Society of America has increased fivefold in the past 40 years. Key: total number of references with abstracts, broken line; references per 1000 with 'variance' in abstract, unbroken line.

Box 1. Jensen's inequality

Jensen's inequality describes how variance depresses the response variable in decelerating functions and elevates the response variable in accelerating functions. For three hypothetical predators, Figs (a)–(c), energy gained from a prey item is a function of prey mass; bigger prey yield more assimilable energy and a 200 g prey item yields 2500 J of energy. However, their functions differ in shape with the first (a) being linear, the second (b) being decelerating (concave down, 2nd derivative is negative) and the third (c) being accelerating (concave up, 2nd derivative is positive).
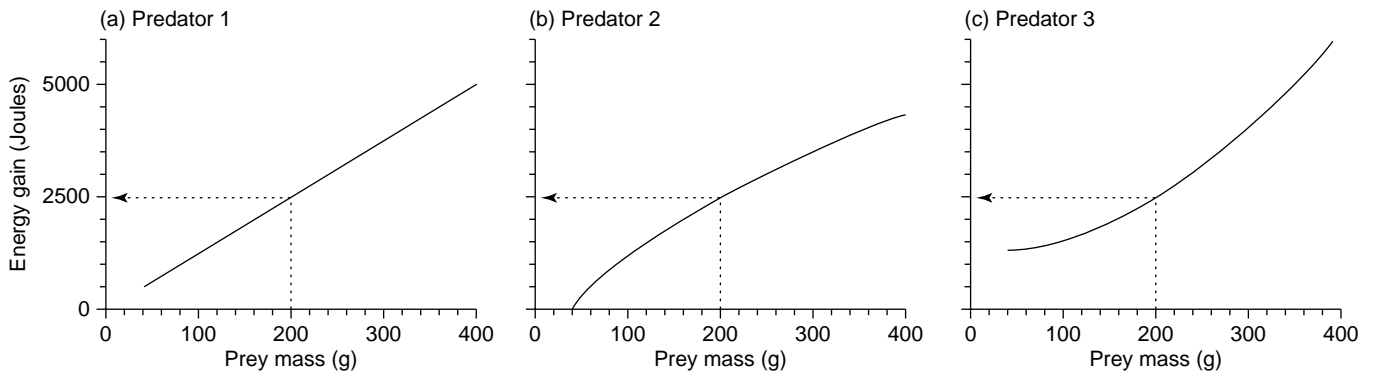
(Online: Fig I)

Trends in Ecology & Evolution

Now consider three groups of prey that each average 200 g per prey item, but differ in variance with group A being uniform, group B somewhat variable and group C highly variable (Table I). Because each group averages 200 g per prey item, does this mean that each predator would gain an average of 2500 J per prey item from consuming each prey group? No. Because the shapes of their assimilation functions differ, variable groups have different consequences for each predator (Table II).

Table I. Mass (g) of prey items in three groups (A–C)

A	B	C
200	160	80
200	180	88
200	180	120
200	200	240
200	220	240
200	220	312
200	240	320

Table II. Average energy gain (J) per prey

	Prey group A	Prey group B	Prey group C
Predator 1	2500	2500	2500
Predator 2	2500	2490	2357
Predator 3	2500	2521	2783

Predator 1 averages 2500 J per prey item for each group because the assimilation function is linear. For any linear function, a unit increase or decrease in X results in the same magnitude change in Y. On average, predator 2 gains less energy per prey item from feeding on the variable groups because, for decelerating functions, a unit decrease in X decreases Y more than a unit increase in X increases Y. Predator 3 gains more energy per prey item from feeding on variable groups because, for accelerating functions, a unit decrease in X decreases Y less than a unit increase in X increases Y. The same phenomenon can apply to populations as well as individuals. If seven predators all had the same assimilation functions as predator 2, and each consumed one prey item from a variable group, the average energy gained per predator would be < 2500 J even though the mean prey mass is 200 g. Although the three example response curves are all increasing functions, Jensen's inequality also applies to decreasing functions. For example, a negative exponential function is a form of an accelerating function (2nd derivative is positive), so increasing variance in the X variable tends to increase the average result of the function (as in predator 3). The direction of the effect of variance on a response variable depends entirely on the form (accelerating versus decelerating) of the response function.

