Ecol Res (2008) 23: 665–671
DOI 10.1007/s11284-007-0425-5

ORIGINAL ARTICLE

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Individual behavioral variation in predator–prey models

Received: 15 March 2007 / Accepted: 24 August 2007 / Published online: 16 October 2007
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Abstract The role of individual behavioral variation in community dynamics was studied. Behavioral variation in this study does not refer to differences in average responses (e.g., average response between presence and absence of antipredator behavior). Rather it refers to the variation around the average response that is not explained by trivial experimental treatments. First, the effect of behavioral variation was examined based on Jensen's inequality. In cases of commonly used modeling framework with type II functional response, neglecting behavioral variation (a component of encounter rate) causes overestimation of predation effects. The effect of this bias on community processes was examined by incorporating the behavioral variation in a commonly used consumer-resource model (Rosenzweig–MacArthur model). How such a consideration affects a model prediction (paradox of enrichment) was examined. The inclusion of behavioral variation can both quantitatively and qualitatively alter the model characteristics. Behavioral variation can substantially increase the stability of the community with respect to enrichment.

Keywords Jensen's inequality · Adaptive behavior · Paradox of enrichment

Introduction

Community dynamics are the product of behavioral processes. In the Lotka–Volterra model and its many variants, behavioral processes such as predation and reproduction are modelled to produce community dynamics. For example, functional responses describe the effect of predation (Holling 1959; Murdoch et al. 2003; Turchin 2003). Suppose we denote R to describe the density of prey; two commonly used functional responses, type I and type II, respectively, are CR and $(CR)/(1 + ChR)$ where C and h represent encounter rate and handling time, respectively.

Regardless of the choice of functional responses, there is a parameter that represents encounter rate C. This parameter describes the encounter rate between predators and prey and is considered to be affected by both predator and prey behavior (e.g., Abrams 1992). For example, a predator's foraging effort such as "rate of movement" may alter the encounter rate with prey (e.g., increase in movement rate may increase C). Similarly, prey may exhibit antipredator behaviors (Lima and Dill 1990; Caro 2005). For example, wolf spiders exhibit a gradient level of activity (e.g., movement speed) in response to the intensity of a predator's (larger spider species) chemical cue (Barnes et al. 2002). If prey exhibit antipredator behavior and decrease their activity, such a behavior can reduce the encounter rate between predators and prey. Considerable attention has been given to understanding how such behaviors might affect community dynamics (Bolker et al. 2003; Werner and Peacor 2003).

In theoretical investigations (mainly differential equation models), one common assumption is that average interactions can effectively approximate the true dynamics. When this assumption is not reasonable, models that are explicit about some ecological factor are developed to accommodate the heterogeneity. For example, suppose large individuals are more efficient in capturing prey than small individuals; ignoring this individual variation and using the average characteristics (e.g., treating all individuals as intermediate size) can then lead to an inaccurate prediction (discussed in more detail below). Thus, size-structured models that explicitly treat this type of individual variation are developed (Tuljapurkar and Caswell 1997; de Roos et al. 2003). Likewise, when prey individuals exhibit distinct defensive behaviors, morphologies or life history changes to avoid predation, models that explicitly incorporate these differences are developed (e.g., Vos et al. 2002, 2004a, b). Other types of explicit models such as stoichiometrical models (e.g., Andersen et al. 2004) and spatial models

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(e.g., Bolker et al. 2000) were developed because it was recognised that variation among individuals caused by those factors is important. The existence of a wide variety of explicit models indicates that ecologists have long been concerned about variations that are observed among individuals.

Despite the attempt to explain variation based on ecological factors, behavioral variation among individuals remains large even with an explicit consideration of those ecological factors. For example, on average, tadpoles move less when they are in the presence of predators than in the absence of predators (Anholt et al. 2000), consistent with assumptions made in some models (e.g., Abrams and Vos 2003). However, among individuals that are in the same condition (e.g., absence of predators), they exhibit a large behavioral variation (Anholt et al. 2000). This type of behavioral variation is common even in controlled laboratory experiments where each organism experiences a nearly identical environment with controlled physiological state (e.g., starvation level). In functional response studies where researchers introduce a pre-conditioned predator into identical environments, predators still exhibit a large variation in the number of prey they capture in a given time (e.g., Putra and Yasuda 2006; Rossi et al. 2006; Kagawa and Maeto 2007). These large behavioral variations among individuals in artificially controlled experiments suggest that such variation is expected to be even larger in the field (even in places that are typically considered homogeneous environments such as agricultural fields).

