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Author(s): N. L. Fowler, R. Deborah Overath and Craig M. Pease

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DETECTION OF DENSITY DEPENDENCE REQUIRES DENSITY MANIPULATIONS AND CALCULATION OF λ

N. L. FOWLER,^{1,3} R. DEBORAH OVERATH^{1,4} AND CRAIG M. PEASE²

¹Section of Integrative Biology, University of Texas, Austin, Texas 78712 USA

²Environmental Law Center, Vermont Law School, S. Royalton, Vermont 05068 USA

Abstract. To investigate density-dependent population regulation in the perennial bunchgrass *Bouteloua rigidiseta*, we experimentally manipulated density by removing adults or adding seeds to replicate quadrats in a natural population for three annual intervals. We monitored the adjacent control quadrats for 14 annual intervals. We constructed a population projection matrix for each quadrat in each interval, calculated λ , and did a life table response experiment (LTRE) analysis. We tested the effects of density upon λ by comparing experimental and control quadrats, and by an analysis of the 15-year observational data set.

As measured by effects on λ and on N_{t+1}/N_t in the experimental treatments, negative density dependence was strong: the population was being effectively regulated. The relative contributions of different matrix elements to treatment effect on λ differed among years and treatments; overall the pattern was one of small contributions by many different life cycle stages.

In contrast, density dependence could not be detected using only the observational (control quadrats) data, even though this data set covered a much longer time span. Nor did experimental effects on separate matrix elements reach statistical significance. These results suggest that ecologists may fail to detect density dependence when it is present if they have only descriptive, not experimental, data, do not have data for the entire life cycle, or analyze life cycle components separately.

Key words: *Bouteloua rigidiseta*; demography; density dependence; density manipulation; finite rate of increase; grass; life table response experiment; LTRE; perennial bunchgrass; population regulation.

INTRODUCTION

The degree to which natural populations are regulated, that is, are affected by negative density-dependent processes, has long been controversial (Nicholson 1933, 1957, 1958, Andrewartha and Birch 1954, Murdoch 1994, Turchin 1999, Berryman et al. 2002, Hixon et al. 2002). (We use the term negative density dependence to refer to negative effects of one individual upon a conspecific individual's survival, fecundity, or growth.) Theory predicts that purely density-independent populations will grow without bound or eventually will go extinct (Smith 1935, Tuljapurkar and Orzack 1980). This implies that negative density dependence must occur at least occasionally, but there remains much empirical uncertainty about the strength of negative density dependence and about the ways in which it operates and should be measured (Godfray and Rees 2002, Sibly and Hone 2002).

In contrast, plant ecologists have tended to assume that density-dependent processes, especially competi-

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³E-mail: nfowler@uts.cc.utexas.edu

⁴Present address: Department of Physical and Life Sciences (ST 312), 6300 Ocean Drive, Unit 5800, Texas A&M University, Corpus Christi, Texas 78412 USA.

tion, play an important role in the dynamics of plant populations (Crawley 1990, Gillman et al. 1993). Perhaps because of this, or because of the difficulty of studying long-lived organisms, there are relatively few studies of the regulation of natural populations of iteroparous perennial species (but see, e.g., Piñero et al. 1984, de Kroon et al. 1987, Burgman and Gerard 1990, Hubbell et al. 1990, Alvarez-Buylla 1994, Silva Matos et al. 1999, Gustafsson and Ehrlén 2003). The majority of published studies that explicitly address the regulation of plant populations are of annuals (e.g., Pacala and Silander 1985, Watkinson et al. 1989, Cousins and Mortimer 1995, Rees et al. 1996, Buckley et al. 2005) or other semelparous plants (e.g., Gillman et al. 1993, Louda and Potvin 1995, Meekins and McCarthy 2002). However, studies of iteroparous perennial species may soon become more common because an understanding of the operation of density dependence is often necessary for realistic predictions about future population sizes of endangered species (e.g., Gillman and Dodd 2000, Hackney and McGraw 2001). In this study, we explicitly investigate the regulation of a natural population of the grass *Bouteloua rigidiseta*, a common perennial species in savannas in central Texas, USA.

Many questions remain about the regulation of natural plant populations, especially about the nature of the algebraic relationship between density and popu-

lation growth rate (including lags [Gillman and Dodd 2000] and spatial effects [Silva Matos et al. 1999, Taylor et al. 2004]), and about the effectiveness of population regulation. In this paper, we address three questions about the regulation of this perennial plant population. (1) How strong was density dependence? (2) How frequently did it occur? (3) At what stage or stages in the life cycle did it regulate population size?

