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Author(s): N. L. Fowler and C. M. Pease
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Temporal Variation in the Carrying Capacity of a Perennial Grass Population

N. L. Fowler[1,*] and C. M. Pease[2]

1. Section of Integrative Biology, University of Texas, Austin, Texas 78759; 2. Environmental Law Center, Vermont Law School, South Royalton, Vermont 05068

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ABSTRACT: Density dependence and, therefore, K (carrying capacity, equilibrium population size) are central to understanding and predicting changes in population size (N). Although resource levels certainly fluctuate, K has almost always been treated as constant in both theoretical and empirical studies. We quantified temporal variation in K by fitting extensions of standard population dynamic models to 16 annual censuses of a population of the perennial bunchgrass *Bouteloua rigidiseta*. Variable-K models provided substantially better fits to the data than did models that varied the potential rate of population increase. The distribution of estimated values of K was skewed, with a long right tail (i.e., a few "jackpot" years). The population did not track K closely. Relatively slow responses to changes in K combined with large, rapid changes in K sometimes caused N to be far from K. In 13%–20% of annual intervals, K was so much larger than N that the population's dynamics were best described by geometric growth and the population was, in effect, unregulated. Explicitly incorporating temporal variation in K substantially improved the realism of models with little increase in model complexity and provided novel information about this population's dynamics. Similar methods would be applicable to many other data sets.

Keywords: Bouteloua rigidiseta, carrying capacity, density dependence, environmental stochasticity, population dynamics, population regulation.

Introduction

Understanding the factors that determine population size, always a core task of ecology, is becoming even more important as we are challenged to understand and to predict the effects of climate change, invasive species, and other anthropogenic impacts on natural ecosystems (Turchin 1999; Hixon et al. 2002; Sibly and Hone 2002; Boyce et al. 2006). Density-dependent processes are often very important in determining population size (Sibly et al. 2005; Brook and Bradshaw 2006), and the inclusion of density dependence in population dynamic models can be critical to their utility in conservation and resource management (Boyce 1992; Hixon et al. 2002; Lorenzen and Enberg 2002; Morris and Doak 2002). A better understanding and better models of density dependence are therefore desirable.

A common assumption of both empirical studies (e.g., Dennis and Otten 2000; Sæther et al. 2000; Todd et al. 2004; Zabel et al. 2006) and mathematical models (e.g., Lande 1993; Kendall 1998; Engen et al. 2005) is that density dependence (usually modeled with K, the carrying capacity) is constant in time. As a result of this assumption, temporal variation in population size (N) has been modeled separately from density dependence, often as additive stochastic variation in N or as stochastic variation in one or more vital rates. Here we test the assumption of constant K and measure the improvement in model realism gained by allowing K to vary in time, using data from a plant population.

An improvement in model realism is not the only potential benefit of allowing K to vary in time. Temporal variation in K represents temporal variation in density dependence and therefore in population regulation. Insights into otherwise inexplicable variation in N may be gained if variation that would otherwise simply be considered environmental stochasticity is discovered to be due to fluctuations in K. The estimates of K at time t (K_t) can provide a description of the environment as experienced by a particular species and can be used in tests of hypotheses about environmental causes of changes in N. Finally, estimates of K_t can be used to measure temporal variation in the effectiveness of density-dependent population regulation, by quantifying how well population size (N) tracks an ever-changing equilibrium population size (K, in our models).

To our knowledge, no one has previously explicitly estimated temporal variation in K in a natural population. However, temporal variation in K is a logical consequence of variation in resource levels. Our data come from censuses of a plant growing in a semiarid environment. Rain-

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[*] Corresponding author; e-mail: nfowler@uts.cc.utexas.edu.

