

# Demographic models reveal the shape of density dependence for a specialist insect herbivore on variable host plants

TOM E. X. MILLER

348 Manter Hall, School of Biological Sciences, University of Nebraska, Lincoln, NE 68588-0118, USA

## Summary

1. It is widely accepted that density-dependent processes play an important role in most natural populations. However, persistent challenges in our understanding of density-dependent population dynamics include evaluating the shape of the relationship between density and demographic rates (linear, concave, convex), and identifying extrinsic factors that can mediate this relationship.

2. I studied the population dynamics of the cactus bug *Narnia pallidicornis* on host plants (*Opuntia imbricata*) that varied naturally in relative reproductive effort (RRE, the proportion of meristems allocated to reproduction), an important plant quality trait. I manipulated per-plant cactus bug densities, quantified subsequent dynamics, and fit stage-structured models to the experimental data to ask if and how density influences demographic parameters.

3. In the field experiment, I found that populations with variable starting densities quickly converged upon similar growth trajectories. In the model-fitting analyses, the data strongly supported a model that defined the juvenile cactus bug retention parameter (joint probability of surviving and not dispersing) as a nonlinear decreasing function of density. The estimated shape of this relationship shifted from concave to convex with increasing host-plant RRE.

4. The results demonstrate that host-plant traits are critical sources of variation in the strength and shape of density dependence in insects, and highlight the utility of integrated experimental–theoretical approaches for identifying processes underlying patterns of change in natural populations.

*Key-words:* Chihuahuan desert; *Narnia pallidicornis*; plant–insect interactions; population dynamics; resource allocation.

*Journal of Animal Ecology* (2007) **76**, 722–729

doi: 10.1111/j.1365-2656.2007.01239.x

## Introduction

Identifying the factors that confer stasis or drive change in population size is a fundamental goal in ecology, with important implications for the management of both rare and over-abundant species. Historically, ecologists have debated whether populations are regulated by density-dependent processes operating at large deviations from some equilibrium population size, or whether populations fluctuate in response to density-independent extrinsic factors (Nicholson 1933;

Andrewartha & Birch 1954; Wolda 1989; Turchin 1999). The controversy is largely resolved, and it is now generally accepted that density dependence plays an important role at some point in time or space for most natural populations (Turchin 1999; Sale & Tolimieri 2000; Brook & Bradshaw 2006). However, a number of key issues in our understanding of density-dependent population dynamics remain unresolved.

One of these issues concerns the shape of the relationship between population parameters and population density (Turchin 1999; Sibly *et al.* 2005; Owen-Smith 2006). Most commonly used theoretical models predict linear effects of density on demographic rates. For example, the logistic model of population growth ( $dN/dt = rN[1 - N/K]$ ) predicts a linear decline in per capita growth rate with increasing population

density ( $N$ ). Alternatively, a concave relationship would result when increases in density have disproportionately stronger effects at small vs. large population sizes. In this case, population growth may quickly decline at low density then level off at higher densities. At the other extreme, population growth may be relatively insensitive to density at low to moderate levels but drop off at high densities, yielding a convex relationship. Accounting for the shape of density dependence is important because, depending on the direction and degree of nonlinearity, linear models may severely bias estimates of population vital rates. Despite well-developed theory for nonlinear density dependence (see Turchin 2003), studies that estimate its shape for natural populations are rare (Leirs *et al.* 1997; Saether, Engen & Matthysen 2002; Sibly *et al.* 2005; Owen-Smith 2006).

A second, related challenge is to identify density-independent, extrinsic factors that mediate the strength of density dependence (Ylloja *et al.* 1999; Saether *et al.* 2002; Brook & Bradshaw 2006) and thus alter the shape of the relationship between density and population parameters. In herbivorous insects, most cases in which density dependence has been detected involve intraspecific competition for plant resources, rather than density-related impacts of predators or parasites (Stiling 1988). This pattern leads to the prediction that host-plant quality should mediate the strength of density dependence in herbivore populations (Larsson, Ekblom & Bjorkman 2000; Rotem & Agrawal 2003; Helms & Hunter 2005). Yet, while the effects of plant quality traits on insect performance are well-established (e.g. Rhoades 1983; White 1984; Rossiter, Schultz & Baldwin 1988), the extent to which these effects scale up to influence population dynamics is a relatively new line of inquiry. Available evidence suggests that understanding the role of density dependence in herbivore population dynamics may require explicit consideration of variation in host-plant quality (Ylloja *et al.* 1999; Larsson *et al.* 2000; Underwood & Rausher 2000, 2002; Agrawal 2004; Agrawal, Underwood & Stinchcombe 2004).