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of high irradiance as the sun passes over gaps in the canopy (sun flecks). Consider hobblebush (*Viburnum alnifolium*), a dominant understory shrub of boreal forests in northeastern North America. If the average light level for the day is used to estimate net daily assimilation, then assimilation is overestimated by >100% (Fig. 2, D.S. Canny *et al.*, unpublished). We refer to this consequence of Jensen's inequality as aggregation bias: systematic errors in the estimate of a biological response [difference between $\overline{f(x)}$ and $f(\overline{x})$] that arise from averaging values of the independent variable over a scale that is coarser than that experienced by the biological system (in this case, a leaf). Plant leaves respond rapidly to changes in irradiance, so the daily carbon budgets

are estimated most accurately if irradiance is measured and recorded at time intervals of seconds to minutes. In the light environment described in Fig. 2 (D.S. Canny *et al.*, unpublished), there was enough temporal autocorrelation of irradiance such that aggregating measurements for up to 10–15 minutes produced less than a 10% error in estimated daily carbon budgets, but aggregating across 60 minutes or more produced >20% error. Aggregation bias can also be introduced by averaging across space.

For *V. alnifolium*, averaging the measurements of three light sensors spaced ten meters apart resulted in overestimation of daily carbon budgets by 14%. This illustrates the need for careful decisions about how to measure, interpret

and report environmental variables such as irradiance. Solar input is frequently reported as a daily or monthly average. However, it is impossible to develop unbiased estimates of daily photosynthesis from average daily or monthly irradiance without making assumptions about the frequency distribution of short-term irradiance. The scale at which aggregation bias becomes severe will be a function of the spatial and temporal autocorrelation of the environmental variable, as well as the strength of nonlinearities in the response functions.

In addition to these practical considerations, Jensen's inequality has some interesting theoretical consequences for the physiological ecology of photosynthesis. For example, two environments with

the same average daily irradiance, but different frequency distributions of short-term irradiance, could yield markedly different carbon budgets for physiologically identical plants. Similarly, the optimization of carbon acquisition strategies (e.g. by adjustment of the light response functions and changes in induction state)[8] could be as strongly influenced by the variability in irradiance as by the average irradiance. Evaluating carbon acquisition strategies and the ecological consequences of changes in light regime requires a careful separation of effects caused by leaf physiology versus the mathematical effects of Jensen's inequality.

Variance in temperature affects animal metabolism

The metabolic rates of poikilotherms tend to increase exponentially as a function of temperature. The accelerating form of these functions implies that variance in temperature will elevate poikilotherm metabolic rates. Temperature regimes, like irradiance regimes, are inherently variable but differ in that temperatures tend to approximate a normal distribution[9]. In an environment where the standard deviation in operative temperatures (i.e. body temperature) is 3–8°C, metabolic rates would be 3–50% greater than in a constant thermal regime with the same average temperature (Fig. 3). The combination of a high Q_{10} (i.e. the factor by which metabolic rate increases over 10°C) and high thermal variation might be selected against because of these rather dramatic increases in maintenance energy requirements. There are predictable patterns in the variability of environmental temperatures. Arid environments and high-altitude environments tend to have very high diurnal variance in air temperatures. Arboreal habitats are more variable than soil habitats, and terrestrial habitats are more variable than aquatic habitats. We predict that poikilotherms adapted to more variable environments will be more likely to employ behavioral thermoregulation (such as microhabitat choice) to minimize variance in their operative body temperatures and will tend to have a lower Q_{10} than related species from low-variance environments. Seasonal changes in behavior and temperature physiology may represent adaptations to minimize the increases in maintenance metabolism that are introduced by seasonal variability in environmental temperature.

