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Covariation between mean vole density and variability drives the numerical

response of storks to vole prey

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Abstract

Hušek et al. (2013, Popul Ecol 55:363–375) showed that the numerical response of storks to vole prey was stronger in regions where variability in vole density was higher. This finding is, at first sight, in contradiction with the predictions of life-history theory in stochastic environments. Since the stork productivity-vole density relationship is concave, theory predicts a negative association between the temporal variability in vole density and stork productivity. Here, we illustrate this negative effect of vole variability on stork productivity with a simple mathematical model relating expected stork productivity to vole dynamics. When comparing model simulations to the observed mean density and variability of thirteen Czech and Polish vole populations, we find that the observed positive effect of vole variability on stork numerical response is most likely due to an unusual positive correlation between mean and variability of vole density.

In a recent issue of Population Ecology (**55**: 363–375), Hušek et al. (2013) reported on the spatial variation in the strength of the numerical response of white storks (*Ciconia ciconia* Linnaeus, 1758) to common voles (*Microtus arvalis* Pallas, 1778). In thirteen regions of Czech Republic and Poland, the numerical response of storks, measured as the correlation between nestling productivity and local vole density, was shown to be stronger in regions where vole numbers were more variable (see Fig. 4 in Hušek et al. 2013).

Life-history theory predicts that temporal variability in resource abundance can positively affect individual fitness (approximated by the long-run population growth rate, $\ln(\lambda)$, or some other appropriate fitness measure; Brommer 2000), but only when the relationship is convex (Pásztor et al. 2000; Koons et al. 2009; Barraquand and Yoccoz 2013). This is due to Jensen's inequality, which we illustrate with a simple graphical model in Fig. 1. Yet, the overall relationship between stork productivity and vole density in the Czech and Polish populations was not convex, but concave (i.e., a logarithmic function fits the data, and this function is concave; see Fig. 2b in Hušek et al. 2013). This finding is at odds with the theory, assuming that variation in fitness in long-lived storks is mainly determined by productivity and less so by high and constant survival (Schaub et al. 2004, Schaub et al. 2005).

Here we discuss an alternative explanation for the positive relationship under the lack of convexity. Namely, we suggest that the positive effect of variability in vole density on the numerical response of storks arises from its co-variation with mean vole density. A major effect of mean density and a smaller effect of variability in prey numbers on population dynamics of predators has been shown in for example the arctic fox (*Alopex lagopus*; Henden et al. 2008) and the long-tailed skua (*Stercorarius longicaudus*; Barraquand et al. 2014).

In Fig. 2, we plot the expected productivity $E[P]$ against both the mean and variability (CV) in vole density over the period 1982–1988 for the thirteen populations of voles studied in Hušek et al.

(2013). $E[P]$ is computed as stork productivity for a given vole density (not accounting for local specialization), and is multiplied by the probability density for the particular vole density value v, and integrated over the whole probability distribution $f(v)$ (Eq. 1; see also Barraquand et al. (2014) for the use of a similar technique). The numerical integration was performed in Matlab using adaptive Gauss-Kronrod quadrature ('quadgk' function). The formula is as follows:

$$E[P] = \int P(v) f(v) \, dv \; ; P(v) = \alpha + \beta \ln(v) \quad (1)$$

with $\alpha = 0$, $\beta = 0.6118$ (estimated from the GAM regression in Hušek et al. 2013).

CV is a somewhat better measure of variability than the S-index (Krebs 2013), unless log-linear models for observation error are used (McArdle and Gaston 1995), even though S-index and CV are rather tightly related. We realistically assume that vole densities follow a lognormal distribution.

Fig. 2 reveals that while the effect of the mean vole density on E(P) is positive and rather large, the effect of CV is negative and small (this small negative effect is due to the abundance distribution asymmetry, see Fig. 5 in Barraquand et al. 2014). The observed increase of productivity with CV and S-index can therefore only be due to the correlation between mean and CV (Pearson's correlation coefficient = 0.76). Note that the use of indices reconstructed from density categories might have removed some noise present in the true CV - mean density relationship (see Tkadlec et al. 2006 for a detailed methodology), thus the reported correlation is only approximate. However, we focus here on the positive sign of the correlation, which is not sensitive to this empirical procedure.