In this paper we also compare the effectiveness of different methodologies commonly used in the study of density dependence. We compare the use of λ with the analysis of individual life history components, finding that the former is much more powerful and even reversed the conclusions of a previous study of this *B. rigidiseta* population (Fowler 1995). We also compare observational vs. experimental approaches to detecting density dependence. Although most ecologists would expect manipulative data to be preferable to observational data, they are more expensive. As a result, much of the literature is based on observational data (e.g., Piñero et al. 1984, Alvarez-Buylla 1994, Silva Matos et al. 1999, Miriti et al. 2001), although there are some experimental studies (e.g., Rydgren et al. 2001, Kivineni 2002, Gustafsson and Ehrlén 2003). Finally, we use a “life table response experiment” (LTRE) analysis to determine the contributions of different elements of population projection matrices to the effects of density upon λ .

METHODS

Species and site

Bouteloua rigidiseta (Steud.) Hitchc. is a small perennial bunchgrass; that is, it grows only by addition of tillers immediately adjacent to the existing cluster of tillers, and does not form new tillers at a distance from the original individual cluster via rhizomes or stolons. It is common in, and frequently dominates, shortgrass communities in central Texas grasslands and savannas. In central Texas, it sets abundant seeds in May and June of most years. Successful seedling establishment usually occurs in October or November, the date depending upon when the soil first becomes continuously moist in the autumn. Seed carryover from one year to the next is negligible because there is no soil seedbank. See Fowler (1986, 1995) for further description of this species.

The data that we report here came from a long-term demographic study of a single population of *B. rigidiseta* (Fowler 1986, 1995). This population was one component of a shortgrass savanna community in Pedernales State Park, Blanco County, Texas. Fowler (1984, 1986) further describes this site and plant community.

Experimental design, annual censuses, and density manipulations

Although we conducted censuses of permanent quadrats in May and June each year beginning in 1982, this

paper concerns only the censuses of 1983–1997 (15 years, 14 annual intervals) and only a subset of the quadrats. During the first two years of the study (1982 and 1983), we conducted a census of four contiguous quadrats (45 × 90 cm) in each of six quadrat-groups. Each of the four quadrats in a group received one of four different density treatments of *B. rigidiseta* (control, seed addition, adult removal, or both seed addition and adult removal). We added two additional quadrats (with density manipulations of *Aristida longiseta* Steud.) to each group of quadrats after the 1983 census; and in 1984, 1985, and 1986, we censused all six contiguous quadrats in each of the six quadrat-groups. In 1987 and subsequent years, we made a census only of the six control quadrats (i.e., one quadrat in each of the six quadrat-groups).

The present paper uses data only from the control quadrats and from two of the density manipulations of *Bouteloua rigidiseta* (the adult removal treatment and the seed addition treatment), a total of 18 quadrats. We omit from further consideration in this paper the quadrats that received both *B. rigidiseta* adult removal and seed addition, because there was no a priori expectation for the direction of the effect of this treatment upon λ and because their inclusion would unnecessarily complicate the analyses and presentation. We also omit the *Aristida* manipulations, because the focus of this paper is density dependence, not interspecific competition.

During the annual census, we mapped all *B. rigidiseta* plants in each quadrat, including seedlings but not ungerminated seeds, onto a clear plastic sheet. Superimposing these maps allowed individuals to be identified from year to year (Fowler 1986, 1995; see also Appendix A for discussion of our correction for “false matches”). When we mapped an individual, we also counted and recorded its tillers, and, if reproductive, the number of spikelet clusters (as a nondestructive estimator of seed set). (However we did not record the number of spikelet clusters per plant in 1982, so we could not construct population project matrices for 1982–1983.) Each year, we estimated the number of seeds per spikelet cluster by collecting and destructively dissecting them from locations near, but not within, the experimental quadrats. We estimated the fecundity of each individual by multiplying the number of its spikelet clusters by the annual average number of seeds per spikelet cluster. We estimated the number of seeds added to each seed addition quadrat by multiplying the annual average number of seeds per spikelet cluster by the number of spikelet clusters added.

Under the *B. rigidiseta* adult removal treatment, we removed approximately half of the adult *B. rigidiseta* plants from each manipulated quadrat. This density manipulation first occurred in November–December 1982 and was repeated in October 1985 (Fowler 1995). Under the *B. rigidiseta* seed addition treatment, the seed addition quadrat in each group had 1000 *B. rigidiseta* spikelet clusters added each summer, 1982–1985, after

that year's census. These manipulations were effective in changing density in the desired directions: on average, the removal treatment reduced the total number of *B. rigidiseta* tillers in a quadrat by 18%, whereas the seed additions, on average, increased it by 20% (Appendix A: Table A1).

Because the effect of a plant on its neighbors depends so strongly upon its size, throughout this paper we use the total number of *B. rigidiseta* tillers per quadrat as our primary measure of density.

Data sets and individual plant histories

For this study, we extracted two data sets from the complete data set. Data Set A includes the four censuses made in 1983–1986 of the control quadrats, the *B. rigidiseta* seed addition quadrats, and the *B. rigidiseta* adult removal quadrats. Because it includes four sequential censuses, it represents three annual intervals. Data Set B includes only the censuses of the control quadrats made from 1983 through 1997, representing 14 annual intervals. The two data sets overlap slightly, because both include the censuses of the six control quadrats made in 1983 through 1986.

