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The route to extinction: population dynamics of a threatened butterfly

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Abstract We compare results of field study and model analysis of two butterfly populations to evaluate the importance of alternative mechanisms causing changes in abundance. Although understanding and predicting population fluctuations is a central goal of population ecology, it is not often achieved because long-term abundance data are available for few populations in which mechanisms causing fluctuations also are known. Both kinds of information exist for two populations of the checkerspot butterfly, *Euphydryas editha bayensis*, which are matched in most ways except for habitat area and topography. We applied results from field study to make predictions about the dynamics of the two populations. Then we tested these predictions using nonlinear modeling of abundance data. Models included endogenous factors, exogenous effects of weather, or both. Results showed that the populations differed in variability and responses to endogenous and exogenous factors. The population in the more homogeneous habitat varied more widely, went extinct first, and fluctuated more severely with climate. Dynamics of the population occupying the topographically diverse habitat were more complex, containing damped oscillations and weaker influences of weather. We draw four main conclusions. First, the routes to extinction for *E. e. bayensis* populations in protected habitat were random walks driven by climatic variability. Climatic influences dominated both populations, but the timing and functional forms of climatic effects differed between populations. Second, topographic diversity reduced weather-induced population variability and increased persistence time. Third, one must explicitly consider both endogenous and exogenous components to fully understand population dynamics. Fourth, resolving the debate over population regulation requires integrating long-term population sampling, model analysis, and investigation of mechanisms in the field.

Keywords *Euphydryas editha bayensis* · Density dependence and density independence · Habitat topography · Nonlinear modeling · Persistence time

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Introduction

Understanding changes in the size of populations is a central objective in ecology. The issue has important theoretical and practical implications related to the nature of biological complexity (Ellner and Turchin 1995; Zimmer 1999), conservation of threatened species (Dennis et al. 1991; Lande 1993), regulation of exploited populations (Ludwig et al. 1993; Higgins et al. 1997), and management of pests (Logan et al. 1998). These applications often require forecasting population changes. When population dynamics are largely stochastic, forecasts of future population size become more uncertain (Lewellen and Vessey 1998), increasing the difficulty of conservation (Mangel and Tier 1994) and management (Higgins et al. 1997; Marion et al. 2000).

Debates about whether population changes are constrained by regulating mechanisms have persisted for decades (Elton 1949; Andrewartha and Birch 1954; Hassell et al. 1976; Dempster 1983; Murray 1994). Until recently, discussion about population regulation was polarized. One position assumed that “density-dependent” factors maintain populations with simple dynamics near constant equilibrium values (Nicholson 1954; Hairston et al. 1960; Hassell et al. 1976). The other argued that equilibria are rare if they exist at all, and that factors independent of population density drive dynamics (Ehrlich and

Birch 1967; Dempster 1983; Den Boer 1991). In recent years, debates about population regulation have approached resolution with an emphasis on identifying mechanisms that cause or limit fluctuations (Murdoch 1994; Turchin 1995, 1999; Kendall et al. 1999). This approach has yielded important unifying results, including evidence that density-dependent factors can act intermittently and that population fluctuations often result from interaction between both kinds of factors (Leirs et al. 1997; Bjørnstad et al. 1999; Bjørnstad and Grenfell 2001; Coulson et al. 2001).

Two developments helped advance the debate. First, more long-term population data sets became available (Inchausti and Halley 2001), especially for insects (Woiwod and Hanski 1992). Second, new mathematical tools were developed to probe data with greater sophistication. Disputes about population regulation were partially resolved by considering the role of nonlinear feedback (Murdoch 1994; Zheng et al. 1998) and by showing that density-dependent mechanisms can account for complex dynamics (Turchin and Taylor 1992). Turchin broadened the debate, suggesting that both the relative importance of density-independent influences and the dynamical complexity of density-dependent factors should be considered. Unfortunately, most analyses have considered density-dependent (endogenous) factors (Hassell et al. 1976; Turchin and Taylor 1992; Woiwod and Hanski 1992) or density-independent (exogenous) factors (Forchhammer and Boertmann 1993; Weiss et al. 1988), but not both. [“Endogenous” factors exert dynamical feedback to population processes, while “exogenous” factors act independently of population history (Turchin and Taylor 1992). These terms are nearly synonymous with “density-dependent” and “density-independent”, but they avoid confusion about density-related processes that occur without feedback (Sale and Tolimieri 2000) or climatic variables that may act in a density-dependent fashion (Andrewartha and Birch 1954).] The importance of both endogenous and exogenous factors has been determined for a few common species (Lewellen and Vessey 1998; Dixon et al. 1999), but rarely for species at risk of extinction.

In this paper, we evaluate endogenous and exogenous mechanisms affecting population dynamics of the Bay checkerspot butterfly, *Euphydryas editha bayensis*. Long-term data exist for just two *E. e. bayensis* populations. Statistical conclusions about relationships between dynamics and causal factors cannot be drawn from simple comparisons of the two populations. Instead, we apply results from field studies to make predictions about their dynamics. We then test these predictions using nonlinear modeling of population data. We use the model results to determine the functional form and relative importance of endogenous and exogenous components. Next, we illustrate dynamical properties of each component by simulating population trajectories and comparing simulations with the data. Lastly, we apply the model results to infer the mechanisms driving *E. e. bayensis* population dynamics.