From an empirical perspective, our results suggest that storks are more likely to choose their diet based on an "estimation" of the average abundance over several years (or using some other "rule of thumb"), than by specializing on voles in places with more temporal variability. From a more general perspective, our results also relate to Taylor's law (its temporal version, see e.g., Kilpatrick and Ives 2003). Taylor's law suggests that most populations fulfill a relationship Variance = $a * $ Mean^b, with the exponent b lying mostly between 1 and 2, which is another way of expressing the correlation between

mean and CV, more familiar to most ecologists. Indeed, CV = (a Mean^b)$^{1/2}$/Mean = a$^{1/2}$ Mean$^{b/2-1}$ and is thus negatively related to the mean if *b/2* < 1, or *b* < 2. There are exceptions to Taylor's law though, and in our particular case, CV is positively related to the mean (Fig. 2), which means *b* > 2. Best-fit estimates of *b*, for the Czech and Polish populations, can be 4 to 6 depending on the estimation method (the log-log regression log(Var) ~ log(Mean) yields a 95% confidence interval [2.22; 7.00]; in any case, it is above 2). Theoretical results show that an exponent of 1 occurs under pure sampling variation, while many population dynamics models generate an exponent closer to 2 (e.g., cyclic autoregressive models). Clearly not all the observed variation in estimates of Taylor's exponent is due to sampling error, and it has recently been suggested that interspecific differences in life histories might drive differences in Taylor's law exponent (Linnerud et al. 2013). Given that a mean-CV positive spatial correlation as observed here drives predator specialization, it seems interesting to check whether positive covariation (equivalently, Taylor's exponent > 2) could occur in more populations.

Even more generally, recent work has focused on whether the environment changes mostly in mean or variability (Garcia-Carreras and Reuman 2013). Our results suggest that spatial covariation between mean and variability of environmental variables, such as food resources or climatic variables, can be paramount to understanding population fluctuations and the evolution of life histories.

Acknowledgements

References

Barraquand F, Yoccoz NG (2013) When can environmental variability benefit population growth? Counterintuitive effects of nonlinearities in vital rates. Theor Popul Biol 89:1–11

Barraquand F, Høye TT, Henden JA, Yoccoz NG, Gilg O, Schmidt NM, Sittler B, Ims RA (2013) Demographic responses of a site-faithful and territorial predator to its fluctuating prey: Long-tailed skuas and arctic lemmings. J Anim Ecol 83:375-387

Brommer JE (2000). The evolution of fitness in life history theory. Biol Rev 75:377–404

García-Carreras B, Reuman DC (2013) Are changes in the mean or variability of climate signals more important for long-term stochastic growth rate? PLoS ONE 8:e63974.

Henden JA, Bårdsen BJ, Yoccoz NG, Ims RA (2008) Impacts of differential prey dynamics on the potential recovery of endangered arctic fox populations. J Appl Ecol 45:1086–1093

Hušek J, Adamík P, Albrecht T, Cepák J, Kania W, Mikolášková E, Tkadlec E, Stenseth NC (2013) Cyclicity and variability in prey dynamics strengthens predator numerical response: the effects of vole fluctuations on white stork productivity. Popul Ecol 55:363–375

Kilpatrick AM, Ives AR (2003) Species interactions can explain Taylor's power law for ecological time series. Nature 422:65–68

Koons DN, Pavard S, Baudisch A, Metcalf JE (2009) Is life-history buffering or lability adaptive in stochastic environments? Oikos 118:972-980

Krebs C J (2013) Population fluctuations in rodents. University of Chicago Press, Chicago

Linnerud M, Sæther BE, Grøtan V, Engen S, Noble DG, Freckleton RP (2013) Interspecific differences in stochastic population dynamics explains variation in Taylor's temporal power law. Oikos 122:1207–1216

McArdle BH, Gaston KJ (1995) The temporal variability of densities: back to basics. Oikos 74:165–171

Pásztor L, Kisdi É, Meszena G (2000) Jensen's inequality and optimal life history strategies in stochastic environments. Trends Ecol Evol 15:117–118

Schaub M, Pradel R, Lebreton JD (2004) Is the reintroduced white stork (*Ciconia ciconia*) population in Switzerland self-sustainable? Biol Conserv 119:105–114

Schaub M, Kania W, Köppen U (2005) Variation of primary production during winter induces synchrony in survival rates in migratory white storks *Ciconia ciconia*. J Anim Ecol 74:656–666