The history of each individual plant was assembled from the maps and census records (Appendix A). Each plant in each year was assigned to one of five size classes: (1) 1–2 tillers, (2) 3–4 tillers, (3) 5–7 tillers, (4) 8–15 tillers, or (5) 16+ tillers. For each size class, in each quadrat, we calculated survival rate, average seed set (i.e., fecundity), and “growth” rates, i.e., the proportions of plants moving into each size class, including the proportion of plants remaining in the same size class. We have previously published an analysis of the effects of quadrat-group and treatment (seed addition, adult removal) upon stage-specific survival, growth, and fecundity during the first four years of the experiment (Fowler 1995).

Population projection matrix construction

We calculated a separate population projection matrix (Caswell 2001) for each quadrat in each annual interval. Because there was only one quadrat of each treatment in each quadrat group, each combination of annual interval \times treatment \times quadrat group had a single unique 5×5 matrix. We employed the five size classes given above in all matrix calculations. In all instances the values of the matrix elements did not include the direct effects of the treatments. That is, plants removed by the investigator were not included in the calculation of any matrix element for the annual interval during which they were removed. And plants arising from seeds added during an annual interval were also not included in the calculation of any matrix element for that interval. Appendix A further describes the methods we employed to construct these population projection matrices.

Finite rate of increase (λ)

Using these matrices, we calculated the finite rate of increase, λ , for each quadrat separately (that is, for each annual-interval \times treatment \times quadrat-group combination separately), as the principal eigenvalue of the population projection matrix. This quantity is perhaps best interpreted as the rate at which the population would eventually multiply if the values of the projection matrix elements did not change from year to year.

We also calculated the actual finite rate of increase of unmanipulated plants, N_{t+1}/N_t , for each quadrat, where N_t and N_{t+1} are the total number of unmanipulated plants in the quadrat at the beginning and end of the interval ($t, t + 1$), respectively. For the calculation of N_{t+1}/N_t in the adult removal quadrats, we adjusted N_t to exclude those plants, if any, that we removed from the given quadrat during the given interval. For the calculation of N_{t+1}/N_t in the seed addition quadrats, we reduced N_{t+1} by subtracting from the observed number of plants in a quadrat at the end of the annual interval the estimated number of new recruits to the population that arose from seed added to the quadrat during the annual interval. We estimated the number of new recruits arising from added seed as (number of new recruits) \times (number of seeds added)/(number of seeds added + number of seeds set naturally). Thus N_{t+1} was not inflated by plants that germinated from added seeds during the interval ($t, t + 1$) (Appendix A).

Tests of density dependence in the density-manipulated quadrats

We employed one-tailed paired *t* tests to test the null hypotheses that seed additions did not reduce λ or N_{t+1}/N_t and that adult removals did not increase λ or N_{t+1}/N_t . We undertook these statistical tests on the experimental data set (Data Set A). To test the effects of seed additions, we paired seed addition and control quadrats by quadrat group, and we paired adult removal quadrats and control quadrats likewise. We separately tested each of the three annual intervals.

Paired *t* tests were also used to test the hypothesis that seed additions and adult removals did not alter the values of individual matrix elements (Appendix C). For these tests, seed addition and control quadrats were paired by quadrat group, as were adult removals and control quadrats, for each of the three annual intervals separately. Available degrees of freedom severely constrained the use of multivariate approaches (including repeated measures) for testing treatment effects on matrix elements. By testing years separately and not pairing quadrats by quadrat group (i.e., not including the term “quadrat group” in the model), we were able to do multivariate analyses of variance (MANOVAs) with sets of 9 or 10 matrix elements.

Test of density dependence in the unmanipulated (control) quadrats

Ultimately, any test of density dependence in an observational time series must look for a correlation be-