Bay checkerspot study system

Life history and habitat relationships

E. e. bayensis is a univoltine butterfly that is restricted to patches of serpentine grassland in the San Francisco Bay Area, California (Ehrlich et al. 1975). In 1987, the subspecies was listed as threatened under the U.S. Federal Endangered Species Act (U.S. Federal Register 1987). The life history of the subspecies features a race against senescence of its larval host plants, *Plantago erecta*, *Castilleja densiflora* and *C. exserta* (Singer 1972). Larvae hatch from eggs in mid-spring, feed briefly, and spend the summer drought in an obligatory diapause (Ehrlich 1965; Singer 1972). Pre-diapause larvae starve unless they reach the fourth instar before host plants senesce. Pre-diapause starvation strongly affects adult abundance in the subsequent year (Singer 1972; Ehrlich et al. 1975; Dobkin et al. 1987). In early winter, larvae break diapause and resume development. After a brief pupation, adults eclose, mate, and lay eggs. Hatching pre-diapause larvae then commence another developmental race.

Climate and topography interact to modulate *E. e. bayensis* phenology and the severity of pre-diapause mortality (Dobkin et al. 1987; Weiss et al. 1988, 1993; Hellmann, unpublished data). Sunny weather supports rapid larval growth, while rainy and cloudy weather slows larval development. Weather conditions affect the phenology of larval host plants in similar ways. During droughts post-diapause larvae become restricted to the coolest slopes, implying that host plants senesce before larvae reach diapause on other slopes. In moderately wet years, larval survival tends to increase and larval distributions tend to expand to warmer slopes. Climate and topography also affect growth of post-diapause larvae in winter, when aspect-determined contrasts in solar exposure are greatest (Weiss et al. 1993). Furthermore, the timing of rainfall within the growing season may be important, because pre-diapause and post-diapause larval stages occur in different months.

Jasper Ridge populations

Populations of *E. e. bayensis* have been studied since 1960 on two patches of serpentine grassland at the Jasper Ridge Biological Preserve (JRBP), Stanford University (San Mateo, Co.), California (Ehrlich et al. 1975; Hellmann et al., unpublished data). Area C is relatively large (9.80 ha) and nearly flat. It supported a widely fluctuating population (JRC) that went extinct in 1991. Area H is smaller (2.55 ha), topographically heterogeneous, and supported a population (JRH) until 1998. Habitats C and H are adjacent and closely matched, sharing similar climates, plant species, and management histories (Ehrlich et al. 1975). They differ primarily in area and topography. Adult dispersal between JRC and JRH averaged less than 2% of total recaptures, and the two populations fluctuated independently (Ehrlich et al. 1975; Hellmann et al., unpublished data). Population sizes of JRC and JRH have been measured annually since 1960, with reliable data continuous from 1969 (Hellmann et al., unpublished data). Analyses below use data on male butterflies because mark-release-recapture data are more reliable for males than females (Ehrlich et al. 1984; Hellmann et al., unpublished data).

Predictions about *Euphydryas* population dynamics

Many factors affecting *E. e. bayensis* populations have been investigated in the field, yielding a mechanistic understanding of their annual fluctuations. This knowledge can be applied to make the following general hypotheses about *E. e. bayensis* population dynamics and specific predictions about dynamics at areas C and H, given differences in topography at those two sites. Below, we test these predictions using long-term *E. e. bayensis* population data.

Hypothesis 1

The importance of climatic factors in *E. e. bayensis* population dynamics is inversely related to heterogeneity in habitat topography.

Prediction 1

Relative to population dynamics in JRH, dynamics in JRC should contain a stronger exogenous component and a weaker endogenous component.

Hypothesis 2

Survival of pre-diapause larvae is the most important demographic bottleneck limiting *E. e. bayensis* populations.

Prediction 2a

Population dynamics should be driven more strongly by weather affecting survival of pre-diapause larvae than by weather affecting subsequent life stages. In particular, changes in adult abundance should be predicted more accurately by growing season weather in the preceding year than by weather in the growing season concurrent with adult flight.

Prediction 2b

The difference in prediction accuracy using weather in the preceding vs current years should be greater for JRC than for JRH because weather affects larval survival more strongly in the relatively flat topography of area C.

Materials and methods

Autocorrelation analysis

We assessed qualitative trends in *E. e. bayensis* populations by analyzing autocorrelation functions (ACFs) of log-transformed (all logarithms in this paper are base *e*) annual population data ($L_t \equiv \log N_t$; Box and Jenkins 1976; Royama 1992). Because JRH appeared to be nonstationary, we also determined ACFs for the log-transformed population growth rates [$r_t \equiv \log (N_t/N_{t-1})$; Royama 1992].

Data manipulation prior to model selection

Truncating the time series

Both populations declined to zero abundance (extinction) late in the sampling period (Hellmann et al., unpublished data). To avoid confounding the analysis with stochastic genetic and demographic factors that affect very small populations, we truncated data for both populations at the first recorded zero population estimate (1988 for JRC; 1996 for JRH). Truncation did not qualitatively affect results, which were similar with data reduced by several additional years. Because the last value in each truncated data set is zero, which is undefined for log-transformations, we added one to all data points.

Detrending

If population trends are entrained by environmental trends, then endogenous dynamics within the trend often are best analyzed independently of the trend itself (Royama 1992; Turchin and Taylor 1992). Alternatively, trends are the dominant feature in the dynamics of some populations, and removing trends prior to analysis can yield misleading conclusions (Pimm and Redfearn 1988; Ariño and Pimm 1995). For example, removing apparent trends from unregulated populations eliminates a central property of their dynamics (Royama 1992). We conducted model analysis for JRC without detrending, because autocorrelation analysis suggested that JRC dynamics were a random walk (see Results), for which detrending is not appropriate (Ariño and Pimm 1995). Autocorrelation analysis was inconclusive about the trend in JRH, so we modeled JRH data with and without detrending. In detrended analysis, the trend was removed by subtracting a linear function in time that had been fitted to log-transformed population data (Turchin and Taylor 1992).