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fall, via its effect on available soil moisture, was an obvious source of variation in a limiting resource, and we predicted that K would track rainfall. Rainfall, mediated through total plant biomass, is also an obvious limiting factor for large herbivores in arid climates. The majority of models that have implicitly incorporated variation in equilibrium population size have done so by incorporating the effects of rainfall into population models of large herbivores (e.g., Illius and O'Connor 2000; Davis et al. 2002; Owen-Smith 2002; Georgiadis et al. 2003; Chamaillé-Jammes et al. 2008). In most cases, the inclusion of rainfall-dependent variation in resource levels has improved the prediction of herbivore population sizes. Similar models have been constructed for rodents (Lima et al. 2006, 2008), for mosquitoes (Yang et al. 2008), and for large herbivores in a wet climate (Coulson et al. 2001; Hone and Clutton-Brock 2007). Stochastic variation in K is also implicit in some plant population studies that have estimated related population parameters (e.g., Freckleton and Watkinson 1998; Freckleton et al. 2000; Turnbull et al. 2004, 2007; Adams et al. 2005). There have also been a few theoretical explorations of the consequences of variation in K and in density-dependent population parameters in general (Turelli 1978; Gyllenberg et al. 1994; Ferriere et al. 2006).

Methods and Models

Data Set

Bouteloua rigidiseta (Steud.) Hitchc. is a bunchgrass (i.e., it has no vegetative reproduction). It is common in and frequently dominates shortgrass communities in central Texas grasslands and savannas. Seed is set in May and June, and successful seedling establishment usually occurs in October or November. We analyzed data from 16 annual early-summer (May/June) censuses of permanent 0.5-m^2 quadrats established as part of a long-running demographic study of *B. rigidiseta* in Pedernales Falls State Park, Texas (30.33°N, 98.26°W; Fowler 1984, 1995; Fowler et al. 2006). For the present analyses, a data set was constructed of 174 (N_t, N_{t+1}) pairs, each pair representing two consecutive annual censuses of a given quadrat. The maximum number of quadrats censused in a single year was 36 quadrats, and the minimum was six. Because the six control quadrats were censused in each of the 16 consecutive years, there are 15 annual intervals in the data set. Some of the other quadrats received experimental manipulations of *B. rigidiseta* density (Fowler et al. 2006). Added *B. rigidiseta* plants were excluded from the calculation of N_{t+1} of the interval in which they were added, and removed *B. rigidiseta* plants were excluded from the calculation of N_t of the interval in which they were removed. Limiting the analyses to the control quadrats would not have changed the qualitative results, with one exception (estimability of K_4), discussed below. The 174 (N_t, N_{t+1}) pairs were not fully independent, as plants that survived for more than 1 year sometimes contributed to more than one (N_t, N_{t+1}) pair. Additional information about census methods, construction of the data set, and the numbers of plants and tillers per quadrat each year is given in appendix A in the online edition of the *American Naturalist*.

The measure of density (N) used in the analyses in this article is the total number of tillers of *B. rigidiseta* in a quadrat. We used total tiller number rather than the number of plants per quadrat because the former is a better estimate of density than the latter for our purposes here. As is usually true of plant populations (Harper 1977), individual plants differed greatly in size (1–200 tillers), with a few large and many small individuals in each quadrat. The effect of a plant on its neighbors is proportional to its size (Fowler 1988). The number of tillers per quadrat is therefore much more closely related to density as it is perceived by a plant than is the number of plants per quadrat. Compared to a size-class-based analysis, our approach is both more tractable (many fewer parameters) and more accurate (because differences among quadrats in the sizes of their largest individuals are not obscured by pooling heterogeneous large plants into a single size class). Using a size-class-based analysis, we had previously discovered that this population experienced negative density-dependent population regulation in at least some quadrats and years, shown by a significant negative relationship between λ (the principal eigenvalue of each population projection matrix) and density (Fowler et al. 2006).

Alternative Models of Stochastic Population Dynamics

Using a maximum likelihood approach to estimate model parameters, we fitted our data set of 174 (N_t, N_{t+1}) pairs to several alternative population dynamic models of the general form $N_{t+1} = f(N_t, R, K) + \varepsilon$ (fig. 1), where ε is the difference between the predicted and observed values of N_{t+1} in each pair, $R + 1$ is the potential finite rate of increase in N, K (carrying capacity) is equivalent to equilibrium population size in these models, and R is the difference equation counterpart of r, the potential rate of population growth. We used the discrete logistic (Ricker 1954), the θ logistic (Gilpin and Ayala 1973; Sæther et al. 2002), and the full and reduced hyperbolic (Yoda et al. 1963; Watkinson 1980) population dynamic models (app. B in the online edition of the *American Naturalist*). Following Ludwig (1975), we included an additional model derived by transforming the coordinate system of the above-mentioned general model to look at the dynamics of small deviations from equilibrium density, $N_{t+1} = K(1 - \beta) + \beta N_t + \varepsilon$, where $f'(K) = \beta$ and equilibrium