The metabolic rate of homeotherms as a function of environmental temperature has a fundamentally different form from that of poikilotherms. Metabolic rates of homeotherms tend to increase both above and below a thermoneutral zone. The slope increases with increasing
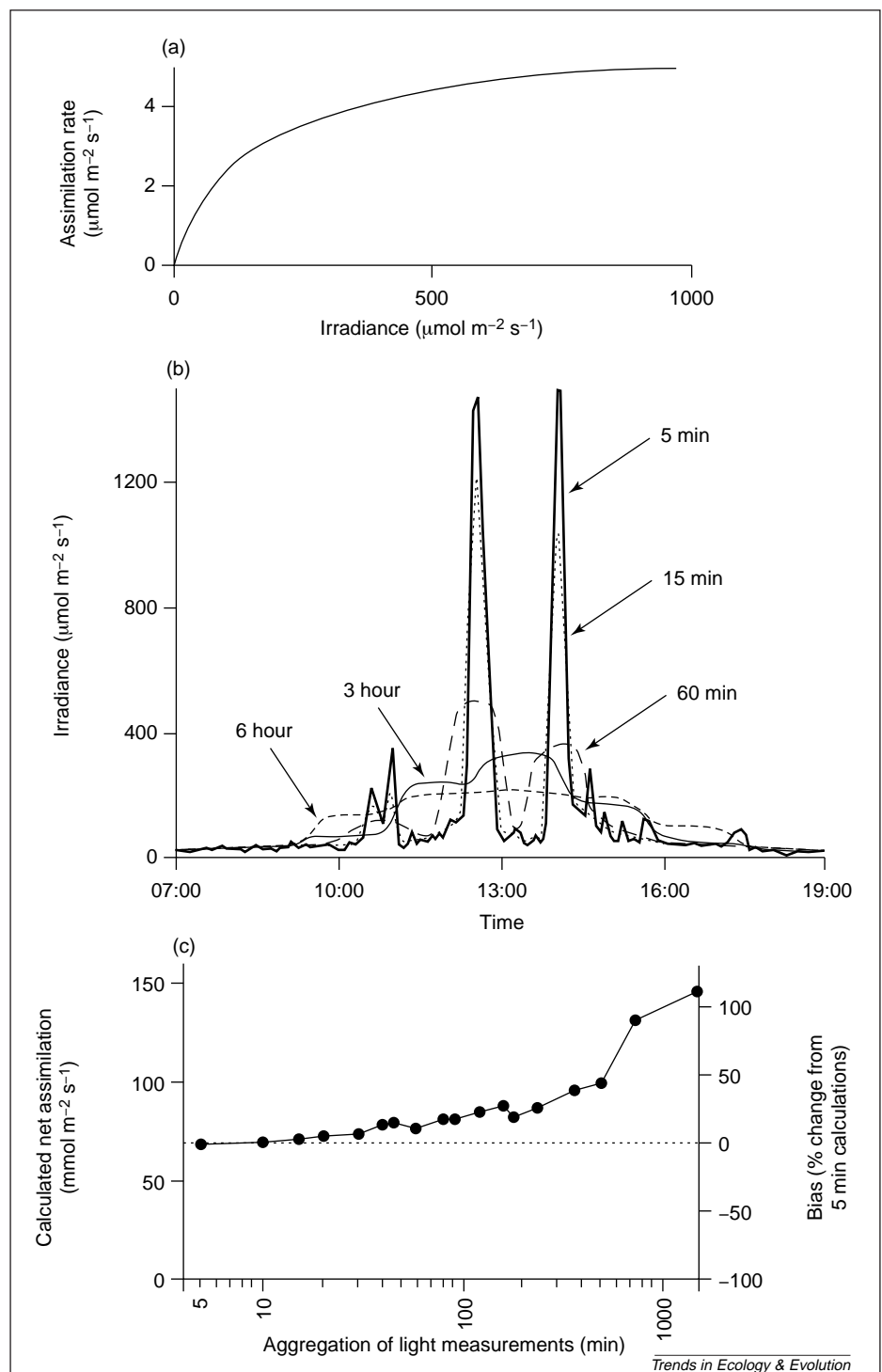

Fig. 2. As with most photosynthetic organisms, carbon assimilation (*A*) by hobblebush, *Viburnum alnifolium*, increases with irradiance as a decelerating function (a). In this case, $A 5 b \bullet I/(1 + a \bullet I) 2 Resp$, where *a* 5 0.0074, *b* 5 0.044, and *Resp* 5 0.22. (b) The light regime of *V. alnifolium's* understory habitat is variable on a timescale of minutes. The irradiance measurements for one day averaged across intervals of 5 min, 15 min, 60 min, 3 h and 6 h show how aggregation of measurements dampens the temporal variation in irradiance. (c) Net carbon assimilation for the day can be calculated based on any temporal aggregation of light measurements from 5 min to 1 day. Because of Jensen's inequality, aggregating light measurements produced a systematic bias in calculated net assimilation. Daily carbon assimilation was overestimated by >twofold using the 24-h average instead of the 5 min measurements. Light response and irradiance data from Canny *et al.*, unpublished.