Many studies of density dependence in animals are based on analyses of population time series (e.g. Hanski 1990; Holyoak & Lawton 1992; Sequeira & Dixon 1997; Brook & Bradshaw 2006). Quantitative methods for detecting density effects from such observational data sets are highly controversial, as the results can be influenced by numerous factors including length of the time series, spatial scale, and choice of statistical test (Hassell, Latto & May 1989; Wolda & Dennis 1993; Dennis & Taper 1994; Ray & Hastings 1996). A more straightforward, though less commonly utilized approach is to directly manipulate densities and quantify the trajectories of experimental populations. This is the approach I have taken.

I studied the population dynamics of a specialist insect herbivore, the cactus bug *Narnia pallidicornis* Stål [Hemiptera: Coreidae], on its host plant, the tree

cholla cactus *Opuntia imbricata* ([Haw.] D.C.), in Chihuahuan desert grassland. Here, I integrate field data from a density manipulation experiment with demographic models to address the following three questions: (1) Which population vital rate, if any, is most responsive to changes in population density? (2) What is the shape of the relationship between density and demographic rates? (3) Does host-plant quality mediate the strength of density dependence, i.e. alter its shape? The combined experimental–theoretical approach employed here provides mechanistic insight into the linkages among insect density, resource quality and population dynamics.

## Methods

### STUDY ORGANISMS

The cactus bug *Narnia pallidicornis* specializes on cacti in the genus *Opuntia*. These haustellate, phloem-feeding insects attack all cactus parts but prefer new growth, especially reproductive structures (Mann 1969). There are two overlapping generations within a year, and juveniles and adults co-occur throughout the growing season. Adults overwinter among debris near the base of the plant and females deposit eggs on cactus spines in late spring. The first cohort of nymphs reaches maturity in June, and the second, larger cohort matures in September. Adults are reluctant but capable fliers and can move among neighbouring plants, while juveniles are flightless and complete their development on a single host (A. Benhumea and T.E.X. Miller, unpubl. data). Both juveniles and adults are susceptible to predation by cactus-dwelling spiders (Salticidae, Therididae, Thomisidae), but these interactions do not influence bug population dynamics (T.E.X. Miller, unpublished).

The tree cholla *Opuntia imbricata* is a common host plant for *Narnia*. This cactus is native to New Mexico, west Texas, and southern Colorado (Kinraide 1978; Benson 1982) and produces cylindrical, photosynthetic stem segments. Early in the growing season, meristems appear in clusters at the terminal ends of stem segments produced the previous year, and these are allocated to either reproductive or vegetative structures. Meristems allocated to reproduction develop into flower buds in late spring and fruits ripen and fall off of plants in early autumn. Meristems allocated to stem segments grow from May through August and produce new meristems the following spring.

Previous work indicated that the proportion of cactus meristems allocated to reproduction, which I term 'relative reproductive effort' (RRE), was an important component of host-plant quality for *Narnia*, and a far better predictor of among-plant variation in abundance than other traits considered (e.g. plant size, number of reproductive structures: Miller, Tyre & Louda 2006). In addition, cactus bug abundance is unrelated to host-plant nitrogen content ( $r = -0.048$ ,  $P = 0.66$ ,  $N = 85$ )

and water content ( $r = -0.023$ ,  $P = 0.83$ ,  $N = 86$ ), suggesting that plant traits more commonly associated with herbivore performance and dynamics have little influence in this system. For these reasons, I focus here on RRE and use this term interchangeably with 'plant quality'. The precise mechanisms that account for the positive effect of RRE on cactus bug dynamics remain unclear, but could include changes in phloem quality or composition associated with increasing reproductive allocation. To date, there is no evidence that insect feeding alters cactus meristem allocation, and so I consider plant quality as a density-independent, extrinsic factor.

#### STAGE-STRUCTURED POPULATION DYNAMICS

The following stage-structured model describes the per-plant dynamics of juvenile and adult cactus bugs in discrete time:

$$J_{t+\Delta t} = r_j(1 - T)J_t + f(r_a A_t + c)$$

$$A_{t+\Delta t} = r_j T J_t + r_a A_t + c \quad \text{eqn 1}$$

In this model,  $J_t$  and  $A_t$  are juvenile and adult bug abundances, respectively, at time  $t$ ;  $r_j$  and  $r_a$  are the retention probabilities of juveniles and adults, respectively;  $T$  is the probability of transition from the juvenile to the adult stage;  $f$  is adult fecundity (juveniles per adult); and  $c$  is the adult colonization rate (adults per  $\Delta t$ ).