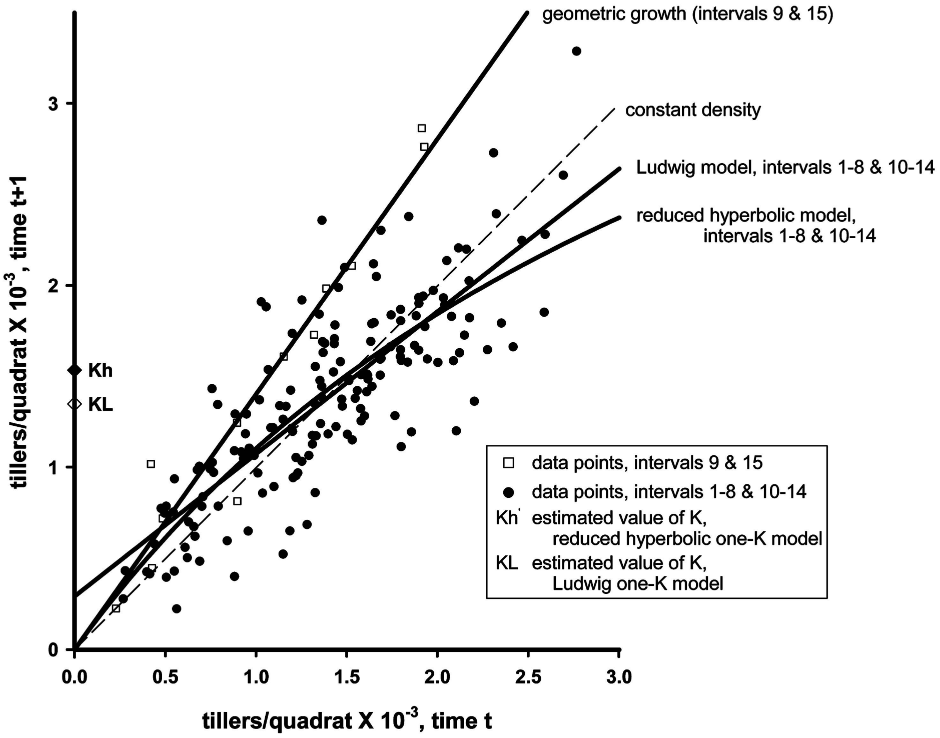

Figure 1: Relationship between density (N) at the beginning (t) and end ($t+1$) of an interval. Each point represents one of the 174 (N_t, N_{t+1}) pairs that comprise the data set. Lines are fitted for the Ludwig one-*K*/one-*R* model (excluding annual intervals 9 and 15), the reduced hyperbolic one-*K*/one-*R* model (also excluding annual intervals 9 and 15), and geometric growth in annual intervals 9 and 15. The dashed line (one-to-one line) represents constant population size. At the point where each of the fitted lines intersects the one-to-one line, the value of N_{t+1} is equal to the estimated value of K in the corresponding one-*K*/one-*R* model. The two estimated values of K are also shown as diamonds on the vertical axis. Note that the Ludwig model does not pass through the origin.

density K is defined as the solution of the equation $f(K) = K$. (Note that β and K do not correspond in a simple way to an intercept and slope, so a simple linear regression is not a useful model; app. B.)

After fitting these six models with both K and R constant (one-*K*/one-*R* models), we fitted models that allowed K, R, or both (or comparable parameters) to take on a different value in each annual interval. The multi-*K* models consistently failed to converge unless population growth in intervals 9 and 15 was modeled as geometric (fig. 1). For all models except the Ludwig, geometric-growth models were obtained by letting $K \rightarrow \infty$ (app. B). Because the Ludwig model does not reduce to a sensible geometric-growth model as $K \rightarrow \infty$, for it we used the geometric-growth model $N_{t+1} = \gamma N_t + \varepsilon$, where γ is a new parameter not in the density-dependent Ludwig model. We verified our identification of intervals best modeled with geometric growth using a procedure that maximized likelihood for each interval separately (app. B).

If the analyses had been limited to the control quadrats ($N = 90$; results not reported), interval 4 would also have required a geometric-growth model; K_4 was so large that it could be estimated only because data from quadrats with very high densities (*B. rigidiseta* seed additions) were available from interval 4. Had we had density-manipulated quadrats in intervals 9 and 15, we might have been able to estimate K_9 and K_{15}.