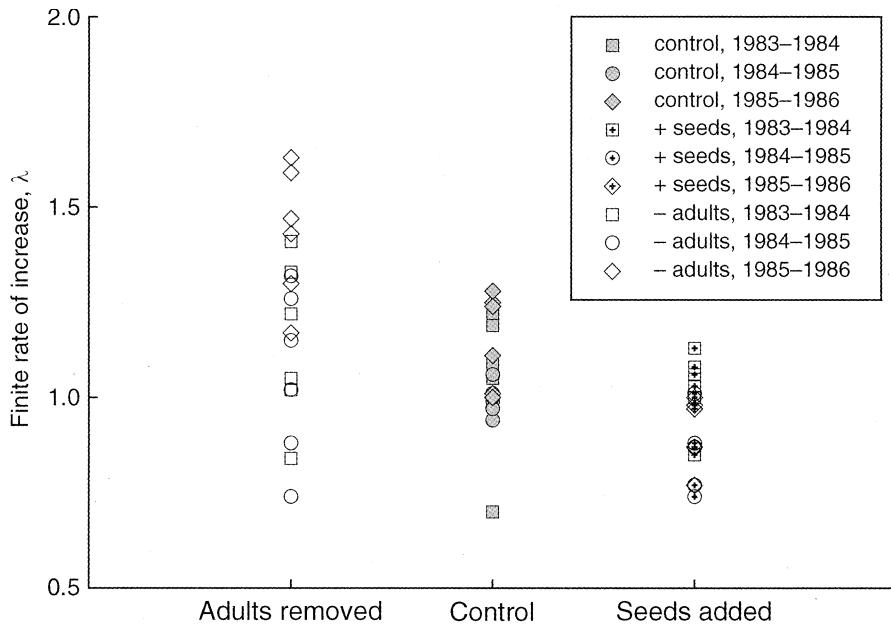


FIG. 1. Effects of the adult removal and seed addition density manipulations on λ , the finite rate of increase. The effect of adult removal was significant in the first and third annual intervals (12 months between censuses); seed addition was significant in the second and third intervals.

tween density (i.e., N_t), and a metric such as λ , N_{t+1}/N_t or ΔN (i.e., $N_{t+1} - N_t$; see Maelzer 1970, St. Amant 1970, Bulmer 1975). To test for density dependence in the 14 annual intervals of data from the control quadrats, we extended the commonly used method of Pollard et al. (1987) that looks for a correlation between density and finite rate of increase, after accounting for the well-known spurious bias in such correlations. Whereas Pollard et al. (1987) described their method for, and applied it to, an unstructured population, our analysis and data are for a stage-structured population. We therefore generalized the method of Pollard et al., as described in Appendix B. Our test statistic is the correlation coefficient of total tiller number at the beginning of the interval with λ , the principle eigenvalue of the population projection matrix, both computed for each annual interval separately. This test statistic was computed for Data Set B, the 15 annual censuses (14 annual intervals) of the control quadrats only.

Alternative test of density dependence in the density-manipulated quadrats

We regard the paired t tests as the definitive test of density dependence in the experimental data set (Set A). Nevertheless, to facilitate a comparison of the two data sets (one experimental and one observational), we calculated correlations between λ and the total number of tillers per quadrat for the experimental data set, in a manner analogous to our analysis of the control data set. See Appendix B for details of this test.

Life table response experiment (LTRE) analysis

To quantify the extent to which different transition matrix elements (representing stage-specific survivor-

ship, fecundity, and growth) contributed to the overall effects of density on λ , we undertook an LTRE analysis (Horwitz et al. 1997, Caswell 2001). We calculated the sensitivity of each transition matrix element, s_{ij} , of each control matrix. We calculated the change in each matrix element induced by the seed addition and adult removal perturbations, Δa_{ij} , by subtracting the value of a matrix element in the control matrix from the value of the same matrix element in a treatment matrix:

$$\Delta a_{ij} = a_{ij,\text{treatment}} - a_{ij,\text{control}}$$

We did this calculation separately for each treatment – control pair in each quadrat-group in each annual interval. We then multiplied these two quantities, and thus calculated $s_{ij}\Delta a_{ij}$ separately for each quadrat group in each annual interval, and also separately for the seed addition treatment and the adult removal treatment.

RESULTS

Finite rates of increase

The principal eigenvalue of each population projection matrix (λ) in the experimental data (Set A) ranged from 0.70 to 1.63, with an overall standard deviation of 0.21 (Fig. 1). This variation reflects quadrat-group-to-quadrat-group and year-to-year variation, as well as the effects of the density manipulations. During the first two annual intervals, average λ of the control quadrats was close to 1.0, but was 1.15 in the third annual interval (Table 1).

Density dependence detected in density-manipulated quadrats

The average value of λ in the quadrats from which half the adults had been removed was greater than that

TABLE 1. Average finite rate of increase (λ) and average change in population size (N_{t+1}/N_t).

Parameter and treatment	1983–1984		1984–1985		1985–1986	
	Value	Diff. from control (%)	Value	Diff. from control (%)	Value	Diff. from control (%)
Average λ						
Control	1.04		0.99		1.15	
Adult removal	1.15*	(+11%)	1.06	(+7%)	1.43**	(+25%)
Seed addition	1.02	(+0%)	0.86*	(-13%)	0.93**	(-18%)
Average N_{t+1}/N_t						
Control	0.81		1.06		1.23	
Adult removal	0.86	(+9%)	1.26*	(+22%)	1.34	(+8%)
Seed addition	0.54**	(-33%)	0.52**	(-48%)	0.40**	(-66%)

Notes: Both λ and N_{t+1}/N_t were calculated using unmanipulated plants only, excluding new recruits attributable to seeds added during the interval, and excluding plants removed during the interval. We calculated λ and N_{t+1}/N_t for each quadrat separately and then averaged ($n = 6$ for each tabled value). Percentage changes are relative to control quadrat values in the same annual interval, calculated for each quadrat separately and then averaged. Treated quadrats were compared to control quadrats by paired *t* tests ($n = 6$) in which quadrats were paired by quadrat-groups; annual intervals were tested separately: * $P < 0.05$; ** $P < 0.01$.

of the control quadrats during each interval, as one would expect if negative density-dependent processes were operating (Table 1, Fig. 1). In the first annual interval, the average λ of the seed addition quadrats was almost equal to that of the control quadrats. In the other two intervals, the average value of λ in the seed addition quadrats was substantially less than that of the control quadrats (13% and 18%, respectively), as one would expect if negative density-dependent processes were operating. The effects of the density manipulations reached significance in four of the six paired *t* tests of λ , and also in four of the six paired *t* tests of N_{t+1}/N_t (Table 1).