As juvenile bugs are flightless and complete development on single plants, there is no juvenile movement in the model. However, late-instar juveniles may eclose into the adult stage and disperse before the next time step. Similarly, adult dispersal can also occur between time steps. These dispersal processes are incorporated into the retention parameters ( $r_j$  and  $r_a$ ), which represent joint probabilities of surviving and remaining on a host plant to be detected at the next time step. Because detecting eggs and differentiating among instars are difficult and time-consuming in the field, the egg stage is not explicitly included in the model and all immature stages are considered collectively in the juvenile (flightless) class. Further discussion of this model is given in Miller *et al.* (2006).

#### DENSITY MANIPULATION EXPERIMENT

To evaluate role of density dependence in cactus bug population dynamics, I manipulated bug densities on individual host plants early in the 2005 growing season and fit the stage-structured model (eqn 1) to experimental data. I consider the insects on a single plant as a replicate cactus bug population, with populations linked by adult movement. The experiment was conducted in a Chihuahuan desert grassland on the Sevilleta National Wildlife Refuge, a Long-term Ecological Research (LTER) site in central New Mexico (34°20'5.3"N, 106°37'53.2"W). In May 2005, I selected

60 similarly sized (*c.* 1.5 m height), mature tree cholla and randomly assigned each plant to one of five levels ( $n = 12$ ) of initial juvenile bug density: 1, 4, 8, 12, or control (unmanipulated). I chose these levels to include and exceed mean and maximum juvenile densities found at this site in May of the previous year (0.88 and 7, respectively). The plants in this experiment exhibited a wide range of natural variation in RRE (minimum: 0.17, maximum: 0.81), but neither RRE nor total available meristems differed among treatment groups (RRE:  $F_{4,55} = 1.08$ ,  $P = 0.37$ ; meristems:  $F_{4,55} = 0.48$ ,  $P = 0.75$ ), indicating that there was no bias in plant quality among treatments. Plant size [estimated volume ( $\text{cm}^3$ )] was also consistent across treatments ( $F_{4,55} = 0.13$ ,  $P = 0.97$ ), and was unrelated to variation in RRE ( $r = -0.055$ ,  $P = 0.67$ ).

On 2 June, I counted naturally occurring juvenile abundances on experimental plants and thinned or added bugs according to the treatment assignment. For most plants, bugs needed to be added and these were collected from plants > 1 km from the experimental site. The manipulations involved only juveniles because this stage is flightless and could therefore be 'confined' to experimental host plants. Adults were rare at this point in the season (mean  $\pm$  SE:  $0.75 \pm 0.16$ ), and so the addition of juveniles likely did not significantly alter population stage structure. Densities were not manipulated any time following the initial treatment, and adults colonized naturally throughout the growing season. I monitored juvenile and adult abundances on three subsequent dates: 1 July, 1 August and 31 August. For presentation, I divided each treatment group into high and low plant quality populations based on whether host-plant RRE was greater than or less than the median value (0.55). Also, because abundances on plants in the control and one-juvenile treatments were statistically identical at the start of the season ( $t_{22} = -0.82$ ,  $P = 0.42$ ), these groups were pooled as 'ambient' for presentation.

#### MODEL-FITTING ANALYSES

I conducted two model-fitting analyses to ask if incremental modifications to the basic demographic structure (eqn 1) provided greater concordance between model predictions and observations from the field experiment. With this approach, I was not trying to detect treatment effects *per se*. Rather, I sought to determine if variation in any demographic parameter was related to variation in density, which was generated experimentally. The time step of the model ( $\Delta t = 30$  days) corresponds to the schedule of data collection. In all analyses, I evaluated explanatory power with Akaike's Information Criterion, corrected for sample size (AICc;  $n = 60$ ), and AIC weights ( $w_i$ ), which give the proportion of evidence in favour of each model out of a given set of candidate models (Burnham & Anderson 1998). Methods for model-fitting are identical to those described in Miller *et al.* (2006).

**Table 1.** Analyses of cactus bug demographic models and results of fitting the models to experimental field data. The analyses were designed to determine (A) which demographic parameter, if any, is most responsive to population density, and (B) if density dependence is linear or nonlinear, and if plant-quality influences its shape. Table entries show the functional form of each demographic parameter (corresponding to eqn 1 in text), the number of parameters ( $P$ ), the minimized negative log-likelihood ( $L$ ), the difference between the AICc of each model and the minimum value of a given set ( $\Delta$ AICc), and the proportion of evidence in favour of each ( $w_i$ ). Within each analysis, best-fitting models are shown in bold. Maximum Likelihood parameter estimates for the overall best model (Model 3 in analysis B) are given in Table 2