We also fitted hierarchical (sensu Clark 2003) models in which K was modeled as a random variable with a mean and variance (σ_K^2) estimated at the same time and by the same maximum likelihood procedure as the other parameters of the model. Normal-*K* models fitted K to a normal distribution in nongeometric-growth intervals. Because the distribution of K obtained from the multi-*K* models (see "Results") suggested that the distribution of K had a right tail, we also constructed lognormal-*K* models, which fitted K to a lognormal distribution in nongeometric-growth intervals.

For each version of each model, we estimated the values of all parameters, including σ_ε^2 (the variance of ε), using the maximum likelihood method implemented by the NLMIXED procedure of SAS (ver. 9.1; SAS, Cary, NC).

Table 1: Selected versions of the two population dynamic models that provided the best fits to *Bouteloua rigidiseta* census data

		BZIC value (no. parameters)				
		Model versions without special treatment for intervals 9 and 15		Model versions with geometric growth in intervals 9 and 15		
Model	Algebraic form	One-*K*, one-*R*	One-*K*, multi-*R*	One-*K*, one-*R*	Lognormal-*K*, one-*R*	Multi-*K*, one-*R*
Ludwig	$N_{t+1} = K \times (1-\beta) + N_t \times \beta$	115.7 (3)	103.8 (17)	87.1 (4)	46.7 (5)	29.4 (16)
Reduced hyperbolic	$N_{t+1} = (1+R)N_t/(1+N_t \times R/K)$	112.8 (3)	92.7 (17)	85.3 (3)	57.8 (4)	41.2 (15)

Note: The lower the Bozdogan's Information Criterion (BZIC) score, the better the fit. The parameter count always includes σ_ε^2. BZIC values include a small-sample-size correction (see "Methods and Models").

In all cases, parameter values were such that intrinsic oscillatory or chaotic behavior would not occur (Case 2000).

Weight of Evidence for Alternative Models

We compared the relative ability of our alternative models to describe our data using Bozdogan's (2000) extension of the Akaike Information Criterion (AIC; Akaike 1973). We rename Bozdogan's (2000) ICOMP(IFIM) as Bozdogan's Information Criterion (BZIC), defined as $-2\log(L) + p \times \log(A/G)$, where L is the likelihood function evaluated at the parameter estimates, p is the number of parameters estimated, A is the arithmetic average of the eigenvalues of F^{-1} (where F^{-1} is the inverse of the Fisher information matrix in Hessian form, i.e., the estimated variance-covariance matrix of the parameter estimates), and G is the geometric mean of the eigenvalues of F^{-1}. Like AIC, BZIC penalizes models with more parameters. However, it also penalizes models that result in parameter estimates with ill-conditioned variance-covariance matrices, which proved to be important for certain models (app. B). Following Burnham and Anderson (2004), we report BZIC values corrected for small sample size: corrected $\text{BZIC} = \text{BZIC} + 2p(p+1)/(N-p-1)$. This correction had little effect on BZIC values (app. B). For convenience, we refer to the model with the lowest BZIC value as the best model.

Proponents of information-theoretic approaches argue that it is better not to employ null hypothesis testing and information-theoretic analyses on the same data but rather to characterize the relative strength of evidence for alternative model I as compared to best model B. Where BZIC scores differ by more than 10, there is essentially no support for the poorer (higher BZIC score) model (Burnham and Anderson 2002).

We recognize that readers may prefer to compare models using other approaches (Burnham and Anderson 2004; Richards 2005; Stephens et al. 2005; Link and Barker 2006). For these readers, appendix B provides (*a*) values of the Bayes Information Criterion (BIC), BIC weights, and Bayes factors (Link and Barker 2006) and (*b*) a significance test of the null hypothesis that K is constant. Uncorrected and corrected AIC values are also provided in appendix B. The use of any of these alternative approaches does not materially affect the conclusions of this article.

Results

Model Comparisons

Among all the versions of all six population dynamic models tested, the Ludwig multi-K model with intervals 9 and 15 fitted with geometric growth provided the best description of the data (lowest BZIC value; table 1). The reduced hyperbolic multi-K model with intervals 9 and 15 fitted with geometric growth provided the second-best description (table 1); we retain it because it provides better estimates of K (see below). Both estimate a separate value of K (carrying capacity) for each of the 13 annual intervals not modeled by geometric population growth.