Only 6% of the paired *t* tests of the separate matrix elements, in contrast, detected density dependence, scarcely more often than one would expect by chance (Appendix C: Table C1). These “significant” tests were scattered among different matrix elements, treatments, and years. MANOVAs on sets of matrix elements were no more successful at detecting treatment effects than paired *t* tests. None of the six MANOVAs (three years \times two treatments) on the matrix elements above the central diagonal ($a_{13}, a_{14}, a_{15}, a_{23}, a_{24}, a_{25}, a_{34}, a_{35}, a_{45}$) had an uncorrected $P < 0.10$; neither did any of the six MANOVAs on the elements on and below the central diagonal ($a_{21}, a_{22}, a_{32}, a_{33}, a_{42}, a_{43}, a_{44}, a_{53}, a_{54}, a_{55}$).

Density dependence not detected in unmanipulated (control) quadrats

From our generalization of the resampling procedure of Pollard et al. (1987) and Data Set B (controls), we obtain an expected value for our test statistic of $r = -0.27$ under the null hypothesis of no density dependence. We expect a negative value for this correlation under the null hypothesis (St. Amant 1970, Bulmer 1975). Our simulation provided a one-tailed, $P = 0.05$ critical value for r of -0.64 ; values less than this are unlikely to appear by chance if the null hypothesis is

true. The actual value of the correlation between λ and density (number of tillers per quadrat) was -0.31 , and is thus not significant (Fig. 2a).

Alternative analysis detected density dependence in density-manipulated quadrats

Applying the method of Pollard et al. (1987) to Data Set A, we obtained an expected value of $r = 0.00$ under the hypothesis of no density dependence, and critical values of $r = -0.40$ (one-tailed, $P = 0.05$) and $r = -0.54$ (one-tailed $P = 0.01$). The expected value is not biased in this case because we analyzed each annual interval separately, computing the correlation across quadrat groups within each annual interval. The actual values of this correlation were between -0.51 and -0.70 and, hence, were significant (Fig. 2b).

LTRE analysis

To check our LTRE analysis, we compared the value of λ computed directly from the transition matrices to the λ predicted from the LTRE analysis (Appendix C). The predicted and directly measured values match quite well, suggesting that the first-order terms in the LTRE analysis adequately describe the density effects.

The overall effect on λ of the adult removals and seed additions was noticeably greater than the contribution of any particular transition matrix element. In the three annual intervals studied, the adult removals induced an average (over six quadrats in each annual interval) increase in λ of $+0.11$, $+0.07$, and $+0.28$ (Table 1). In contrast, most elements contributed less than $+0.01$ to $\Delta\lambda$ (Appendix C: Table C5). The same was true in the seed additions (Appendix C: Table C7).

Because the predicted change in λ ascribable to transition matrix element ij is estimated by the product $s_{ij}\Delta a_{ij}$ (Caswell 2001), a relatively large effect on λ can be due either to a relatively high sensitivity of a life history component, s_{ij} , or to the relatively large effect