Model	Demographic parameters						$P$	$L$	$\Delta$ AICc	$w_i$
	Juvenile retention	Transition	Adult retention	Fecundity	Colonization					
A	1	$r_j$	$T$	$r_a$	$f$	$c$	5	1594.40	14.57	0.0007
	<b>2</b>	<b><math>a-bD</math></b>	<b><math>T</math></b>	<b><math>r_a</math></b>	<b><math>f</math></b>	<b><math>c</math></b>	<b>6</b>	<b>1585.88</b>	<b>0.00</b>	<b>0.99</b>
	3	$r_i$	$a-bD$	$r_a$	$f$	$c$	6	1593.12	14.49	0.0007
	4	$r_i$	$T$	$a-bD$	$f$	$c$	6	1594.06	16.37	0.0003
	5	$r_i$	$T$	$r_a$	$a-bD$	$c$	6	1594.19	16.62	0.0002
	6	$r_i$	$T$	$r_a$	$f$	$a-bD$	6	1594.40	17.05	0.0002
B	1	$a-bD$	$T$	$r_a$	$f$	$c$	6	1585.88	13.60	0.001
	2	$a-bD^\theta$	$T$	$r_a$	$f$	$c$	7	1584.00	12.41	0.002
	<b>3</b>	<b><math>a-bD^{\alpha \times \text{RRE}}</math></b>	<b><math>T</math></b>	<b><math>r_a</math></b>	<b><math>f</math></b>	<b><math>c</math></b>	<b>7</b>	<b>1577.79</b>	<b>0.00</b>	<b>0.99</b>

In the first analysis, I asked if a model incorporating density dependence provided a better fit to the experimental data than a density-independent model and, if so, which parameter was most responsive to density. I constructed six different model versions in which all parameters were density-independent, or each parameter was a linear function of density (Table 1A). The intercept of the linear function represents the parameter value at zero density, and a nonzero slope would indicate that the parameter value changes with density. This analysis indicated that the juvenile retention parameter was density-dependent (see Results).

In the second analysis, I asked if a nonlinear relationship between density and juvenile retention provided a better fit than a linear one, and if host-plant quality influenced the shape of this relationship. To do this, I compared the explanatory power of the linear model with that of two nonlinear models in which density was raised to an exponent,  $\theta$ . If  $0 < \theta < 1$ , the relationship is concave and the parameter value decreases sharply at low density then levels off. If  $\theta > 1$ , the relationship is convex and the parameter value decreases slowly and drops off at high density. In the two nonlinear models,  $\theta$  was either a constant or a function of plant quality ( $\theta = \alpha \times \text{RRE}$ ; Table 1B). For a given  $\alpha$ , density dependence becomes increasingly convex with increasing plant quality. In preliminary analyses, the intercept of this function was estimated as 0, and so I removed the intercept parameter from the model. I incorporated plant quality effects through the density exponent ( $\theta$ ) because modifications to the slope ( $b$ ) led to implausible parameter estimates with large or incalculable confidence limits.

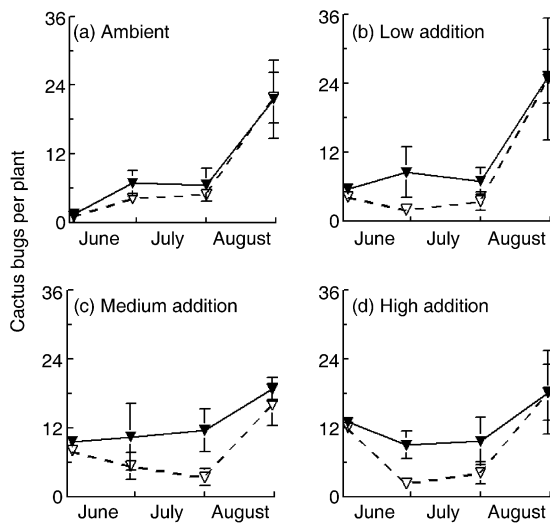
I used this incremental method rather than conducting a single large model contest in order to avoid problems associated with many candidate models relative to sample size (Burnham & Anderson 2002). In all density-dependent models, density was defined as

total bug abundance (juvenile + adult) at the current time step (i.e. no lagged density effects). To facilitate parameter convergence for models in which retention and transition probabilities were functions of density, I rescaled bug densities to an index from 0 to 1 by dividing each total bug count by the maximum observed (44). The sign of parameters for density effects was not constrained, and so this approach could identify either positive or negative density dependence.

It is possible that RRE has no effect on density dependence but does directly influence other demographic parameters. In this case, the model with density raised to a function of plant quality (Model 3, Table 1B) may provide the best fit simply because the parameter  $\alpha$  is accommodating RRE effects elsewhere in the life cycle. To evaluate this possibility, I generated additional Maximum Likelihood estimates for  $\alpha$  when each of the other demographic parameters ( $t, r_a, f, c$ ) could also vary with RRE as a linear function. If there is a true effect of plant quality on the shape of density dependence, then  $\alpha$  should not change when additional parameters can also respond to host-plant RRE.