Further support for temporal variation in K is provided by the finding that for each of the six models (Ludwig, Ricker, etc.) its multi-K version outperformed both its one-K/one-R version and its multi-R version. A complete set of BZIC values, differences in BZIC values, and evidence ratios is provided in appendix B for each version of each model.

Temporal variation in K was also modeled as a random variable in a hierarchical model. In all instances, the multi-K version of a model provided a better fit to the data (lower BZIC value) than did the version of the same model that treated K as a normally or lognormally distributed random variable. Because BIC imposes a much more severe penalty for parameter number than do AIC and BZIC, the Ludwig lognormal-K model with geometric growth in intervals 9 and 15 had the lowest BIC value (app. B).

Distribution of K

The distribution of values of K was skewed, with a long right tail (fig. 2). The largest values of K were not estimable

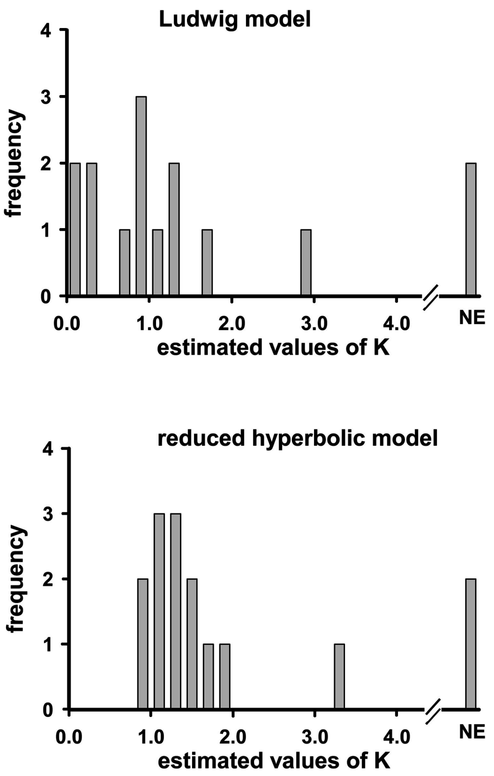

Figure 2: Distribution of the estimated values of K, for the Ludwig multi-K model and the reduced hyperbolic multi-K model; K was not estimable (*NE*) in two of the 15 intervals.

because they occurred in annual intervals in which geometric growth provided the best fit to the data. Even during the annual intervals in which K was estimable, the distribution of K was quite skewed, as evidenced by the better fit of the lognormal-K versions of models than the normal-K versions of models (app. B) and inspection of figure 2. In other words, most years were poor years, some were better years, and a few were excellent years for this species. The variation in K was large relative to N: $\sigma_K \simeq 0.5N$.

Relative Magnitude of Variation in K *versus Other Variation in* N

Our estimate of σ_ε^2 from the multi-K Ludwig model provides an upper bound for the density-independent annual variation in reproduction and survival since it includes all sources of variation not otherwise explicitly included in the model. Under it we estimated $\sigma_\varepsilon = 247$ tillers/quadrat (t/q), whereas the 13 estimated K_t values of the Ludwig model yielded $\sigma_K = 752$ t/q (reduced hyperbolic: $\sigma_\varepsilon = 259$ vs. $\sigma_K = 632$ t/q), so σ_K was at least three times larger than density-independent variation in N. Had we been able to estimate K_9 and K_{15}, the estimated annual variation in carrying capacity would likely have been even larger.

Tracking of K *by* N

Population size, N, was larger than K at least half the time (fig. 3), primarily because K dropped more quickly than did N. One measure of the strength of density dependence is $(K - N)/K$, which takes values from 1 (weakest density dependence, $N \rightarrow 0$) to 0 (when $N = K$) to $\ll 0$ (when $N \gg K$). Because under the Ludwig model estimated values of K are related to estimated Y-axis intercepts (which are equal to $K_t \times (1 - \beta)$ in this model; fig. 1), the reduced hyperbolic model provides better estimates of K for this purpose. Under the reduced hyperbolic model, the median value of $(K_t - N_{t+1})/K_t$, where N_{t+1} is density at the end of the $(t, t + 1)$ annual interval and K_t is the value of K estimated for the $(t, t + 1)$ interval, in the 13 intervals in which K was estimable, was -0.07, indicating on average strong density dependence in these intervals. In these 13 intervals, density dependence was weaker in intervals 4, 13, and 14 ($(K - N)/K = 0.41$, 0.36, and 0.38, respectively) and stronger in intervals 1–3, 5–8, 10, and 11.