Modeling population dynamics

We used response surface methodology (RSM; Box and Draper 1987; Turchin and Taylor 1992; Turchin 1996) to quantify *E. e. bayensis* population dynamics and to determine the relative importance of endogenous and exogenous factors. RSM predicts a response variable using generalized polynomial regression of transformed independent variables. We chose RSM because its flexibility with functional form and model dimensionality (number of variables included) allows detection of nonlinearities and time lags in population dynamics (Turchin 1995). Other methods sharing these advantages (Sugihara and May 1990; Ellner et al. 1991) require longer time series than those available for *E. e. bayensis*. All one- and two-variable models analyzed in this paper had at least 10 residual degrees of freedom (18 for JRH), meeting or exceeding the minimum recommended by Perry et al. (1993).

We developed three kinds of response surface models corresponding to different causes of fluctuations in *E. e. bayensis* populations. As described below, three kinds of variables and variable combinations defined the models: (1) time-lagged population data, (2) growing season rainfall data, and (3) combinations of population and rainfall data.

Models of endogenous dynamics

The endogenous component in *E. e. bayensis* dynamics was reconstructed with models containing time-lagged population data, N_{t-i}, following Turchin (1996). This method approximates the endogenous effects of multiple factors with an equation containing multiple time lags in a single variable. Equation 1 represents per capita rate of population change, N_t/N_{t-1}, as a function of populations in d previous years, N_{t-i}, and exogenous noise, ε_t:

$$N_t/N_{t-1} = f(N_{t-1}, N_{t-2}, ..., N_{t-d}, \varepsilon_t). \quad (1)$$

The response surface is constructed by approximating f, using polynomial combinations of Box-Cox transformed predictor variables ($X \equiv N_{t-1}^{\theta_1}$) and log-transformed rate of population change, $r_t \equiv \log_e(N_t/N_{t-1})$. To illustrate, Eq. 1 reduces to Eq. 2 for a two-dimensional model (d=2) with quadratic dependence (q=2) on transformed predictor variables $X \equiv N_{t-1}^{\theta_1}$, $Y \equiv N_{t-2}^{\theta_2}$:

$$r_t = a_0 + a_1 X + a_2 Y + a_{11} X^2 + a_{22} Y^2 + a_{12} XY + \varepsilon_t. \quad (2)$$

Model dimension (d), polynomial degree (q), and variable transformations (θ_i) were determined in two steps to avoid selecting spuriously complex models. First, d was selected while holding θ constant among predictor variables. Then θ_i and q were selected, with θ_i allowed to differ between predictor variables. Model selection was conducted using ordinary cross-validation, which optimizes prediction accuracy by minimizing one-step prediction error (Efron and Tibshirani 1993; Turchin 1996). Prediction accuracy was measured with the prediction coefficient of determination, R_p^2 (Turchin 1996) for log-transformed population size ($L_t = \log N_t$), which depends on the ratio of the mean square prediction error to population variance,

$$R_p^2 = 1 - \frac{\sum_i (L_i - \hat{L}_i)^2}{\sum_i (L_i - \bar{L})^2}, \quad (3)$$

where $\hat{L}_i$ is abundance predicted in year i, and $\bar{L}$ is the mean of the log-transformed abundances L_i. Potential values for R_p^2 range from 1, indicating perfect prediction, to $-\infty$. Models yielding R_p^2 =0 are equivalent to using the mean population size as a simple predictor, models with positive R_p^2 successfully extract some component of the dynamics, and models with negative R_p^2 attempt to fit noise instead of predictable population changes. Furthermore, RSM includes a given variable only if that variable increases prediction accuracy.

Models of exogenous dynamics

Models for exogenously driven changes in *E. e. bayensis* populations contained total growing season rainfall (Oct.–Apr.) for each year as a predictor variable. Values for growing season rainfall were derived from monthly precipitation data recorded at the Woodside Fire Station, California (NOAA 1995; National Climatic Data Center 2000), adjacent to JRBP. Exogenous models included rainfall data from either the current growing season (W_t), the growing season in the year preceding adult flight (W_{t-1}), or both. Rainfall in the current growing season can affect adult population size by influencing post-diapause larval development and the survival of pupae and adults (Weiss et al. 1993). Rainfall in the preceding growing season affects the survival of pre-diapause larvae (Weiss et al. 1988; Hellmann, unpublished data).

Procedures for construction, selection, and analysis of exogenous models were similar to those for endogenous models, described above. Equation 4 is an exogenous analog of Eq. 1 containing rainfall in both current and preceding years:

$$N_t/N_{t-1} = f(W_t, W_{t-1}). \quad (4)$$

Box-Cox transformations were applied to exogenous predictor variables ($X \equiv W_t^{\theta_1}$, $Y \equiv W_{t-1}^{\theta_2}$) to obtain an exogenous equivalent of Eq. 2. Single variable exogenous models contained either W_t or W_{t-1}.

Models with "seasonal" rainfall

If weather during a particular "season" is the primary exogenous influence on *E. e. bayensis* populations, then including rainfall from other months would add noise and hence decrease model fit. We evaluated seasonal relationships qualitatively with a series of scatter plots of population growth rate (r_t) versus rainfall in each season. Seasons with apparent relationships were spring (March–April) in year t–1 and winter (January–February) in year t. Models containing other rainfall variables produced no discernible pattern. Hence, we repeated RSM modeling procedures described above using winter and spring rainfall variables. For example, the exogenous model $f(W_t, W_{t-1})$ becomes a seasonal exogenous model $f(w_{t\{JF\}}, W_{t-1})$ by replacing total rainfall in the current growing season (W_t) with winter (January–February) rainfall in the current year ($w_{t\{JF\}}$).