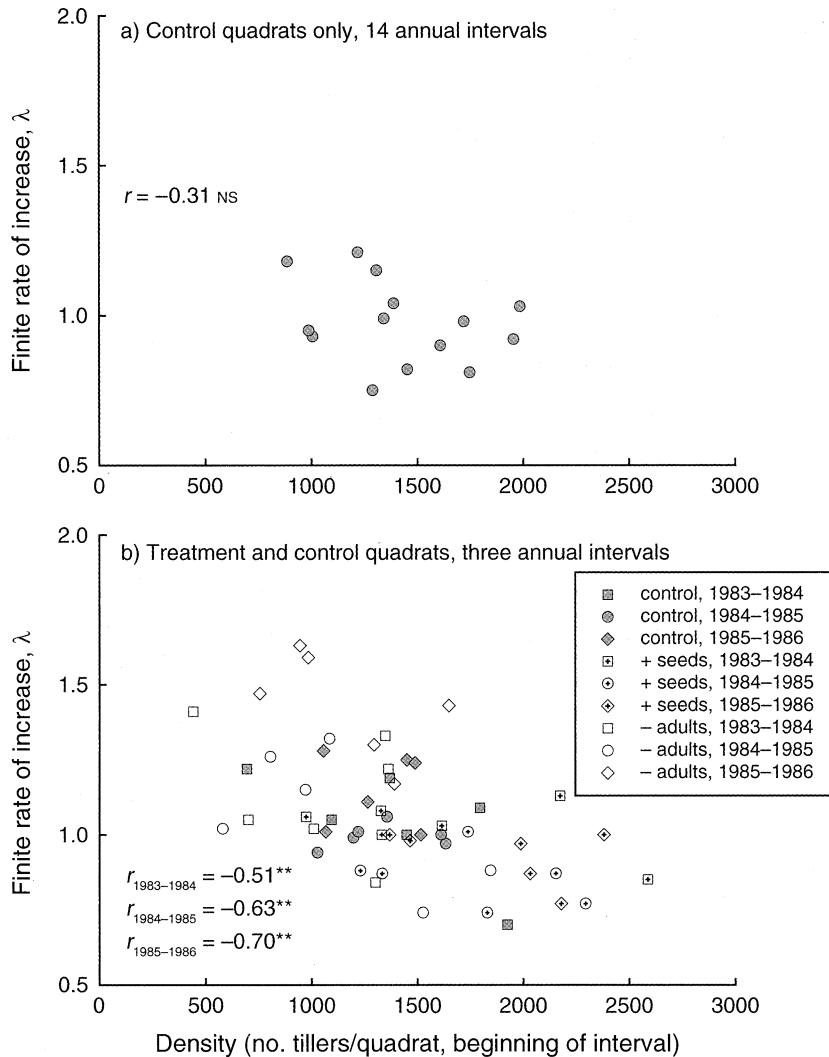


FIG. 2. (a) The finite rate of increase was not significantly related to density for the 14 annual intervals of data from control quadrats only (Data Set B). (b) The finite rate of increase was significantly related to density in the experimental data (Data Set A), in each of the three annual intervals.

that the manipulation has on that component, Δa_{ij} , or both. In the first and second annual intervals, the largest contributors to the effects of adult removal on λ were matrix elements representing the growth and survival of the largest plants, which had higher sensitivities (Appendix C: Tables C3 and C5). In the third annual interval, most of the larger contributions to the overall adult removal effect on λ were made by elements representing the fecundity of large plants, due to the greater effects of the treatment upon these matrix elements (Appendix C: Tables C4 and C5).

In the second and third annual intervals, the two intervals in which the seed addition treatment significantly affected λ , relatively large contributions were made by a_{54} and a_{55} , reflecting their relatively large sensitivities, and a_{44} (1984–1985) and a_{42} and a_{25} (1985–1986), reflecting relatively large treatment effects on them (Appendix C: Tables C3, C6, and C7).

Element a_{25} primarily reflects the production of recruits of size class 2 by an adult of size class 5.

DISCUSSION

Density dependence was strong

The present analysis found statistically significant effects of density on λ and on N_{t+1}/N_t in two-thirds of the tests (Table 1). Density dependence was strong, as shown by a comparison of the magnitudes of the effects on λ with the magnitudes of the manipulations. In the adult removal quadrats, λ was, on average, 14% larger than it was in the paired control quadrats, not far from the 18% reduction in density created by the removals. In the seed addition quadrats, λ was, on average, 10% less than in the paired control quadrats, half the value of the 20% increase in density caused by the seed additions (compare Table 1 with Table A.1 in Appendix

A). We therefore conclude that this population was being quite effectively regulated. Effective density-dependent regulation is also consistent with the fact that the values of λ in the control quadrats throughout the 15 years of this study tended to cluster around 1.0, although with considerable spatial and temporal variation.

There is no reason to expect that this population or the years in which the experiment was conducted were unusual; therefore these results are consistent with a hypothesis that strong density-dependent population regulation is relatively common in populations of iteroparous (i.e., "perennial") herbaceous plant species. There are not yet enough comparable published studies, however, to know whether this hypothesis is true. Results from the few comparable studies have been mixed. Gustafsson and Ehrlén (2003) found a weak relationship: reductions in density of 50–75% increased λ by only 8% in a manipulative study. deKroon et al. (1987) reported strong density dependence, but did not separate the effects of (conspecific) density from simultaneous increases in the densities of other species. Gillman and Dodd (2000) also found strong density dependence, but only as a time-lagged effect: the rate of increase in an orchid population was related to densities four years earlier. Menges and Dolan (1998) reported a positive relationship between density and the finite rate of increase, presumably because high-density sites were more favorable in other ways, reflecting a limitation of purely observational studies of density dependence like theirs. Hackney and McGraw (2001) found positive, not negative, density dependence in an experimental study of American ginseng (*Panax quinquefolius*), probably caused by pollinator limitation.