## Results

Despite the wide range of initial, experimentally generated densities on tree cholla cacti, cactus bug populations quickly converged upon similar growth trajectories, with all populations reaching similar peak abundances late in the season (Fig. 1). Cactus bugs tended to be more abundant on high- vs. low-quality plants (greater vs. less than median RRE), and plant quality appeared to influence rates of change following the initial density manipulations. Populations that began at ambient densities increased on both high- and low-quality plants between the first two censuses, while those that began at the highest densities (12 juveniles) decreased on both high- and low-quality plants

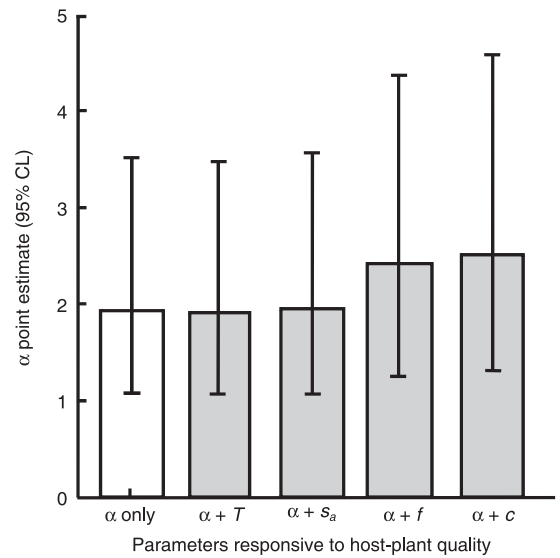


**Fig. 1.** Results of density manipulation experiment for cactus bug populations on tree cholla cactus, sorted by density treatment (a–d). Open shapes/dotted lines represent populations on low-quality plants (relative reproductive effort < median) and filled shapes/solid lines represent populations on high-quality plants (RRE > median). The ‘ambient addition’ panel (a) shows pooled results from control and 1-juvenile treatments. Low, medium, and high addition panels (b–d) show results from the 4-, 8- and 12-juvenile addition treatments, respectively.

(Fig. 1). Interestingly, populations at intermediate levels of addition (four and eight juveniles) tended to increase on high-quality plants and decrease on low-quality plants. Juveniles outnumbered adults throughout the season (data not shown).

In the first model-fitting analysis, the model that defined juvenile retention ( $r_j$ ) as a decreasing linear function of density received substantially more support from the data than either a density-independent model, or models that included density dependence through other demographic parameters (Table 1A). In the second analysis, the experimental data strongly supported a nonlinear relationship between juvenile retention and density, and an effect of host-plant quality on the shape of this relationship (Table 1B). The model with density raised to a function of RRE provided a significantly better fit than either the linear model or the nonlinear model with density raised to a constant, based on Akaike weights. The parameter that described the effect of RRE on density dependence ( $\alpha$ ) was generally insensitive to RRE effects on additional demographic rates, indicated by the large overlap of 95% confidence intervals for  $\alpha$  when additional parameters could vary with RRE (Fig. 2).

Parameter estimates and 95% confidence intervals for the best-fitting model (Model 3 in Table 1B) are given in Table 2. The upper confidence limit for the intercept of the juvenile retention function ( $a$ ) could not be estimated (the likelihood profile was L-shaped), and so I set the upper confidence limit as 1.0, the upper bound for this parameter. Figure 3A shows that the



**Fig. 2.** Point estimates and 95% confidence limits for the parameter  $\alpha$ , which determines how host-plant quality (RRE) influences the relationship between cactus bug density and juvenile retention. The white bar shows the estimate from the original model (Table 1B) in which only  $\alpha$  responds to RRE; grey bars show variations on this model in which additional parameters can respond to RRE.

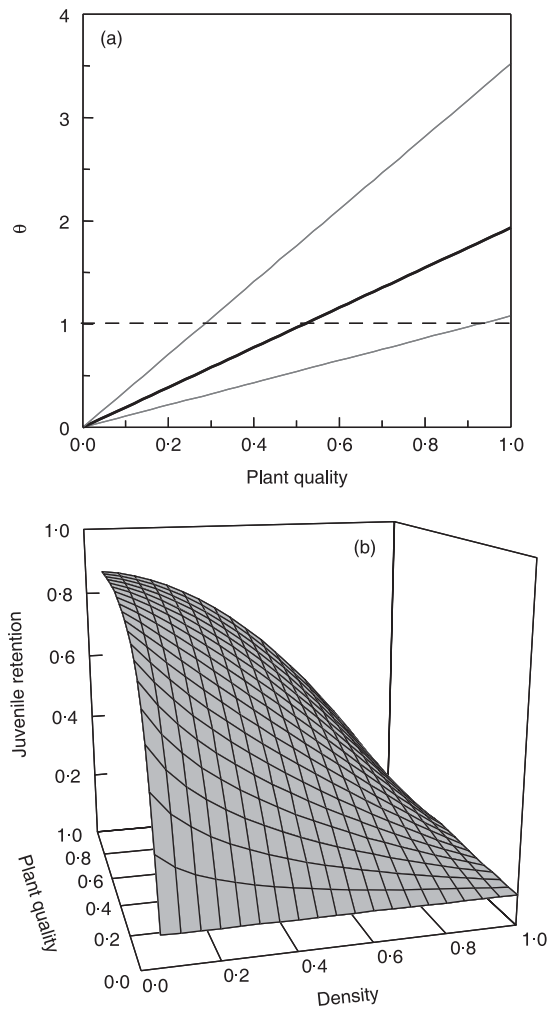
**Table 2.** Maximum likelihood parameter estimates and 95% confidence limits corresponding to the best-fitting model structure (Table 1B, Model 3)