Mixed endogenous-exogenous models

The third class of models included both lagged population size and seasonal or total growing season rainfall as predictor variables. Equation 5 is a two-variable mixed model containing the endogenous variable N_{t-1} and the exogenous variable, W_{t-1}:

$$N_t/N_{t-1} = f(N_{t-1}, W_{t-1}). \quad (5)$$

We did not consider models with three predictor variables for JRC, e.g. $f(N_{t-1}, W_t, W_{t-1})$, because too few residual degrees of freedom would have resulted (Perry et al. 1993). Results with 2D models for JRH (see below) suggested that we consider three predictor variables in mixed models. We repeated RSM model selection for three-variable models, in which $X \equiv N_{t-1}^{\theta_1}$, $Y \equiv N_{t-2}^{\theta_2}$, and $Z \equiv W^{\theta_3}$, where W is winter, spring, or total growing season rainfall. 3D models contain up to 15 estimated quantities (polynomial order, 3 transformations, and 11 parameters), leaving 12 residual degrees of freedom.

Simulating population dynamics

Simulations of population trajectories reveal dynamical properties extracted by each kind of model. We initialized all simulations at the 1969 population estimate. We ran simulations over time periods represented by the data: 1970–1988 for JRC, and 1970–1996 for JRH. Simulations were run freely, without correcting prediction errors. We measured simulation accuracy with the coefficient of determination, R^2=1–(residual SS/total SS).

Results

E. e. bayensis population data: qualitative patterns

Since 1969, both populations fluctuated widely and declined to extinction (Fig. 1). Fluctuations in JRC had greater amplitude, with 10-fold greater variance in abundance and 2.5-fold greater variance in growth rate than JRH (Hellmann et al., unpublished data). Correlation of growth rates in the two populations was weak: r =0.317 for growth rates over the interval 1970–1988 (Pearson product-moment correlation, P =0.186).

Autocorrelation analysis

JRC data contain no significant autocorrelation at any lag beyond zero; the autocorrelation function (ACF) for

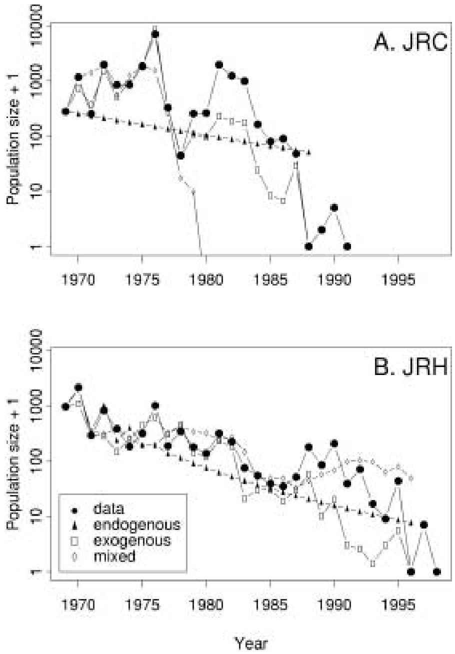

Fig. 1A, B Annual population data and simulated population trajectories for *Euphydryas editha bayensis* adult males at Jasper Ridge Biological Preserve, Stanford University, California. Simulations were generated using endogenous, exogenous, and mixed endogenous-exogenous models (Eqs. 1, 4, 5). Simulations were initialized at 1969 abundances and subsequent abundances were generated using the models and rainfall data. Simulation errors were not corrected prior to predicting subsequent abundances. Simulations were terminated in the first year that field populations dropped to zero abundance (1988 for Jasper Ridge C *JRC*, 1996 for Jasper Ridge H *JRH*). **A** Area C, extinction occurred in 1991. Endogenous simulations initialized at other abundances converged to trajectories parallel to the one plotted here. The exogenous simulation used Eq. 4, plotted in Fig. 4A. The mixed simulation used Eq. 5, plotted in Fig. 4C. **B** Area H, extinction occurred in 1998. Endogenous simulations initialized at other abundances followed similar damped oscillations toward trajectories parallel to the one shown. The exogenous simulation used the seasonal model $f(w_{t\{JF\}}, w_{t-1\{MA\}})$ plotted in Fig. 4B. The mixed simulation used Eq. 5 plotted in Fig. 4D

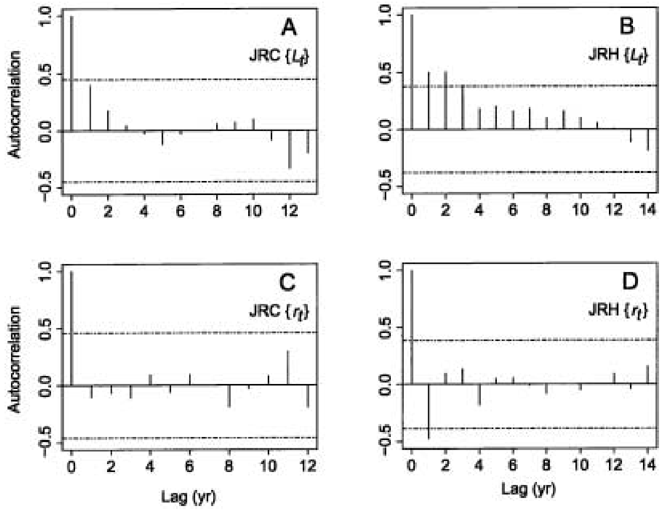

Fig. 2A–D Autocorrelation functions (ACFs) for log-transformed data (L_t=log N_t) and log-growth rates [r_t=log (N_t/N_{t-1})] for JRC and JRH. By definition, ACF(0) = 1. *Dashed lines* mark the Bartlett band, which delineates 95% confidence intervals for zero autocorrelation

{L_t} is confined within the Bartlett band delineating the 95% confidence interval of zero autocorrelation (Fig. 2A). In addition, the ACF for {r_t} decays rapidly (Fig. 2C), as expected for stationary time series. Although the mean growth rate for JRC was negative, the variance was large (Hellmann et al., unpublished data). Consequently, mean (r_t) did not differ significantly from zero (*t*-test, *P* =0.45). These properties suggest that fluctuations in JRC were a simple random walk (Royama 1992). Because long-term trends are the primary statistical feature of random walks, detrending JRC data prior to model analysis would not have been appropriate (Ariño and Pimm 1995).