The purpose of this study is to discuss the role of behavioral variation in community dynamics. In this study, "behavioral variation" refers to the background behavioral variation (e.g., variation not described by some experimental treatments) discussed above. Thus, commonly treated variation (e.g., difference in mean effect—presence vs absence of antipredator behavior) is not the focus (e.g., Vos et al. 2004a). First, I discuss Jensen's inequality as it is one mechanism describing how such variation affects the model prediction. I then extrapolate such variation in a common predator–prey model (i.e., Rosenzweig–MacArthur model) and discuss the effect of behavioral variation on community dynamics.

Jensen's inequality

One of the ways that behavioral variance affects the model expectation is through Jensen's inequality (Ruel and Ayres 1999; Inouye 2005). Suppose predation is characterized by a type II functional response, $(CR)/(1 + ChR)$, and we want to predict how the predation rate changes with varying foraging effort. If we assume encounter rate linearly increases with foraging effort, $C = ac$ where c is foraging effort (e.g., movement rate) and a is a scaling parameter that converts foraging effort to an encounter rate, then the functional response is a concave down function in foraging effort (Fig. 1, left).

Suppose these predators practice a biphasic foraging pattern (e.g., low activity or high activity) where individuals that forage at low effort gain a low reward (A) and individuals that forage at high effort gain a high reward (B). If half the population forages at low effort and the other half forages at high effort, resource gain is $(A + B)/2$ on average. However, if we ignore the behavioral variation and use the average foraging effort, the model predicts much higher prey intake, $F > (A + B)/2$, (Fig. 1, left). Similarly, one can show that the variation in handling time causes an underestimation of the actual effect (Fig. 1, right). These examples clearly show that ignoring behavioral variation can cause quantitative bias in model prediction; summarizing behavioral trait by an average leads to an inaccurate model prediction.

Actual behavioral variation is not always as extreme as in the example (e.g., high or low) and is represented by a number of different outcomes (e.g., Barnes et al. 2002; Rossi et al. 2006). If we describe the variation in foraging effort c with a probability distribution, $c \sim f(\cdot)$, the expected effect of the functional response is

$$E\left(\frac{CRN}{1+ChR}\right) = \int_x \frac{axRN}{1+axhR} f(x)\,\mathrm{d}x \qquad (1)$$

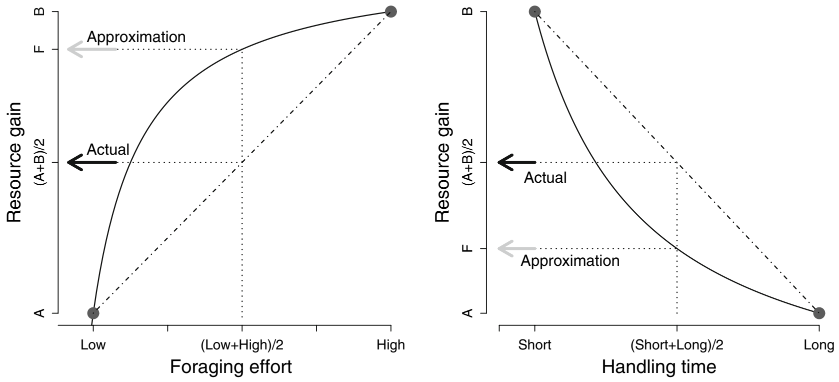

Fig. 1 An example illustrating the difference in expectation of type II functional response when behavioral variance is explicitly considered or average behavioral trait is used. The *solid line* shows the relationship between resource gain and foraging effort (*left*) and handling time (*right*) based on type II functional response

by using a standard probability property. In general, when the effect function (e.g., functional response) is concave down as in the example, ignoring variation will results in overestimation of effect,

$$E\left(\frac{CRN}{1+ChR}\right)<\frac{aE(c)RN}{1+aE(c)hR} \tag{2}$$

On the other hand, when the effect function is concave up (e.g., effect of variation in handling time h in type II functional response; Fig. 1, right), the inequality direction changes.