In these simple one-dimensional population dynamic models, the eigenvalue, β, associated with the stable internal equilibrium characterizes the linearized dynamics near K. A population originally at density $K + \Delta K$ will approach K with dynamics $N_{t+1} = K + \Delta K^{\beta}$. We estimated $\hat{\beta} = 0.79$ (Ludwig model) and $\hat{\beta} = 1/(1 + \hat{R}) = 0.71$ (reduced hyperbolic model), implying that each year the population traversed only 21%–29% of the distance from N to K.

Correlations with Precipitation

Climate data from Johnson City, Texas, 16 km from the site (National Climatic Data Center, NOAA), were used. Average July and August temperatures there are 28°C; average January temperature is 9°C. Annual precipitation there averaged 860 mm during the study. Average density of *Bouteloua rigidiseta* in the control quadrats in a given census was positively correlated with total precipitation during the 12 months preceding that census, that is, from June to May ($r_s = 0.18$, $N = 15$; fig. 4). Total precipitation from June to the following May was also positively correlated with the value of K_t during that interval (reduced hyperbolic model: $r_s = 0.48$; Ludwig model: $r_s = 0.26$; $N = 15$ intervals).

Discussion

Density dependence varied over the 16 years of this study of a perennial grass population. Models that incorporated

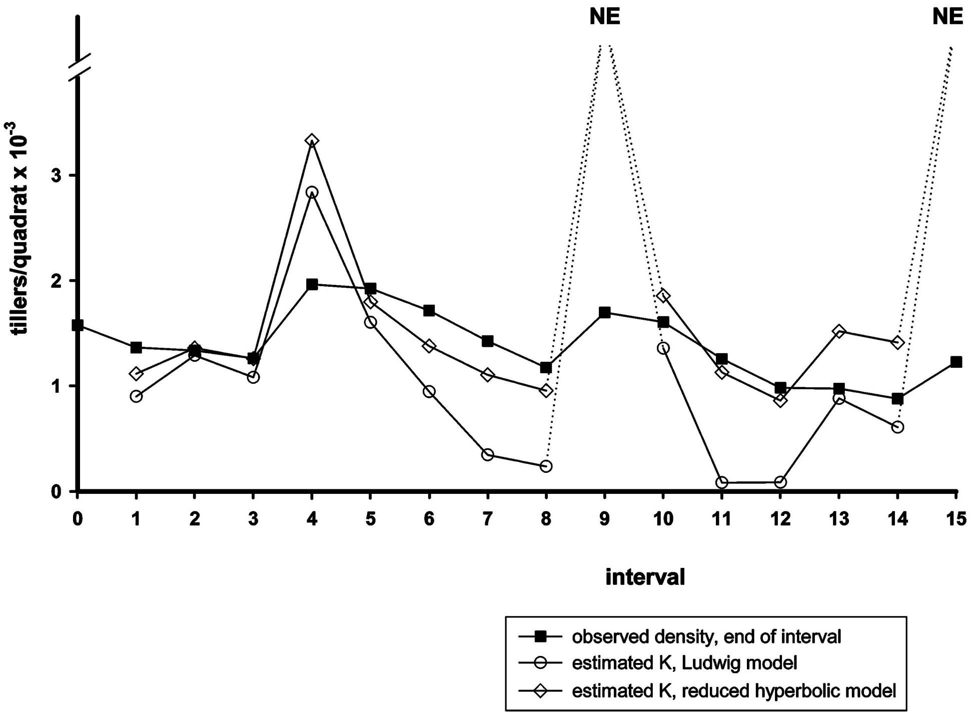

Figure 3: Observed average density at the end of the interval (N_{t+1}) and estimated K_t of that interval; K was too large to be estimated ($NE = K$ not estimable) in two of the 15 intervals.

temporal variation in K (carrying capacity; equilibrium population size in our models) provided better fits to annual census data than did models that incorporated temporal variation only as variation in N (i.e., in ε) or models that incorporated temporal variation only in R (the potential finite rate of increase in N). As far as we are aware, an explicit comparison of these modeling approaches has not been made, so this may be the first explicit test of temporal variation in K and hence in density dependence.