temperature around both ends of the thermoneutral zone (slope goes from negative to zero at the lower critical temperature and from zero to positive at the upper critical temperature), so when temperature variation spans either the

upper or lower critical temperature, average metabolic rate will be greater than in a constant thermal regime with the same average temperature. Therefore, temperature variability tends to have the same qualitative effect on
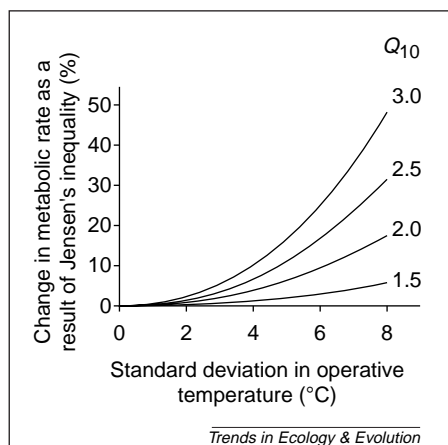
Fig. 3. The effect caused by Jensen's inequality of changes in temperature variability on the metabolic rate of poikilotherms. Here, metabolic rate = $a \cdot 10^{rt}$, where t = temperature, a = rate at $0°$ C, and r = rate of increase with temperature. Q_{10} is the factor by which a biological process increases over $10°C$. Metabolic rates (and many other physiological processes) tend to have a Q_{10} of 2–3. Increases of up to 50% in average metabolic rate result from increases in the variance of operative temperature without any change in average temperature. Results assume a normal distribution of temperatures.

metabolism maintenance in homeotherms as in poikilotherms.

Poikilotherm development rate is also a nonlinear function of temperature. The generalized temperature response function is accelerating at low temperatures, approximately linear at intermediate temperatures and decelerating at high temperatures[10]. Consequently, the effects of temperature variation as a result of Jensen's inequality will tend to be positive at low temperatures, minimal at intermediate temperatures and negative at high temperatures. These effects are a recognized source of error in degree-day models of insect development and plant phenology, and have been referred to as the Kaufmann effect[11]. We hypothesize that differences among environments in temperature variability will select for changes in the acceleration rate, inflection point and deceleration rate of poikilotherm developmental responses to temperature. These evolutionary responses would have the effect of altering subsequent phenotypic responses to changes in temperature variability. If so, the same change in temperature variance could have different ecological effects on, for example, aquatic insects versus terrestrial insects.

Herbivores encounter variable hosts

Intraspecific variance in host tissue quality is common[12–16]. The causes of variance in foliage quality include microsite and genetic differences between plants, plant ontogeny, leaf ontogeny, inducible responses and somatic mutation[13,14,17–19].

Insect responses to this variance include selective feeding, modified consumption rates and the evolution of locally adapted demes[20–22].

Although variance in host quality can affect herbivores in many ways, we will discuss only how variance in the ingested tissue affects herbivore performance via Jensen's inequality. The variance actually experienced by a herbivore is a function of the scale at which variability occurs, the mobility of the herbivore and the discrimination capacity of the herbivore. Host tissue quality can vary among plant populations, plants within a population, leaves within a plant and even areas within a single leaf[20,23,24]. Variability beyond the scale of foraging by an individual will tend to exert its effects at the population level (e.g. if fecundity as a function of leaf chemistry is nonlinear, then mean population fecundity will differ from that predicted from the mean leaf chemistry). Variability at a finer scale can exert effects at the level of the individual (e.g. if development time as a function of leaf chemistry is nonlinear, then development time for an individual can differ from that predicted by the average chemistry of ingested leaves). Behavioral responses that allow herbivores to exploit resources with higher average tissue quality[16,20,25] will tend to reduce the variance experienced by the herbivores. Such behaviors reduce the impact of Jensen's inequality, but do not eliminate it unless the realized variability is reduced to zero. It is also possible that other behaviors actually increase the variance experienced by the herbivore and hence increase the importance of Jensen's inequality.