In this example (i.e., $C = ac$), expectation of type I functional response is not affected by variation in c because the relationship between the type I functional response and c is linear. Nevertheless, this does not mean that behavioral variation is not important in cases of type I functional response. For example, in cases of predators' movement pattern; it is possible that movement affects the encounter rate in a nonlinear manner (e.g., $C = ac/(b + c)$, where a and b are parameters). Theoretical studies suggest that a common surrogate of foraging effort may not linearly relate to encounter rate (Travis and Palmer 2005; Ruxton 2005). This type of consideration is important, especially when one tries to connect theory and data, but here I will not focus on the relationship of how a particular realization of behavior relates to a model.

The model

The example I use to illustrate the effect of behavioral variation on community dynamics is the paradox of enrichment (Rosenzweig 1971). I use the Rosenzweig–MacArthur model (Rosenzweig and MacArthur 1963),

$$\frac{dR}{dt}=rR\left(1-\frac{R}{K}\right)-\frac{CRN}{1+ChR} \tag{3}$$

$$\frac{dN}{dt}=\frac{bCRN}{1+ChR}-dN \tag{4}$$

where the simple encounter rate assumption $C = ac$ of predators on prey is assumed. N and R are predator and prey densities, respectively. Other parameters, r, K, h, b, d, indicate intrinsic rate of prey growth, carrying capacity of the environment for prey, predators' handling time, predator conversion efficiency, and the density-independent death rate of predators, respectively.

Paradox of enrichment

In this model, the predator isocline ($dN/dt = 0$) is vertical at $R_{\text{pred}} = d/[C(b - dh)]$, and the prey isocline is symmetrically hump-shaped, where the tip of the hump is at $R_{\text{tip}} = [K - 1/(Ch)]/2$ (Fig. 2). It is well known that when predator isocline intersects with prey isocline of negative slope (i.e., $R_{\text{pred}} > R_{\text{tip}}$; e.g., K_{small} in Fig. 2), Jacobian analysis shows that equilibrium to be stable, and when predator isocline is left of the hump, it is unstable (Rosenzweig and MacArthur 1963; Hastings 1997). Because an increase in K does not affect predator isocline, the increase in K will eventually place the predator isocline left of the hump, $R_{\text{pred}} < R_{\text{tip}}$, making the equilibrium unstable (Fig. 2), leading to a limit cycle. Further increasing K will increase the amplitude of the limit cycle, making the community unstable. This theoretical prediction is confirmed by laboratory studies (Bohannan and Lenski 1997; Fussmann et al. 2000), but field studies do not tend to support this pattern (e.g., Murdoch et al. 1998). This inconsistency may be attributed to a number of factors, and a variety of models that include some specific details (e.g., existence of refuge, alternative prey, density-dependent death rate of predators, inducible defenses) to resolve the inconsistencies have been created (Abrams and Walters 1996; Genkai-Kato and Yamamura 1999; Vos et al. 2004a, b).

Here I examine how the inclusion of behavioral variation affects the model conclusion. As a comparison to an existing model, I used the model developed by Genkai-Kato and Yamamura (1999), where they show that inclusion of alternative prey species of a specific benefit effectively reduces the effect of enrichment discussed above. In this model, predators always attack the primary prey species but attack the secondary (less beneficial) prey species only when the primary species density is sufficiently low (for the derivation of this theory, see Stephens and Krebs 1986). The specific description of their model is given in the Appendix.