Autocorrelation analysis suggested that fluctuations in JRH occurred within a trend. The ACF for log-transformed JRH data decays slowly, with positive values until year 12 and negative values thereafter (Fig. 2B). When JRH data are divided into equal halves corresponding to early and late sampling periods, ACFs for both intervals decay more rapidly. This tendency for more rapid decay in shorter data sets suggests that JRH data are nonstationary (Royama 1992). Similar to JRC, the mean growth rate for JRH was negative but not significantly different from zero (*P* =0.29). The ACF for {r_t} is significantly negative at lag 1 and is within the Bartlett band at longer lags (Fig. 2D). These results suggest two alternative interpretations. First, JRH could have followed a generalized random walk; generalized random walks show a greater tendency for long-term drift than simple random walks (Royama 1992). Second, JRH may have undergone endogenous oscillations about a declining trend caused by long-term environmental change. Detrending JRH data is appropriate under the second interpretation, but not under the first.

Models of endogenous dynamics

The two populations differed in the endogenous component of their dynamics, as determined by RSM models. Endogenous dynamics in JRC were one-dimensional (d = 1), and fit the data poorly relative to exogenous and mixed models discussed below (Table 1). In contrast, the endogenous model selected for JRH was two-dimensional (d =2) and obtained a better fit than the endogenous model for JRC. Nevertheless, the endogenous model for JRH did not perform as well as models with at least one exogenous variable, discussed below.

Models of exogenous dynamics

Responses of both populations to rainfall were convex, with abundance declines following dry or very wet weather and increases following intermediate conditions

Table 1 Summary of models fitted to data on Jasper Ridge *Euphydryas editha bayensis* populations. Response surface methodology (RSM) models were developed from Eqs. 1, 4, and 5. Model dimension (*d*), polynomial order (*q*), and transformations (θ_i) were selected to maximize the prediction coefficient of determination (R_p^2). Models for JRH containing the variable D_{t-1} were fitted to data that were detrended by subtracting a linear decline fit to log-transformed values: $D_t = L_t - (7.11 - 0.160t)$. R^2 "model fit" is for the fitted model, using selected values for *d*, *q*, and θ_i. R^2 "simulation" is the coefficient of determination for simulated abundances, $R^2 = 1 -$(residual SS/total SS). Negative values for R^2 simulation resulted when simulation errors exceeded the variability in population data. The far right column lists figures showing response surfaces (Fig. 4) and simulation results (Figs. 1, 4) generated by selected models

Kind of model	Population	Variable(s)	*d*	*q*	θ_1	θ_2	R_p^2	R^2 model fit	R^2 simulation	Figures
Endogenous	JRC	N_{t-1}	1	1	2		0.33	0.16	–0.31	1A
	JRH	N_{t-1}, N_{t-2}	2	1	0.5	0.5	0.40	0.26	0.29	1B
		D_{t-1}, D_{t-2}	2	1	1	–2	0.12	0.65	–0.36	
Exogenous	JRC	W_t, W_{t-1}	2	2	–1	2	0.53	0.82	0.83	4A, 1A
		$w_{t\{JF\}}, W_{t-1}$	2	2	2	–0.5	0.73	0.81	0.28	
		$w_{t\{JF\}}, w_{t-1\{MA\}}$	2	2	0.5	1	0.33	0.40	–0.39	
	JRH	W_t, W_{t-1}	2	2	–2	0	0.46	0.32	0.29	
		$w_t\{JF\}, W_{t-1}$	2	2	1	–1	0.43	0.38	0.51	
		$w_{t\{JF\}}, w_{t-1\{MA\}}$	2	2	0	–0.5	0.51	0.54	0.65	4B, 1B
Mixed endogenous-exogenous	JRC	N_{t-1}, W_t	2	1	2	–2	0.37	0.25	–0.28	
		N_{t-1}, W_{t-1}	2	2	0	1	0.58	0.74	0.18[a]	4C, 1A
	JRH	N_{t-1}, W_t	2	1	2	3	0.43	0.14	0.36	
		N_{t-1}, W_{t-1}	2	1	2	1	0.47	0.26	0.78	4D, 1B
		D_{t-1}, W_t	2	1	0	0.5	–0.12	0.50	–1.21	
		D_{t-1}, W_{t-1}	2	1	1	2	–0.10	0.61	0.08	