Insect herbivores are affected by host variance in nitrogen

Insect growth performance as a function of dietary nitrogen concentration, [N], is often nonlinear[2,21,26]. This implies that variance in host [N] has direct consequences for insect herbivores. The responses are decelerating saturation functions for the southern armyworm (*Spodoptera eridania*) and gypsy moth (*Lymantria dispar*)[2,21]. In these cases, variance in [N] should depress performance and this has been experimentally demonstrated for gypsy moths[2]. In the western spruce budworm (*Choristoneura occidentalis*), the response functions for survival and female pupal mass are complex, accelerating at low [N] and decelerating at high [N][26]. Therefore, the effect of host variance on budworm performance would tend to be positive at low average [N] and negative at high average [N]. Insect growth performance can also be linear[27], in which case there are no direct effects of variance in dietary nitrogen. Variance in [N] can exert direct effects on herbivores,

but the magnitude and direction of the effects will differ among taxa because taxa differ in the shape of their response functions.

Insect herbivores are affected by host variance in secondary metabolites

Herbivore performance as a function of secondary metabolite concentrations also includes a range of functions from linear to complex (having both accelerating and decelerating regions)[28–33]. For example, growth rate and survival of the leaf beetle (*Chrysomela falsa*) decreased linearly with condensed tannins from birch (*Betula resinifera*)[29]. Oviposition success of the southern pine beetle (*Dendroctonus frontalis*) was a negative exponential (accelerating) function of tree resin flow[33]. Survival of the cabbage looper (*Trichoplusia ni*) was a decreasing decelerating function of diester concentration[28]. Larval mass of the tobacco budworm (*Heliothis virescens*) declined with increasing concentrations of two different diterpene acids but the functions were decelerating at low levels and accelerating at higher levels[32].

The fact that many of these response functions are nonlinear suggests that variance in host secondary metabolite concentrations has direct consequences for herbivores. In the studies we examined, the performance response of herbivores to secondary metabolite concentrations tended to be accelerating functions rather than decelerating functions (ten cases of accelerating functions versus three decelerating functions, two complex functions and eight linear functions). This suggests that many herbivores will benefit from variance in secondary metabolite concentrations because of Jensen's inequality. In some systems, Jensen's inequality could result in selection for plants to decrease variance (perhaps by distributing resources evenly). Karban *et al.*[5] suggested that induced defenses in plants are a means of elevating variance in host tissue that are selectively favored because of Jensen's inequality. If so, induced defenses should be most common in systems where herbivore performance is a decelerating function of metabolite concentration.

The form of insect response functions is relevant to plant breeding and pest management. In the case of cotton (*Gossypium hirsutum*), herbivore performance tends to decline with allelochemical concentrations[30], so deploying strains of cotton with a high average concentration of allelochemicals could reduce damage by insects. However, because herbivore performance tends to decline as a negative exponential function (an accelerating function) and plant tissue concentrations tend to be variable, the reduction in

herbivory would be less than expected based on mean concentrations of allelochemicals.

The shape of herbivore performance functions could change with evolutionary time. Because of physiological and biochemical constraints, we expect that changes in the slope of performance functions and shifts in the function peaks will be more common than changes from decelerating to accelerating or vice versa. If evolutionary and behavioral responses to host variance do not commonly change the sign of the 2nd derivative of a performance function (i.e. accelerating versus decelerating), they cannot influence the direction of the effect of host variance on a herbivore.

Variable phytochemistry and the frequency of nonlinear responses by herbivores to phytochemistry suggest a strong role for Jensen's inequality in plant–herbivore interactions. Simple simulations can calculate the effects of Jensen's inequality; these only require estimates of the response function and of the frequency distribution of the driving variable. In general, the magnitude of Jensen's inequality will increase with increasing nonlinearity (absolute value of the 2nd derivative) and increasing variance in the driving variable, but many response functions will be more complex than a simple exponential model and many environmental variables have non-normal distributions. In these cases, there is probably no substitute for simulations developed around empirical frequency distributions. The net effect of host variance depends on the combination of the response functions for all relevant compounds and, for a given herbivore, the shapes of these functions might differ for different host compounds. Simulations can be developed around response surface models[34] whenever herbivore performance is influenced by interactions among host traits (e.g. when there are interacting effects of dietary nitrogen and secondary metabolites[35]).

Conclusions and prospects

Jensen's inequality deserves consideration in many more areas of ecological research than we have discussed here. For example, photosynthesis is a decelerating function of temperature and many plants respond to increased atmospheric carbon dioxide concentration $[CO_2]$ with increased maximum assimilation, a shift in the optimal temperature and a narrowing of the peak in the temperature response[36]. One consequence suggested by Jensen's inequality is that natural variance in temperature will cause a greater depression in assimilation under increased $[CO_2]$ than at ambient $[CO_2]$ because of the narrowing of the peak. Estimated effects based solely on maximum assimilation or assimilation at a given temperature will overestimate the effect of increased $[CO_2]$.