Inclusion of behavioral variation

Because a typical surrogate of foraging effort, such as movement rate, is represented by a non-negative real

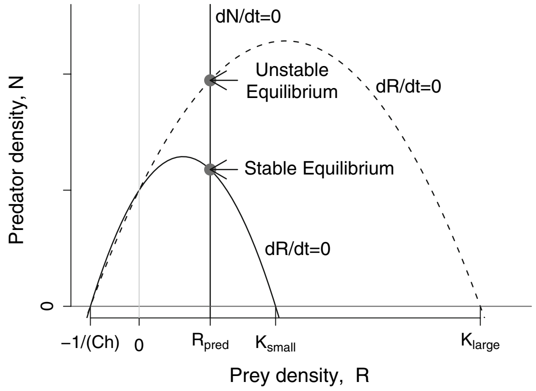

Fig. 2 Phase-plane for Rosenzweig–MacArthur model for two different carrying capacities, with all other parameters held constant. In this example, when carrying capacity is small (K_{small}), the equilibrium is stable (see text), but when carrying capacity is increased (K_{large}), the equilibrium becomes unstable. Predator isocline ($dN/dt = 0$) is a vertical line (i.e., $R = R_{\text{pred}} = d/[C(b - dh)]$) and is not affected by carrying capacity

value, gamma distribution was used to describe the variation in foraging effort c,

$$c \sim \mathrm{Gamma}(\alpha, \beta) \tag{5}$$

where $E(c) = \alpha\beta$ and $V(c) = \alpha\beta^2$. I examined the effect of behavioral variation based on the expectation (e.g., Eq. 2) of the original model,

$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR\left(1 - \frac{R}{K}\right) - \int_0^\infty \left(\frac{axRN}{1 + axhR}\right) f(x)\mathrm{d}x \tag{6}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \int_0^\infty \left(\frac{baxRN}{1 + axhR}\right) f(x)\mathrm{d}x - dN \tag{7}$$

where $f(x) = \mathrm{Gamma}(\alpha, \beta)$.

To compare the behavior of the model (Eqs. 6, 7) with the results of Genkai-Kato and Yamamura (1999), the same parameters used in their model were used. The average encounter rate C used in their model was 1. To make the expectation of encounter rate the same, I used $E(c) = 0.5$ and $a = 2$ such that the expected encounter rate $E(C)$ is the same for both models.

Types of behavioral variation

Little is known about how variance $V(c)$ changes with environmental variables because most studies have focused on how the environment affects the mean response. I considered two simple scenarios representing density-independent and density-dependent behavioral variation.

Density-independent behavioral variation is a scenario where $V(c)$ is fixed regardless of the environmental variables. When $V(c)$ is fixed to zero, it is reduced to the original Rosenzweig–MacArthur model. In the density-dependent behavioral variation model, I assumed that the behavioral variation changes with density of prey and conspecifics. Variance of foraging effort was assumed to decrease with resource density and increase with conspecifics density, $V(c) = 2.5\mathrm{e}^{-0.5R/N}$. For both types of behavioral variation, the parameters of gamma distribution were obtained by using the method of moment (i.e., $\alpha = m^2/v$, $\beta = v/m$ where m and v are the mean and variance of gamma distribution).

Results

In the standard Rosenzweig–MacArthur model without alternative prey or behavioral variation, even the lowest carrying capacity considered in this study (i.e., $K = 4$) leads to an oscillation. Increases in K lead to a larger amplitude of the cycle that goes through very low density, making populations vulnerable to stochastic extinction (Fig. 3a).