Stochastic population dynamic models are central to many studies of population dynamics and are used to guide conservation (e.g., estimates of extinction probabilities of endangered species) and resource management (e.g., of fisheries; Sibly and Hone 2002; Lande et al. 2003). We suggest that the inclusion of temporal variation in K might improve the realism of these population dynamic models without increasing their complexity, as it did in this study. The methods we used to quantify variation in K require only spatial replication of estimates of N each census (spatially replicated time series), not estimates of individual survival and reproduction, and therefore are potentially widely applicable (Saitoh et al. 1997; Bjørnstad et al. 1999).

Inclusion of temporal variation in K is not dependent on the particular density-dependent model (discrete logistic, Ricker, etc.) used and could be easily adapted for any similar population dynamic model. In this study, the best fit was provided by the Ludwig model, followed by the hyperbolic model (table 1). We are uncertain of the reason why the Ludwig model performed better than the hyperbolic model. However, note that the Ludwig model includes a constant term and therefore is the only model under which N_{t+1} can be positive when $N_t = 0$ (fig. 1; table 1). Density-independent immigration of seeds, perhaps from areas immediately adjacent to the study quadrats, may have been frequent enough for the inclusion of this constant term to improve model fit. Alternatively, the success of the Ludwig model may have arisen from the fact that it characterized low- and high-density behavior with separate parameters (γ for geometric growth and β for the rate of approach to K, respectively).

Because of the relatively low maximum finite rate of increase in population size (estimated to be ~40% per year), all of the models we tested predicted that had K been constant, there would have been a smooth approach to K over time. Oscillations or chaos would be possible under some of our models if R were larger (Case 2000), although constantly changing values of K would likely prevent this behavior from being apparent.

The effect of variation in K on population dynamics

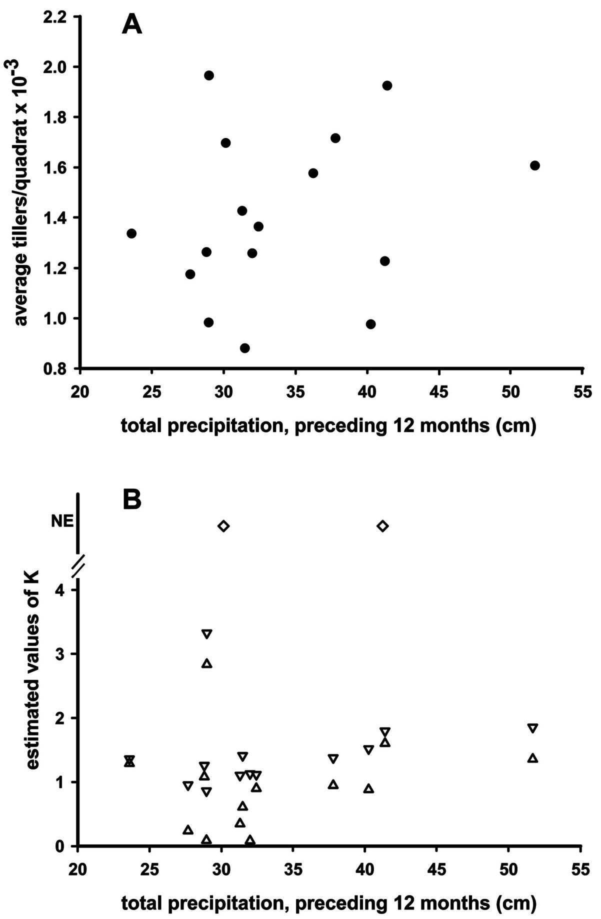

Figure 4: *A*, Average number of tillers per quadrat versus total precipitation in the 12 months preceding each census (June–May). *B*, Estimated values of *K* for each annual interval versus precipitation during the interval. *Triangles* = Ludwig multi-*K* model; *inverted triangles* = reduced hyperbolic multi-*K* model; *diamonds* = *K* not estimable.