Tkadlec E, Zbořil J, Losík J, Gregor P, Lisická L (2006). Winter climate and plant productivity predict abundances of small herbivores in central Europe. Clim Res, 32:99–108.
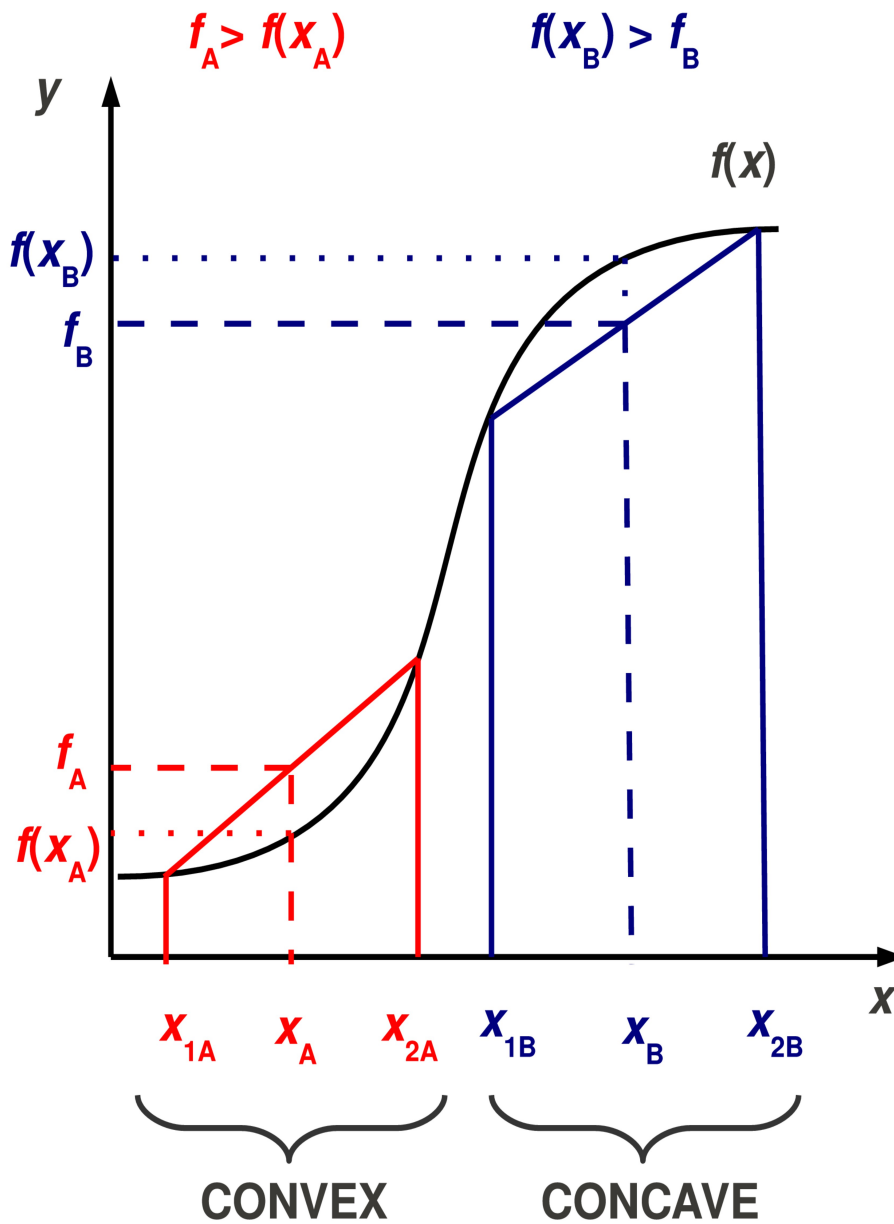
Figures