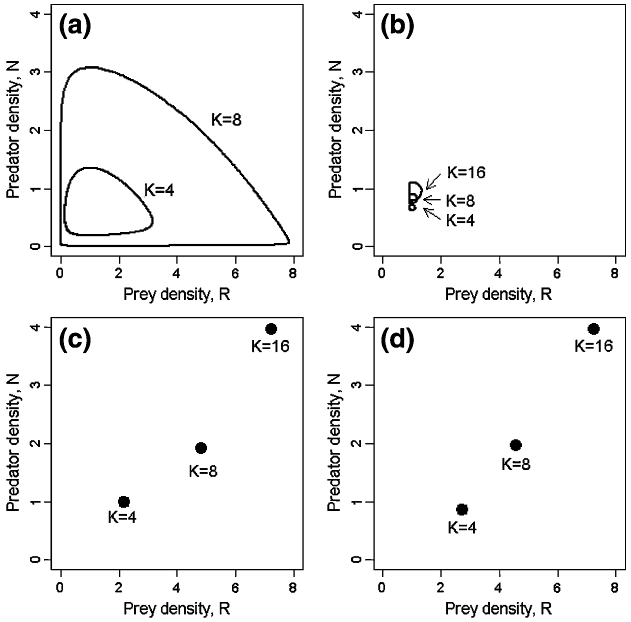

Fig. 3a–d Community response to enrichment (i.e., increase in K). **a** Standard Rosenzweig–MacArthur model. **b** Inclusion of moderately profitable alternative prey (Genkai-Kato and Yamamura 1999). **c** Inclusion of density-independent variance in individual behavior. Variances were arbitrarily chosen such that the system is stable at each level of carrying capacity [$V(c) = 0.4, 0.8, 1$ for increasing level of K]. **d** Inclusion of density-dependent variance in behavior. In **c** and **d**, *dots* indicate stable equilibrium. For the parameter values used in the models, see Appendix

Inclusion of alternative prey that are moderately profitable effectively reduces the amplitude of the cycle (Fig. 3b). This result is taken directly from Fig. 2 of Genkai-Kato and Yamamura (1999). They found that the community dynamics are sensitive to the profitability of the two prey types, and when the less profitable prey is "moderately profitable", the system becomes stable. This occurs because when the primary prey density becomes sufficiently low, predators include the second prey type in their diet. Due to the dilution effect, this helps the primary prey population to increase faster than in the absence of the secondary prey type (e.g., decreasing the size of oscillation). The profitability of the secondary prey determines the timing of foraging strategy switch (i.e., include or exclude the secondary prey). When the secondary prey is profitable, inclusion of the secondary prey occurs faster, which also increases the predator density and the amplitude of the oscillation. Thus, the key elements of the model are the predator's optimal foraging behavior and the profitability of the alternative prey species.

When behavioral variance $V(c)$ is constant, the predator isocline remains vertical and is not affected by the carrying capacity; however, increase in the variance moves the predator isocline to the right (Fig. 4a).

The prey isocline is also affected by behavioral variation, but behavioral variation does not affect the qualitative model prediction because R_{tip} is not affected

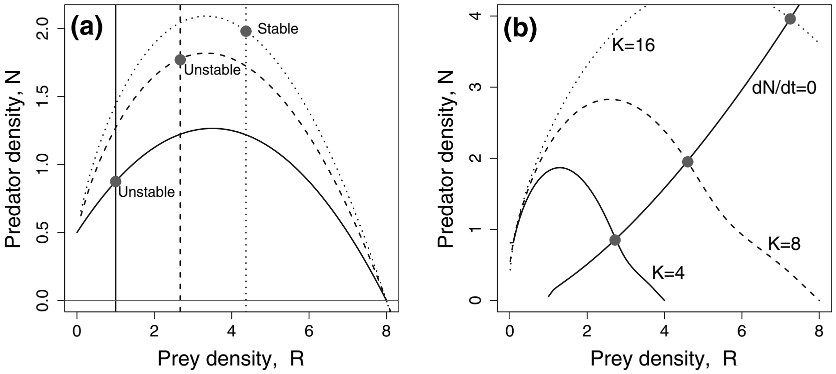

Fig. 4a,b Phase-plane diagrams. **a** Constant behavioral variation when $K = 8$. *Vertical lines* are predator isoclines for variable behavioral variances. *Hump shaped lines* are associated with prey isoclines. Behavioral variances, $V(c)$, used are 0 (*solid*), 0.5 (*dashed*), and 0.75 (*dotted*). **b** Density-dependent behavioral variation. This phase-plane corresponds to Fig. 3d. *Hump shaped lines* are prey isoclines for varying carrying capacity. Predator isocline is the same for all carrying capacity levels

(Fig. 4a). Therefore, behavioral variation would have a generally stabilizing effect by shifting the predator isocline to the right of the hump although it can shift the predator isocline beyond the right side of the hump, which will exclude the predator population from the community.

It is worth noting that if behavioral variation reduces the foraging efficiency on average, a similar effect can be produced by assuming that the variance is negligible as in conventional models [i.e., $V(c) = 0$] but also assuming a lower attack efficiency a. In fact, lowering the attack efficiency a will have a similar effect as increasing the behavioral variance. Thus, in this simple example, qualitative model prediction can potentially be examined with the model without behavioral variance if we recognize the mechanistic effect of the variance.