[a] Simulation crashed to extinction in year 1980

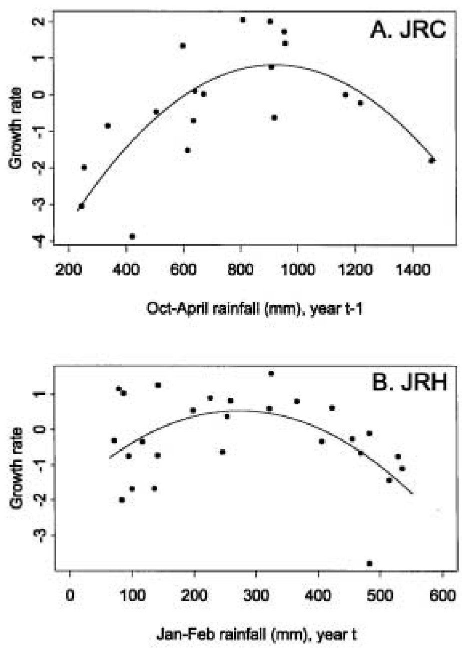

Fig. 3A, B Response functions for single variable exogenous models. Observed growth rates [r_t=log (N_t/N_{t-1})] are plotted as *solid circles*. Response functions $f(W_{t-1})$ and $f(w_{t\{JF\}})$ are shown for JRC (**A**) and JRH (**B**), respectively

(Fig. 3). The populations differed in the timing of their responses: JRC dynamics were dominated by rainfall in the preceding growing season (W_{t-1}) and JRH varied most closely with winter rainfall in the current growing season ($w_{t\{JF\}}$). Although these single-variable results are informative, we focus on two-variable exogenous models because they have greater prediction accuracy (R_p^2).

The 2D exogenous model fitted JRC data markedly better than did the endogenous model (Table 1). The exogenous model for JRC also exceeded the equivalent model for JRH in prediction accuracy (R_p^2) and fit (R^2). Preceding growing season rainfall dominated the JRC model, accounting for 73.2% of the explained variance (60.3% of total variance), with current growing season rainfall accounting for 0.5% (0.3% of the total) and interaction between the two variables accounting for the remaining 26.4% (21.7% of the total). The shape of the response surface generated by the JRC exogenous model (Fig. 4A) reflects these results. It varies mostly with W_{t-1} in a convex arc similar to the analogous 1D model (Fig. 3A). These results are consistent with previous work suggesting that fluctuations in JRC were driven by weather-determined survival of pre-diapause larvae (Ehrlich et al. 1975; Dobkin et al. 1987).

For JRH, exogenous models performed better than the endogenous model, and they were improved by including winter or spring rainfall variables (Table 1). The best exogenous model for JRH contained winter rainfall in the current year and spring rainfall in the preceding year: $f(w_{t\{JF\}}, w_{t-1\{MA\}})$. In this model, $w_{t\{JF\}}$ accounted for 27.7% of explained variance (14.9% of total), $w_{t-1\{MA\}}$ accounted for 5.4% (2.9% of total), and interaction between the two variables accounted for the majority, 66.9% (36.0% of total). The surface generated by this model is relatively flat in both rainfall dimensions, except where it dips sharply for dry weather in both years (Fig. 4B). Qualitatively similar results were obtained with the JRH exogenous model containing total growing season rainfall, $f(W_t, W_{t-1})$. The dominance of interaction terms in exogenous models for JRH suggests that climatic effects on JRH were more complex than those on JRC.

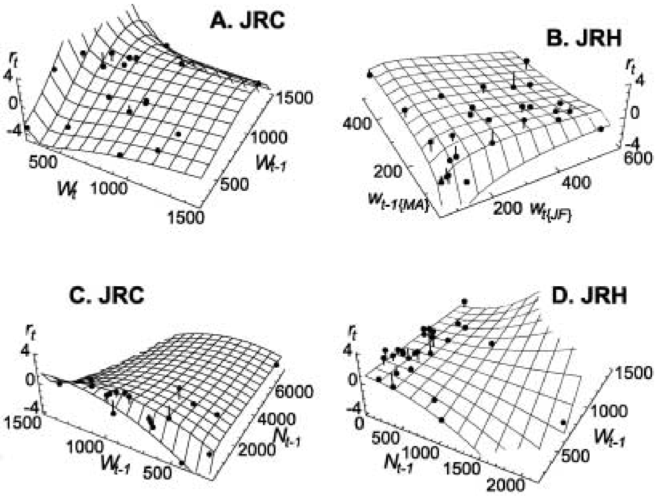

Fig. 4A–D Response surfaces for growth of *Euphydryas editha bayensis* populations, as determined by the exogenous model Eq. 4 and the mixed endogenous-exogenous model Eq. 5. Estimated growth rate (r_t) is plotted against preceding population size (N_{t-1}) and/or rainfall variables. Observed growth rates are plotted as *solid circles*. Lines connecting data points to the surface show residual variation. **A** JRC, exogenous model; **B** JRH, seasonal exogenous model; **C** JRC, mixed endogenous-exogenous model; **D** JRH, mixed endogenous-exogenous model

Models of combined endogenous-exogenous dynamics

The best mixed endogenous-exogenous models for both populations contained rainfall in the preceding growing season (W_{t-1}; Eq. 5). For JRC, prediction accuracy and fit were comparable to the exogenous model (Table 1), and most of the accuracy and fit were exogenously determined. W_{t-1} accounted for most of the explained variance (69.5%; 51.6% of total), with the remainder divided evenly between N_{t-1} (15.4%; 11.4% of total) and interaction between the two variables (15.2%; 11.2% of total). Accordingly, the surface for JRC is convex in the W_{t-1} dimension (Fig. 4C), similar to the exogenous model (Fig. 4A). For JRH, interaction between the two variables accounted for most of the explained variance (55.2%; 14.1% of total). Following dry years, the JRH model predicts population increase if the population size is small and decrease if it is large (Fig. 4D).