Density dependence throughout the life cycle

Density dependence may appear in any stage of the life cycle, but especially in seedling recruitment and survival (e.g., Silva Matos et al. 1999), in juvenile growth and survival (e.g., Hubbell et al. 1990, Gustafsson and Ehrlén 2003), and in adult fecundity (e.g., Alvarez-Buylla 1994). The effects of density on different life stages may differ in strength (Gustafsson and Ehrlén 2003) and may even be in different directions (Hackney and McGraw 2001). In this population, we found that no single life stage was consistently responsible for the effect of density on λ . There was a pattern of relatively small density effects at many points in the life cycle, rather than a few large density effects on one or two stages in the life cycle. (It was because most of these small effects were in the same direction that the effect on λ was large.) There was also considerable variation among years and treatments in the magnitude of the contributions made by different life stages. Therefore we do not single out any particular stage or stages as the "important" one(s) for the regulation of this population, and indeed doubt whether it would be meaningful to do so.

Sensitivity plays a central role in connecting individual life history components to measures of finite rate of increase (de Kroon et al. 1986, 2000, Caswell 2001). One approach to quantifying this connection is to compare the sensitivities and/or elasticities of different matrix elements (e.g., Silva et al. 1991, Silvertown et al. 1993, Dinnétz and Nilsson 2002, Raimondo and Donaldson 2003). However, sensitivity (or elasticity) is an incomplete characterization of this connection, because one also needs to know the extent to which density or some other factor alters each transition matrix element: if the magnitude of the element is invariant under the density manipulation, its sensitivity is irrelevant. Although one can undertake an analysis that arbitrarily alters the magnitude of certain matrix elements (e.g., Esparza-Olguín et al. 2002), without empirical data one does not know how large a perturbation in each matrix element is reasonable. An LTRE analysis (Horwitz et al. 1997, Ehrlen 1999, Caswell 2001) avoids these difficulties because it analyzes sensitivity in conjunction with actual empirical variation in matrix elements, as we did in this study. Our LTRE analysis revealed that, in this population, the separate, individual contributions of the various matrix elements to the change in λ induced by the density manipulations were mostly small. They were, however, mostly consistent in direction, which allowed them to have, collectively, a large effect. Neither sensitivity alone nor Δa_{ij} alone was a particularly good predictor of the contribution of a particular matrix element.

We were wrong

An earlier study of this *Bouteloua rigidiseta* population (Fowler 1995) concluded that density dependence in this population was weak, probably intermittent among years, and involved most stages in the life cycle. As a result of the analyses described in this paper, we now know that at least the first of these conclusions was wrong, and the second is at least questionable, given that we found significant density effects in the experimental data set (Set A) in all three annual intervals; the third conclusion is compatible with the results of this study. The previous paper was based upon the same four-year experimental data set (Set A) analyzed in this paper, but in the earlier paper, only the effects of density upon separate life history components (rates of survival, growth, and reproduction, and numbers of new recruits to the population) were analyzed. If density affects λ , it must necessarily be affecting at least some components of the life history and, hence, some elements of the population projection matrix. We next discuss why it was not detected in them.

λ rules!

Analyses of the finite rate of increase in population size (λ) and of the actual rate of change in numbers of nonmanipulated plants (N_{t+1}/N_t) proved to be much more powerful methods of detecting density depen-

dence in this population than were either the analysis of separate matrix elements (see *Results*), or the previously published analyses of separate life history components (Fowler 1995). Why was density dependence detected using λ , but not using the underlying life history variables of which it is composed, or in the matrix elements that are functions of one or more life history variables? We suggest two, not mutually exclusive, reasons.

First, many small responses to the treatments in individual life history components summed to a much larger response in λ . This need not be the case: if there were no density dependence, small positive and small negative differences in individual life history components between treatment and control would be expected, on average, to cancel each other out. Instead, what happened was that most of the responses, although small, were in the same direction (positive, in response to the reduction of density by adult removal; or negative, in response to the increase in density by seed additions). This was quantified by the LTRE analysis.

Second, the sampling error of λ relative to $\Delta\lambda$ is likely to be less than the sampling error of the separate matrix elements relative to Δa_{ij} , so that the ratio $\Delta\lambda/\sigma_\lambda$, as a general rule, will be greater than $\Delta a_{ij}/\sigma_a$. This is a general property of these parameters, not specific to a given statistical test or to our data. For further discussion of the mathematical properties of the sampling errors of $\Delta\lambda$ and Δa_{ij} , please see Appendix C.

In our data, this can be demonstrated by comparing coefficients of variation (cv, i.e., standard deviation/mean, which is effectively the inverse of the ratios $\Delta a_{ij}/\sigma_a$ and $\Delta\lambda/\sigma_\lambda$). For example, the cv of λ for the 84 control quadrat matrices was 23.6, while the cv values of the 25 individual matrix elements of these 84 matrices varied from 21.2 to 519.0, with a median value of 122.7 ($N = 25$). All but one matrix element (a_{55}) had a cv larger than the cv of λ .

Experiments rule!