Density-dependent behavioral variance affects the isoclines in a qualitatively different manner. For example, predator isocline is no longer a vertical straight line (Fig. 4b). This occurs because, at a particular prey density, R, an increase in predator density will increase behavioral variance by the model assumption, which decreases the fitness of predator individuals on average. Thus, unlike the previous examples, the per capita fitness of predators depends on their own density. The prey isocline's hump shape becomes larger than the in the case where $V(c) = 0$. This is because the behavioral variation makes the predation pressure weaker, and thus prey can sustain themselves at higher predator density. In addition, the tip of the hump moves to left. Although increasing K arbitrarily would eventually place their intersection left of the hump (i.e., unstable equilibrium), the combination of these two isoclines' characteristics makes it more likely that the two isoclines intersect in a stable manner (Fig. 4b). Furthermore, the tilted predator isocline no longer assures that the system is unstable even when the isoclines intersect left of the hump, further enhancing the stability of the community.

Discussion

In this study, I demonstrated that behavioral variation can cause a substantial shift in community dynamics. I discussed how behavioral variation affects a component of model prediction with Jensen's inequality (Fig. 1) and extended the results into a common consumer-resource model. Although I used a particular example to illustrate the effect of behavioral variation, Jensen's inequality is a statistical fact, and thus the variance effect would appear in any model with a nonlinear effect function. Because behavioral variation is particularly large, it is likely to affect the model prediction in a profound manner.

Although I focused on the variance of the foraging effort (parameter c in the model), all other parameters exhibit variation. For example, a predator's optimal foraging behavior was a key component of the model of Genkai-Kato and Yamamura (1999). In the past, variation around this behavior caused some debate about how to contrast theoretical prediction and data (Krebs et al. 1977; Stephens 1985). Thus, even at behavioral level processes, existence of variation make it difficult to test model predictions (Stephens 1985). At community level processes, variation is around multiple parameters, each of which may behave independently or be dependent on one other. Empirical characterizations of variations as well as further theoretical investigations are needed to fully appreciate the importance of individual variations in community processes.

In the constant variance scenario, I explained how behavioral variance could be effectively examined without explicitly considering it. This kind of exercise is important, especially when one tries to connect theory and data. For example, in the analysis of differential equations, it has become common to assume parameters that are obtained empirically (mean estimates) to explore the behavior of the models. Although simple models may qualitatively predict system behavior (e.g., how it responds to an increase in a particular parameter), it can be misleading to make quantitative arguments (e.g., whether it is stable) by simply substituting empirically estimated parameters in the model. For example, a set of parameters may indicate that the community is unstable based on a model without behavioral variation (e.g., Eqs. 3, 4), but this quantitative prediction is biased when behavioral variance is present, and the community may be stable when the variance is explicitly considered (Fig. 4a). Similarly, although rarely discussed, even when examining the qualitative behavior of the model, researchers must make some kind of quantitative argument. For example, suppose one examines how the community responds to an enrichment (i.e., increase in K), one must make sure that the range of K examined is wide enough to include the bifurcation point (e.g., a point in K that divides the system into stable or unstable)—a quantitative argument. In some systems, certain factors may move the bifurcation point high enough that it is biologically unfeasible to test it even if it exists theoretically.

In the density-dependent behavioral variance, I assumed a specific form because we know little about how behavioral variance is affected by exogenous and endogenous factors. Although I employed the predator–dependent variance expression as an example and obtained results that are qualitatively similar to those where predator dependence is directly modelled as the mean response (Beddington 1975; DeAngelis et al. 1975), any density-dependent form of variance would qualitatively alter the model prediction. The distinction between predator- or prey-dependent functional response has been discussed before (Abrams and Ginzburg 2000), and the mechanistic interpretation of models (e.g., events occurring continuously) is used against predator dependence (Jensen and Ginzburg 2005). The explicit consideration of behavioral variance may provide some reconciliation, as predators' basic behavioral expressions (e.g., movement rate) may respond to graded environmental cues quickly.