Parameter	Point estimate (95% CL)
Juvenile retention $r_j$	$\left\{ \begin{array}{l} a \quad 0.87 (0.65, 1.0) \\ b \quad 0.78 (0.51, 1.0) \\ \theta \quad 1.93 (1.08, 3.52) \times \text{RRE} \end{array} \right.$
Transition	$T \quad 0.09 (0.03, 0.14)$
Adult retention	$r_a \quad 0.09 (0.04, 0.14)$
Fecundity	$f \quad 7.89 (6.13, 10.48)$
Colonization	$c \quad 0.8 (0.61, 1.01)$

density exponent,  $\theta$ , shifts from < 1 (concave) to > 1 (convex) with increasing plant quality. The inflection point occurs at approximately RRE = 0.5 (half of meristems allocated to reproduction). Incorporating this variation in  $\theta$  into the juvenile retention function yields the surface shown in Fig. 3(B), which describes juvenile retention in relation to bug density and host-plant quality (RRE). Estimated retention ranged from 0.87 on low-density – high-quality plants to 0.09 on high-density – low-quality plants, and the relationship was curvilinear in both dimensions. Juvenile retention declined with small increases in density on low-quality plants, but did not decline until very high densities were reached on high-quality plants.

**Discussion**

I integrated data from a density manipulation experiment with multimodel inference techniques to evaluate



**Fig. 3.** (a) Variation in the density exponent ( $\theta$ ) in relation to host-plant quality [relative reproductive effort (proportion of meristems allocated to reproduction)]. Black line corresponds to predictions based on the Maximum Likelihood point estimate for the slope parameter  $\alpha$ , and thin grey lines represent the 95% confidence limits. The shape of density dependence is concave below and convex above the horizontal dotted line ( $\theta = 1$ ). (b) Fitted surface of juvenile cactus bug retention in relation to bug density (scaled from 0 to 1) and host-plant quality (RRE).

competing hypotheses for the role of density dependence in cactus bug population dynamics, and the effect of plant resource quality on its strength and shape. The field data showed a strong response by cactus bug populations to experimentally elevated densities and this response appeared to be influenced by host-plant quality (Fig. 1). It is unclear why the difference in cactus bug abundance between high- and low-quality plants diminished late in the season. It is possible that the reliability of relative reproductive effort (RRE) as an indicator of plant quality decreased as the plants in this experiment began dispersing their fruits in August.

Fitting models to the field data allowed me to identify likely demographic mechanisms underlying these patterns. The model-fitting analyses clearly indicated that juvenile bug retention was negatively influenced by

the densities of co-occurring conspecifics, and a non-linear decreasing function best described this effect. The shape of the relationship between juvenile retention and density varied along a gradient of RRE, shifting from concave to convex with increasing allocation of cactus meristems to reproduction (Fig. 3). As RRE increases, higher densities are required to achieve equal reductions in juvenile retention. Thus, negative effects of density are 'diluted' by plant quality at all but the highest densities. The fact that the parameter  $\alpha$  was generally insensitive to RRE effects elsewhere in the life cycle (Fig. 2) suggests a real effect of this plant-quality trait on the shape of density dependence.

These results support suggestions that host-plant traits are critical sources of variation in density dependence in insects (Underwood 2000; Agrawal *et al.* 2004), and key components to understanding spatio-temporal variation in insect population abundance (Larsson *et al.* 2000; Underwood & Rausher 2000; Helms & Hunter 2005). Indeed, cactus bug abundance varies dramatically across adjacent years and across sites distributed throughout New Mexico, and this variation is correlated with differences in meristem allocation among host-plant populations (Miller *et al.* 2006). The results of this study suggest that concomitant differences in the strength of density dependence among host-plant populations may underlie observed patterns of cactus bug dynamics through time and space.