In this study, experimental data proved to be much more powerful than observational data for the detection of density dependence, even though they were collected over a much shorter period of time (four vs. 15 years). We detected density dependence not only when we analyzed values of λ from the experimental data with paired *t* tests (a method appropriate for experimental data), but also in our experimental data when we calculated the correlation between density and λ (a method appropriate for purely observational data). In contrast, we did not detect density dependence in the purely observational (i.e., control quadrats only) data using a modification of standard methodology. Why was density dependence detected using the experimental, but not the observational, data?

Although the details will differ, any statistical approach to detecting density dependence must compare the magnitude of changes in finite rate of increase due

to density fluctuations to the magnitude of the changes caused by all other factors, known and unknown (a.k.a. "error"). Our experimental data set not only involved larger differences in density than did the observational data set (Fig. 2), but also compared the effects of these to smaller differences arising from uncontrolled factors, making statistical significance easier to achieve. Differences due to uncontrolled factors were smaller because the experimental data set controlled more factors than did the observational data set: it controlled some spatial variation because experimental and control quadrats were paired in each quadrat group, and it also controlled some variation related to differences between annual intervals. Relatively small fluctuations in density and relatively large fluctuations due to uncontrolled factors unrelated to density are probably common in observational data sets, including most time series, suggesting that density dependence often may be relatively more difficult to detect in such data sets. Much longer time series than ours may enable one to overcome these difficulties; unfortunately, such long time series are rare in ecology.

Murdoch (1994) reported that the method of Pollard et al. (1987) detected density dependence in only 17 of 92 data sets that he analyzed, and he interpreted this as evidence against density dependence in these time series. Our results, however, suggest that this low percentage may be due to the methodological weakness of observational data. Uncontrolled factors may even produce spurious positive density dependence. For example, Menges and Dolan (1998) did not manipulate density and found that finite rates of increase were greater in sites with higher densities, presumably because these sites were more favorable in other ways. Finally, we note that correcting for the well-known bias of the correlation between density and changes in finite rate of increase (Maelzer 1970, St. Amant 1970, Bulmer 1975, Pollard et al. 1987), while essential, does not address all the limitations of observational data sets for the detection of density dependence.

Methodological conclusions

We have no reason to suspect that this population of *Bouteloua rigidiseta* is unusual in ways that would make density dependence hard to detect. Therefore the results of this study suggest that experimental manipulations, collection of data from all stages of the life cycle, and the calculation of λ or a comparable summary parameter may all be necessary to detect even relatively strong density dependence in many natural populations. Unfortunately, properly replicated experiments usually require more labor and are logically more complex than observational studies, and measuring all of the life history components and constructing and analyzing population models are also labor intensive.

There are situations in which some or all of these labor- and time-intensive approaches are unnecessary

for the detection of density dependence in natural populations, but the results of this study suggest that they are uncommon, for the following reasons.

1. Using observational instead of manipulative approaches.—Fifteen years was not enough even to come close to statistically significant density dependence in our time series, suggesting that much longer runs of data would be required for time series analyses for this and other short-lived perennial species.

2. Studying individual life history components.—If the response to density consistently occurs only in one or two life history components (and there were some way of knowing a priori which they were), one would only need to measure those life history component(s). However, if the response to density is the sum of many small responses spread throughout the life cycle, as it was in this population, it probably will be necessary to gather the data required to estimate λ or a comparable summary statistic and, hence, to measure or estimate all life history components.

3. Using N_{t+1}/N_t instead of λ .—In this study, the ratio N_{t+1}/N_t was as effective as λ in detecting density dependence in experimental data. Note, however, that N_{t+1} must be corrected to exclude manipulated (removed or added) plants. It was easy to identify which individuals were removed, but not which arose from added seed. To estimate the latter quantity, we had to measure the fecundity and size of each reproductive individual, the number of deaths in each size class, and the number of new recruits of each size class each year. Therefore, using only N_{t+1}/N_t instead of λ would not have reduced the labor involved in this study, but it might with a species in which seeds can be reliably marked and remain identifiable around their seedlings.

With this sole exception, the results of this study strongly support what may seem like a platitude, that there are no reliable shortcuts to the study of population regulation. They also support the conjecture that the failure to find density dependence may often be the result of weak methodology, rather than weak population regulation.

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APPENDIX A

Methods of population projection matrix construction, including “false match” correction, and direct effects of the density manipulations (*Ecological Archives* E087-037-A1).

APPENDIX B

A generalization to stage-specific population matrices of Pollard et al.’s (1987) bootstrap method for time-series data, and a description of the comparable method used as a supplementary analysis of the experimental data (*Ecological Archives* E087-037-A2).

APPENDIX C

The control matrices, the values of s_{ij} , Δa_{ij} , and $s_{ij}\Delta a_{ij}$ for each matrix, results of tests of density effects on individual matrix elements, additional results of the alternative analysis of density effects in the manipulated quadrats, results of the check of the linearity assumption of the LTRE, and a discussion of the sampling errors of λ and the separate matrix elements (*Ecological Archives* E087-037-A3).