One source of variation may be the foragers' decision process. Suppose that foraging effort c depends on resource and predator densities (Abrams 1992). In such models, foragers choose their foraging effort based on the density of predators and prey (i.e., mean of behavior, c, is a function of predator and resource densities). If foragers guess (perceive) actual densities of predators and resources based on their experiences (e.g., encounter events), then the higher the densities of predators and resources, the smaller the variance in experience among foragers. Although understanding how such internal perception is shaped and how it affects actual behavioral expression is a future research topic, decision–theoretical models are promising tools with which to gain mechanistic understanding of the variation because of their explicit consideration of uncertainty (Dall et al. 2005). Furthermore, density-dependent variance expression may evolve as part of an optimal foraging strategy where not only mean but also variance is a trait that can be modified by animals. Theoretically examining these details may be worthwhile in order to utilize behavioral data more efficiently.

Variation is typically treated as a nuisance in most studies. Prevalent use of nonparametric statistics in behavioral studies, for example, indicates our disinterest in actual distributions of data as well as the existence of a potentially rich distribution of behavioral expressions among individuals. While interest in uncovering the effect of individual behavior on population and community level processes has been solid (Bolker et al. 2003; Werner and Peacor 2003), we have largely ignored the ubiquitous large variance that we see in empirical documentation. Paying attention to variation (in addition to mean) and thus utilizing the data more (instead of throwing variance away as a nuisance) may shed light on many of outstanding ecological problems.

Acknowledgments I thank Ben Bolker, Chris Jensen, and an anonymous reviewer for their insightful comments.

Appendix: Model from Genkai-Kato and Yamamura (1999)

There are two prey species R_1 and R_2 and predators N that consume them.

$$\frac{\mathrm{d}R_1}{\mathrm{d}t} = r_1 R_1 \left(\frac{K_1 - R_1 - \alpha_{12} R_2}{K_1} \right) - \frac{p_1 C_1 R_1 N}{1 + p_1 C_1 h_1 R_1 + p_2 C_2 h_2 R_2} \tag{8}$$

$$\frac{\mathrm{d}R_2}{\mathrm{d}t} = r_2 R_2 \left(\frac{K_2 - \alpha_{21} R_1 - R_2}{K_2} \right) - \frac{p_2 C_2 R_2 N}{1 + p_1 C_1 h_1 R_1 + p_2 C_2 h_2 R_2} \tag{9}$$

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \frac{b_1 p_1 C_1 R_1 N}{1 + p_1 C_1 h_1 R_1 + p_2 C_2 h_2 R_2} + \frac{b_2 p_2 C_2 R_2 N}{1 + p_1 C_1 h_1 R_1 + p_2 C_2 h_2 R_2} - dN \tag{10}$$

Parameter description follows the basic model described in the main text. New parameters are competition coefficients, α_{12} and α_{21} that describe the competitive effect of prey species 2 on species 1 and vice versa, respectively. p_1 and p_2 are the probability that predators will attack prey species 1 and species 2, respectively. For this behavioral strategy of predators, optimal foraging behavior was assumed. Assuming that species 1 is more profitable (i.e., $b_1/h_1 > b_2/h_2$), predators should always attack species 1 (i.e., $p_1 = 1$). The theory suggests that p_2 is either 0 or 1 and does not hold an intermediate value (Stephens and Krebs 1986) and can be determined by the following rule,

$$p_2 = \begin{cases} 0 & \text{if} \quad \frac{b_1 C_1 R_1}{1 + C_1 h_1 R_1} > \frac{b_2}{R_2} \\ 1 & \text{otherwise} \end{cases} \tag{11}$$

Parameter values used in this study were $r_1 = 0.5$, $r_2 = 0.25$, $d = 0.25$, $\alpha_{12} = 0.1$, $\alpha_{21} = 0.4$, $C_1 =$

$C_2 = 1, b_1 = b_2 = 0.5, h_1 = 1, h_2 = 2.083$. In Fig. 3b, dynamics for R_1 and N is plotted. For the model with behavioral variance, the same parameter values for the prey species 1 were used.

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