The use stage-structured models allowed me to identify where in the life cycle conspecific density had the greatest effects on population dynamics. This is in contrast to the common use of more phenomenological models, in which single parameters [e.g.  $r$  (intrinsic rate of increase) or  $K$  (carrying capacity)] incorporate multiple demographic processes. Similar approaches to those employed here will likely be useful in understanding density-dependent population dynamics in other organisms with complex life histories (Hellriegel 2000; Larsson *et al.* 2000). It is worth noting, however, that the juvenile cactus bug retention parameter represents the joint probability of surviving and remaining on a host plant to be detected at the next time step. While juveniles generally complete development on their natal hosts, they may eclose and disperse between censuses. From my data, I cannot determine whether density influenced juvenile mortality, postnatal dispersal, or both. Density-dependent dispersal is common in herbivorous insects (Denno & Roderick 1992; Herzig 1995) and could play a role in this system. In addition, the temporal variation in the experimental data (Fig. 1) suggests that parameter values may not be constant across the growing season, as is assumed here. A time-varying model may have provided a better fit to the data, but would have had the disadvantage of requiring many more estimated parameters.

Cactus meristem allocation is likely driven by a combination of factors including winter climate, local resource conditions, plant history (i.e. costs of reproduction in previous years), and genotype (Miller

et al. 2006). Herbivory does not alter current or future meristem allocation (unpubl. data), and so I considered host-plant quality as a density-independent, extrinsic factor. However, the view of plant quality traits as density-independent factors may not be broadly applicable (but see Price & Hunter 2005). Herbivore damage often does influence resource quality to co-occurring or subsequent feeders via induced plant responses (Karban & Baldwin 1997; Underwood 2000; Underwood & Rausher 2002; Viswanathan, Narwani & Thaler 2005), suggesting the potential for complex feedbacks among herbivore damage, plant quality, and the strength of density dependence. Extending the influences of plant quality to include such feedbacks remains an important challenge in our understanding of herbivore population dynamics in both natural and managed systems.

### Acknowledgements

Funding for this work was provided by the Initiative for Ecological and Evolutionary Analysis at the University of Nebraska – Lincoln and from the Sevilleta LTER (NSF DEB-0217774). Rene Aguilera and Max Smith provided valuable assistance in collecting wily insects off of very spiny plants. Drew Tyre provided valuable instruction, and Chad Brassil, Jim Eckberg, Aaron Gassman, Svata Louda, Diana Pilson, Holly Prendeville, Brigitte Tenhumberg, and two anonymous reviewers offered helpful comments on this manuscript. TEXM was supported by a training grant from the US Department of Education (Graduate Assistance in Areas of National Need).