Because the endogenous component of JRH dynamics was two-dimensional, we considered 3D mixed endogenous-exogenous models containing two endogenous variables. The RSM model selection protocol indicated that 3D mixed models were appropriate for JRH: R_p^2 was greatest for 3D models even with θ constant among variables. Prediction accuracy and fit of 3D mixed models exceeded all 2D JRH models considered: R_p^2 =0.61 and R^2 =0.68 for the model $f(N_{t-1}, N_{t-2}, w_{t\{JF\}})$, and R_p^2 =0.55 and R^2 =0.74 for the model $f(N_{t-1}, N_{t-2}, W_{t-1})$. The endogenous component accounted for 84.0% and 67.0% of the explained variance (56.9% and 49.4% of total) in the two models. Lagged population size (N_{t-2}) accounted for more than 40% of explained variance (30% of total) in both cases. Models for JRH with more than three variables would leave insufficient residual degrees of freedom.

Simulated dynamics

Model simulations showed that JRC and JRH differed qualitatively in the endogenous component of their dynamics. The endogenous model for JRC produced no fluctuations (Fig. 1A), similar to endogenous model simulations for other species dominated by exogenous noise (Turchin and Taylor 1992). In contrast, the endogenous model for JRH generated damped oscillations about a declining trend (Fig. 1B). The oscillatory tendency of JRH also appears in its autocorrelation function (Fig. 2D) and in the raw data (Fig. 1B). Nevertheless, endogenous simulations for both JRBP populations differed markedly from the data.

Most exogenous models tracked observed population trajectories better than did the endogenous models (Table 1, Fig. 1). The simulation using the exogenous model, Eq. 4, for JRC was the most accurate of all models for either population (R^2 =0.83). The simulated trajectory closely resembled observed JRC dynamics until 1979, when the model underestimated population growth (Fig. 1A). Although the model predicted subsequent growth rates accurately, the 1979 error propagated through the rest of the simulation. (Simulation accuracy increased to R^2 =0.87 if the 1979 error was corrected during the simulation.) Error propagation also affected simulation with the JRC seasonal exogenous model $f(w_{t\{JF\}},W_{t-1})$, in which the error occurred in the second year. Propagation of prediction errors in uncorrected simulations is common (Lewellen and Vessey 1998).

The exogenous model containing seasonal rainfall in both years simulated JRH dynamics most accurately (Table 1; Fig. 1B). Similar to JRC simulations, error propagation reduced simulation accuracy for JRH exogenous models. For JRH, the largest prediction errors were caused by the influence of the 1996 decline to zero abundance, when r_t was at least twofold smaller than in all other years. If the 1996 outlier was omitted prior to model selection and fitting, simulation accuracy with the seasonal rainfall model $f(w_{t\{JF\}},w_{t-1\{MA\}})$ improved from R^2 =0.65 to 0.81.

Simulation accuracy with mixed endogenous-exogenous models was low for JRC and relatively high for JRH (Table 1). The JRC model, Eq. 5, predicted an erroneously large decline following the 1976–1977 drought, which caused the simulation to crash to extinction (Fig. 1A). If this error was corrected and the simulation allowed to continue, persistence to the end of the simulation resulted. Simulation with the analogous model for JRH was more accurate. This model simulated intermediate and long term trends in JRH reasonably well, but it did not predict many of the annual fluctuations (Fig. 1B).

Models with detrended data

Detrending did not qualitatively affect the behavior of the JRH endogenous model. Both original and detrended models were two-dimensional and generated damped oscillations during simulations. Nevertheless, detrending consistently reduced prediction accuracy in all JRH models (Table 1). Prediction accuracy (R_p^2) for the detrended endogenous model was positive, but less than a third of the original endogenous model. Prediction accuracy of mixed endogenous-exogenous models was negative. In addition, simulation accuracy with detrended models was low (Table 1). These results imply that detrended JRH models fit noise in the data, suggesting that the trend was integral to JRH dynamics.

Discussion

Analysis of three decades of abundance data for two *E. e. bayensis* populations showed that the relative dynamical importance of endogenous and exogenous factors differs even between populations of the same subspecies in adjacent habitats. We found that the populations also differed in variability and qualitative and quantitative responses to endogenous and exogenous factors. The population in the large relatively flat habitat (JRC) varied more widely and went extinct sooner. The population in the topographically more diverse habitat (JRH) varied less widely but more regularly, and persisted longer. Effects of weather dominated JRC dynamics, with a minor influence from endogenous factors. In particular, JRC dynamics were most strongly correlated with total growing season rainfall in the year prior to adult flight. In contrast, JRH dynamics were influenced by both endogenous and exogenous factors, and in ways that differed from JRC. While the endogenous component extracted from JRC data was a simple one-dimensional decline, the endogenous component in JRH was two-dimensional and generated damped oscillations. The exogenous components in JRC and JRH differed in the timing of their effects. JRC fluctuations were driven by rainfall in the preceding year, while JRH responded more strongly to rainfall in the growing season concurrent with adult flight. This analysis supports conclusions from field study that JRC dynamics were volatile and density independent, while JRH dynamics were more complex and buffered somewhat from climatic variability.

Response surface models for *E. e. bayensis* performed comparably to similar models for other species, despite substantial differences in mechanisms causing population fluctuations. For example, simulation accuracy of *E. e. bayensis* models was within the range obtained with short-term models of white-footed mice (Lewellen and Vessey 1998). Models for both species contained endogenous and exogenous components, including large weather effects. In addition, prediction accuracy (R_p^2) in our models was comparable to endogenous models of vole populations in northern Europe (Turchin 1996).

Comparing model results with field predictions

Prediction 1

Relative to JRH, JRC dynamics will contain a stronger exogenous component and a weaker endogenous component.