has been investigated theoretically. Depending on assumptions about its distribution, random variation in *K* can reduce long-term average population size (Chesson 1991). Variable-*K* populations exhibit growth-catastrophe dynamic behavior (rapid population growth followed by a crash; Gyllenberg et al. 1994; Fagerholm and Högnäs 2002; Ferriere et al. 2006). Variable-*K* populations tend to be either small or large, rather than spending long time periods at intermediate densities (Ferriere et al. 2006). Though this perennial grass did not exhibit growth-catastrophe behavior, we can see its skeleton. Had the population quickly tracked *K* in one of the years when it was growing geometrically, it would have crashed the following year when *K* returned to a more normal level. Its failure to track *K* closely prevented dramatic crashes. Variation in *K* in annual species, a category that includes most insects, would be more likely to produce growth-catastrophe population dynamics.

When *K* represents equilibrium population size, as it does in our models, temporal variation in *K* represents variation in the equilibrium size of a population over time. Variation in *K* may provide insights into mechanisms underlying population regulation, especially if variation in *K* accounts for a substantial portion of the variation in *N*, as it did here (σ_K was at least three times the variation in *N* from all other sources). Previous models that have implicitly incorporated variation in *K* have done so by making resource levels a function of one or more climatic variables, often rainfall, usually with good success (e.g., Illius and O'Connor 2000; Davis et al. 2002; Owen-Smith 2002; Georgiadis et al. 2003; Lima et al. 2006, 2008; Hone and Clutton-Brock 2007; Chamaillé-Jammes et al. 2008; Yang et al. 2008). *Bouteloua rigidiseta* readily adds tillers in response to rain and dies back in response to drought (N. L. Fowler, personal observation). We therefore expected rainfall to be a good predictor of variation in *K*. As expected, precipitation during a 12-month interval was positively correlated with the value of *K* calculated for that interval (fig. 4). The correlations were lower than we expected, however (hyperbolic model: $r_s = 0.48$; Ludwig model: $r_s = 0.26$). The positive direct effects of rainfall on *B. rigidiseta* may have been partially countered by negative effects due to greater interspecific competition in wetter years (Adler and HilleRisLambers 2008; Lima et al. 2008). Visual inspection did not indicate greater rates of disease in wetter years, but we cannot rule it out. We also cannot rule out complex relationships with rainfall that were not captured by our simple analyses.

Fitting models that included temporal variation in *K* provided quantitative estimates of the distribution of *K*. Variation in *K* when it was estimable was substantial ($\sigma_K \simeq 0.5N$) and highly skewed with a very long right tail (fig. 2); *K* was even larger but not estimable during the annual intervals in which the population was best described as growing geometrically and therefore effectively unregulated. This occurred 13%–20% of the time (two of 15 intervals; three of 15 intervals in the control quadrats). Geometric growth could, in theory, also occur when a merely good year (moderate *K*) begins with a very low *N*; however, the values of *N* we observed were not particularly low preceding geometric-growth intervals (fig. 2). Because *K* is necessarily inestimable in geometric-growth intervals, it is not possible to quantify how fat-tailed the distribution of *K* was. Nevertheless, it is clear that *K* was usually relatively low, with some good years and an occasional jackpot year. Because the distribution of rainfall is often skewed in arid and semiarid regions, similarly skewed distributions of *K* may be common among species in those places.

Variation in K can increase the amount of time that a population is either substantially larger or substantially smaller than K, as it did for this grass population. We were aware before this analysis that N varied widely from year to year and suspected that this was due to variation in K. However, it surprised us to learn how poorly N had been tracking K (fig. 2). Mathematically, this appears in the estimated magnitude of the parameter β, which revealed that N moved only 21%–29% of the distance to K each year. The combination of ineffective tracking and the temporal variation in K made both overshoots ($N > K$) and lags ($N < K$) common; K changed so much faster than N that the size of this population (N) was like a slow soccer (football) player, trundling up and down the field after a rapidly moving ball (K) but never reaching it except when, by happenstance, the ball came flying past. We are not aware of comparable data but suspect that this may not be uncommon in natural populations. In general, poor tracking will tend to reduce temporal variation in population size, including the likelihood of large overshoots and crashes. It will also tend to make observed population sizes rather poor guides to resource levels and to other factors that determine equilibrium population size and will therefore increase the value of estimating K explicitly.

Acknowledgments

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