### References

- Agrawal, A.A. (2004) Plant defense and density dependence in the population growth of herbivores. *The American Naturalist*, **164**, 113–120.
- Agrawal, A.A., Underwood, N. & Stinchcombe, R. (2004) Intraspecific variation in the strength of density dependence in aphid populations. *Ecological Entomology*, **29**, 521–526.
- Andrewartha, H.G. & Birch, L.C. (1954) *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago, IL.
- Benson, L. (1982) *Cacti of the United States and Mexico*. Stanford University Press, Stanford.
- Brook, B.W. & Bradshaw, J.A. (2006) Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology*, **87**, 1445–1451.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*, 2nd edn. Springer, New York.
- Dennis, B. & Taper, M.L. (1994) Density dependence in time series observations of natural populations: estimation and testing. *Ecological Monographs*, **64**, 205–224.
- Denno, R.F. & Roderick, G.K. (1992) Density-related dispersal in planthoppers: effects on interspecific crowding. *Ecology*, **73**, 1323–1334.
- Hanski, I. (1990) Density dependence, regulation, and variability in animal populations. *Philosophical Transactions of the Royal Society, London (Series B)*, **330**, 141–150.
- Hassell, M.P., Latto, J. & May, R.M. (1989) Seeing the wood for the trees: detecting density dependence from existing life table studies. *Journal of Animal Ecology*, **58**, 883–892.
- Hellriegel, B. (2000) Single- or multistage regulation in complex life cycles: does it make a difference? *Oikos*, **88**, 239–249.
- Helms, S.E. & Hunter, M.D. (2005) Variation in plant quality and the population dynamics of herbivores: there is nothing average about aphids. *Oecologia*, **145**, 196–203.
- Herzig, A.L. (1995) Effects of population density on long-distance dispersal in the goldenrod beetle *Trirhabda virgata*. *Ecology*, **76**, 2044–2054.
- Holyoak, M. & Lawton, J.H. (1992) Detection of density dependence from annual censuses of bracken-feeding insects. *Oecologia*, **91**, 425–430.
- Karban, R. & Baldwin, I.T. (1997) *Induced Response to Herbivory*. University of Chicago Press, London.
- Kinraide, T.B. (1978) The ecological distribution of cholla cactus (*Opuntia imbricata* (Haw.) DC) in El Paso county, Colorado. *Southwest Naturalist*, **23**, 117–134.
- Larsson, S., Ekbom, B. & Bjorkman, C. (2000) Influence of plant quality on pine sawfly population dynamics. *Oikos*, **89**, 440–450.
- Leirs, H., Stenseth, N.C., Nichols, J.D., Hines, J.E., Verhagen, R. & Verheyen, W. (1997) Stochastic seasonality and non-linear density-dependent factors regulate population size in an African rodent. *Nature*, **389**, 176–180.
- Mann, J. (1969) *Cactus-feeding Insects and Mites*. Smithsonian Institution, Washington, DC.
- Miller, T.E.X., Tyre, A.J. & Louda, S.M. (2006) Plant reproductive allocation predicts herbivore dynamics across spatial and temporal scales. *American Naturalist*, **168**, 608–616.
- Nicholson, A.J. (1933) The balance of animal populations. *Journal of Animal Ecology*, **2**, 132–178.
- Owen-Smith, N. (2006) Demographic determination of the shape of density dependence for three African ungulate populations. *Ecological Monographs*, **76**, 93–109.
- Price, P.W. & Hunter, M.D. (2005) Long-term population dynamics of a sawfly show strong bottom-up effects. *Journal of Animal Ecology*, **74**, 917–925.
- Ray, C. & Hastings, A. (1996) Density dependence: are we searching at the wrong spatial scale? *Journal of Animal Ecology*, **65**, 556–566.
- Rhoades, D.F. (1983) Herbivore population dynamics and plant chemistry. *Variable Plants and Herbivores in Natural and Managed Systems* (eds R.F. Denno & M.S. McClure), pp. 55–68. Academic Press, New York.
- Rossiter, M., Schultz, J.C. & Baldwin, I.T. (1988) Relationships among defoliation, red oak phenolics, and gypsy moth growth and reproduction. *Ecology*, **69**, 267–277.
- Rotem, K.A. & Agrawal, A.A. (2003) Density dependent population growth of the two-spotted spider mite, *Tetranychus urticae*, on the host plant *Leonurus cardiaca*. *Oikos*, **103**, 559–565.
- Saether, B., Engen, S. & Matthysen, E. (2002) Demographic characteristics and population dynamics patterns of solitary birds. *Science*, **295**, 2070–2073.
- Sale, P.F. & Tolimieri, N. (2000) Density dependence at some time and place? *Oecologia*, **124**, 166–171.
- Sequeira, R. & Dixon, A.F.G. (1997) Population dynamics of tree-dwelling aphids: the importance of seasonality and time scale. *Ecology*, **78**, 2603–2610.
- Sibly, R.M., Barker, D., Denham, M.C., Hone, J. & Pagel, M. (2005) On the regulation of populations of mammals, birds, fish, and insects. *Science*, **309**, 607–610.
- Stiling, P. (1988) Density-dependent processes and key factors in insect populations. *Journal of Animal Ecology*, **57**, 581–593.
- Turchin, P. (1999) Population regulation: a synthetic review. *Oikos*, **84**, 153–159.
- Turchin, P. (2003) *Complex Population Dynamics*. Princeton University Press, Princeton, NJ.

- Underwood, N. (2000) Density dependence in induced plant resistance to herbivore damage: threshold, strength, and genetic variation. *Oikos*, **89**, 295–300.
- Underwood, N. & Rausher, M. (2000) The effects of host-plant genotype on herbivore population dynamics. *Ecology*, **81**, 1565–1576.
- Underwood, N. & Rausher, M. (2002) Comparing the consequences of induced and constitutive plant resistance for herbivore population dynamics. *American Naturalist*, **160**, 20–30.
- Viswanathan, D.V., Narwani, A.J. & Thaler, J.S. (2005) Specificity in induced plant responses shapes patterns of herbivore occurrence on *Solanum dulcamara*. *Ecology*, **86**, 886–896.
- White, T.C.R. (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia*, **63**, 90–105.
- Wolda, H. (1989) The equilibrium concept and density dependence tests. What does it all mean? *Oecologia*, **81**, 430–432.
- Wolda, H. & Dennis, B. (1993) Density dependence tests, are they? *Oecologia*, **95**, 581–591.
- Ylloja, T., Roininen, H., Ayres, M.P., Rousi, M. & Price, P.W. (1999) Host-driven population dynamics in an herbivorous insect. *Proceedings of the National Academy of Sciences of the USA*, **96**, 10735–10740.

*Received 3 December 2006; accepted 28 February 2007*