In any system in which nonlinear processes are common, Jensen's inequality describes and predicts direct implications of environmental variance. A dominant theme in ecosystem science is the development of models that can be driven by readily obtained data, such as monthly average temperatures, but can still capture the behavior of dynamic biological systems that are sometimes intrinsically nonlinear[37]. With estimates of the response functions and the variance experienced, Jensen's inequality can be used to estimate the error involved in averaging at different scales and aid in choosing the appropriate scale for calculation steps in the model.

Because resources are often distributed unevenly (spatial variance), Jensen's inequality has been implicated in explanations of saltatory search and risk-sensitive foraging[3,4]. In population ecology, functional responses, numerical responses and intraspecific interference tend to be nonlinear and population densities are often aggregated and highly variable[38]. Results of stochastic population models will systematically differ from results of equivalent deterministic models whenever the models include nonlinearities[39]. Community ecology includes extensive consideration of nonlinearities in species interactions and evolutionary ecology involves the study of nonlinear fitness surfaces.

In conclusion, Jensen's inequality has broad relevance for understanding the effects of environmental variance on ecological and evolutionary processes. It deserves consideration whenever a study system includes nonlinear processes. The inequality is not a biological phenomenon *per se* but instead a mathematical consequence of the nonlinear form of many biological functions and the variance inherent in many environmental factors. Progress in our understanding of the role of environmental variance in ecology and evolution will be accelerated if Jensen's inequality becomes as familiar to ecologists as the central limit theorem.

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The behaviour–conservation interface

Tim Caro

In the past four years, there have been several attempts to apply studies of animal behaviour to conservation. Knowledge of individuals' behaviour has the potential to alter understanding of how populations fare in fragmented habitats, the responses of populations to exploitation and disturbance, disease susceptibility, effective population size, captive breeding and reintroduction efforts, and population monitoring and modelling. It can even be useful in understanding human conservation actions.

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Enormous advances in understanding animal behaviour have yet to penetrate attempts to conserve animal populations. First, conservation biology has successfully emerged from population ecology (incorporating measures of birth, death, immigration and emmigration), from population genetics (using genetic variation and genetic population structure) and from systematics (relying on traditional and molecular techniques to reconstruct phylogenies) without incorporating much animal behaviour. Second, any use of behavioural knowledge has never been expounded by the behavioural community or explicitly recognized by conservation biologists. Third, there is a conceptual divide between the study of variation in behaviour of individuals and the study of the response of populations to deterministic and stochastic events. Finally, there is a view among ethologists and behavioural ecologists that conservation biology lacks theoretical backbone. So, is there any conceptual or practical point in bridging these two disciplines? Three recent edited volumes, five reviews and a special edition of a journal totalling 106 authors think that there is[1–9]. Although none of them is suggesting that behavioural study has the answer to all conservation problems[10], there is a breaking wave of enthusiasm for linking these fields. Here, I discuss this interdisciplinary interface by demonstrating how practical and conceptual issues in conservation biology can benefit from a knowledge of indiviual behavior and pinpoint where future research would be most profitable.

Fragmented habitats

The principal cause of species' extinctions is habitat loss and fragmentation[11]. Conservation biologists have developed metapopulation dynamics to predict populations' responses to fragmentation[12] and these require assumptions about ranging behaviour and individual dispersal distances. For instance, colonization of unoccupied habitats, 'rescue' effects of low density patches, and source–sink effects depend on factors such as dispersal distance, the influence of landscape on individual movements and conspecific attraction. There are several studies with data on dispersal distances and a few on environmental and social factors affecting movement and settlement patterns that could be fed into metapopulation models or used in practical management plans. In general, however, few empirical data on ranging and dispersal have been collected in fragmented habitats (but see Ref. 13) leaving controversial models, such as those for the spotted owl (*Strix occidentalis*), open to challenge by opposing interests[14].

Reserve design has dogged conservation biology for years, initially in the form of the 'single large or several small' debate, and now in regard to connectivity between reserves or habitat patches[15]. If we knew more about species' ranging