Fig 1. Illustration of Jensen's inequality with a two-point sample. The x-axis can represent any environmental variable, here it is best interpreted as vole density, while the y-axis should be interpreted as a measure of individual fitness (here, stork productivity). In the convex part (red in the online version) of the sigmoid curve, the mean function f_A is above the function of the mean $f(x_A)$, and any increase in variance will therefore increase the mean function f_A. It is the reverse in the concave part (blue in the online version).
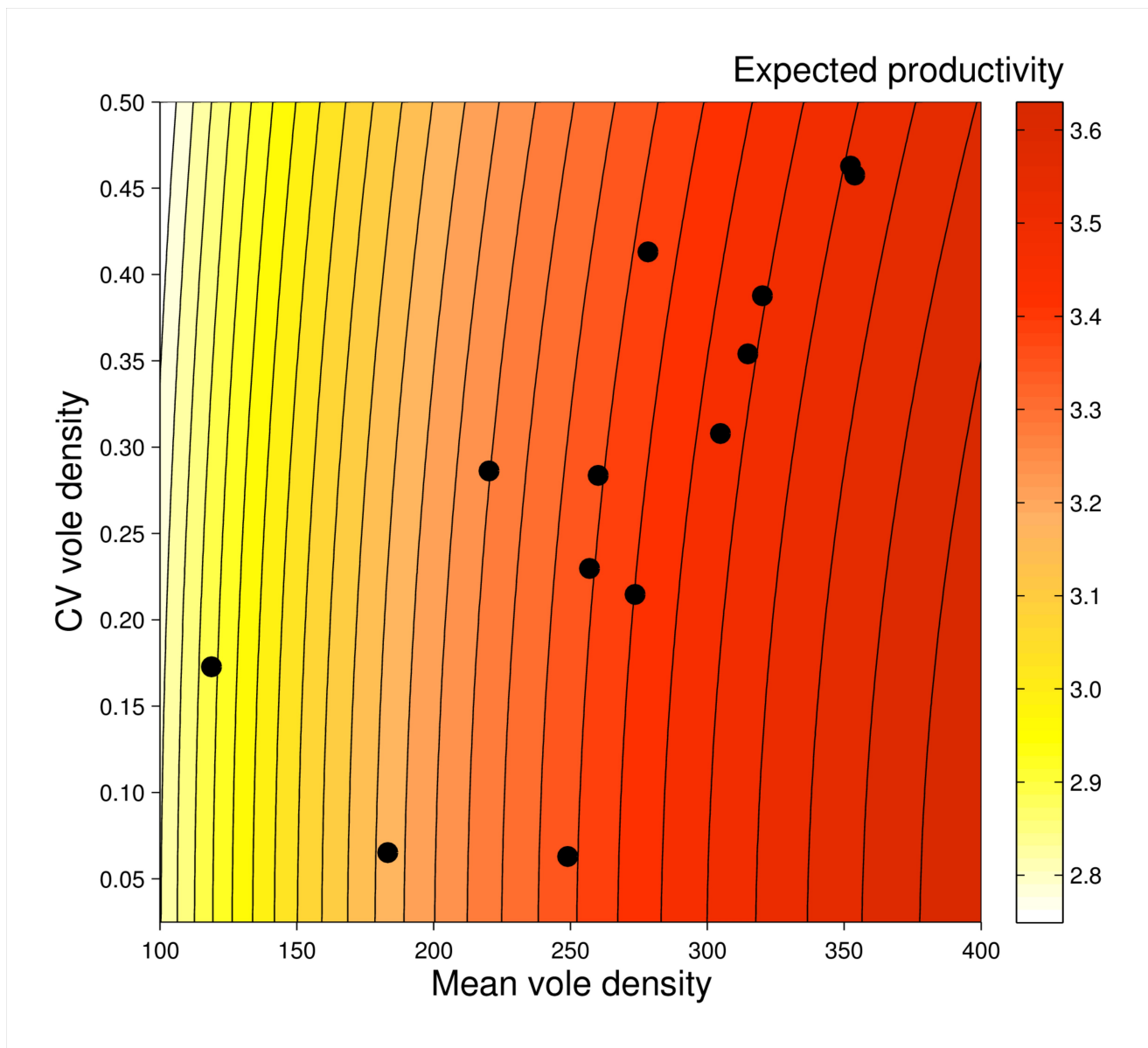
Fig 2. Expected productivity and its comparison with empirical data. The surface and contour plot shows $E[P]$ as a function of mean and CV of vole density, under the classic assumption of a log-normal distribution of vole density values (v). $P(v) = \alpha + \beta \ln(v)$, $\alpha = 0$, $\beta = 0.6118$ (estimated from the GAM regression in Hušek et al. 2013). Black circles represent the empirical mean and CV values for the thirteen Czech and Polish populations over the period 1982–1988, which are positively correlated (Pearson's $r = 0.76$).