Accuracy in model fit, prediction, and simulation confirm this prediction. The best exogenous model for JRC performed better than the best exogenous model for JRH in all three criteria. Conversely, the endogenous model for JRH exceeded the endogenous model for JRC in the same three criteria. Exogenous models for JRC performed markedly better than the endogenous model, with up to fivefold better fit and twofold greater accuracy in one-step-ahead prediction and simulation (Table 1). Qualitatively similar results were obtained for JRH models, but the difference was smaller than for JRC models. Mixed endogenous-exogenous models also showed greater importance of exogenous influences on JRC than on JRH. For JRC, rainfall accounted for most of the variance explained by the best mixed model, Eq. 5. For JRH, interaction between endogenous and exogenous variables accounted for most of the explained variance.

Prediction 2

(a) Weather conditions in the year prior to adult flight (t–1) will influence population size in JRC more than weather in the current year (t). (b) This difference will be less evident in JRH because area H has greater topographic diversity.

Results from several kinds of models confirm these predictions. The exogenous model, Eq. 4, for JRC showed that effects of rainfall in the preceding year far exceeded effects in the current year. In the equivalent model for JRH, rainfall in the 2 years were approximately equal in importance. Comparable results were obtained with seasonal exogenous models. With mixed endogenous-exogenous models, fit and accuracy for JRC were much greater when the model contained rainfall in the preceding year than rainfall in the current year. For JRH, results were slightly better with models containing preceding year rainfall, but this difference was small relative to JRC.

Mechanistic interpretation

Identifying mechanisms that cause various classes of population behavior is a central goal of the study of population dynamics (Lawton 1992; Bjørnstad and Grenfell 2001). We now use data obtained in the field and population modeling to describe mechanisms driving dynamics of *E. e. bayensis* populations at Jasper Ridge.

First consider the dynamics in area C, where diversity of slope aspect is limited. Direction and magnitude of population fluctuations were determined primarily by survival rates of pre-diapause larvae. Because area C is relatively flat, conditions for larval development were nearly uniform throughout the habitat. [We ignore microtopographic variation in the order of 10 cm (Dobkin et al. 1987), because it exists in all habitats.] During moderately wet years, conditions for survival of pre-diapause larvae were favorable throughout JRC, and adult abundance subsequently increased. During droughts and exceptionally wet years, conditions were unfavorable throughout the habitat and the population declined. Hence, JRC dynamics were a simple random walk, with successive values in the series generated by a quadratic function of prior growing season rainfall. In hindsight, the extinction of JRC in 1991 after a series of four dry years was not surprising.

In contrast, JRH dynamics were more complex, but less variable. Initially, two mechanisms appear plausible. The first invokes a combination of endogenous and exogenous factors, with endogenous oscillations induced by stochastic perturbations due to weather. The second extends the mechanism of climatic influence on JRC described above to the more diverse topography at area H. Closer inspection of model results rules out the first mechanism and supports the second.

Irregular oscillations in many populations result from the combined action of oscillatory density-dependence and exogenous perturbations (Higgins et al. 1997; Dixon et al. 1999; Lima et al. 1999; Bjørnstad and Grenfell 2001). Two results argue against this mechanism as the cause of irregular oscillations in JRH. First, models fitted to detrended data performed poorly. Low prediction accuracy of detrended models implies that detrending removed much of the predictable pattern, causing the models to fit noise instead. Second, the endogenous model without detrending produced damped oscillations throughout the range of observed population sizes. Hence, JRH oscillations depended on deviations from the trend, not on absolute population density. This eliminates biotic mechanisms of endogenous feedback that operate in proportion to absolute density, such as food limitation or mortality from predators and parasitoids. Therefore, JRH dynamics cannot be explained by the combined action of oscillatory density-dependence and exogenous perturbations.

The second mechanism, interacting effects of weather and topography on larval growth and survival, accounts for both the low prediction accuracy of detrended models and JRH dependence on abundance relative to the trend. Climatic variation affects *E. e. bayensis* populations by shifting the relative suitability of various habitat slopes (Singer 1972; Weiss et al. 1988). Hence, weather effects on adult abundance in a topographically heterogeneous habitat are indirect, mediated through larval distributions. Changes in adult populations correlate with expansion and contraction of larval distributions (Weiss et al. 1993), leading to apparent endogenous effects. These effects are in proportion to relative population size instead of absolute population density, however. Larval distributions expand or contract relative to the previous distribution of larvae, rather than the previous absolute number of larvae or adults. Consequently, changes in adult abundance in JRH appeared to depend on the relative abundance of adults in previous years, but this dependence was likely mediated by the spatial distribution of surviving larvae. As a result, prediction accuracy for JRH data was greatest with models containing surrogates for larval distributions: either rainfall variables from two growing seasons or both rainfall and relative population size. The effective dependence of JRH on more than one exogenous variable represents a generalized random walk (Royama 1992). In sum, both JRC and JRH dynamics were driven largely by climatic variables. The climatic influence on JRC dynamics was strong and simple, while climatic influences on JRH were weaker and more complex.

Limitations and sources of error

Although differences in the dynamics of JRBP populations may suggest causal relationships between dynamics and habitat characteristics, inferences cannot be made with confidence by comparing only two populations. Instead, we used model analysis to test predictions from field study, and we drew mechanistic conclusions from the test results. While our analyses confirmed these predictions, we caution against drawing general conclusions about relationships between dynamics and habitat heterogeneity from our results alone. Such conclusions will require the identification of mechanisms for other species, such as Kindvall's (1996) work on the bush cricket *Metrioptera bicolor*, and Kadmon's (1993) study of the desert annual *Stipa capensis*.

Our analysis supports the caution of Perry et al. (1993) against combining data from different populations unless they have similar dynamics. The dynamics of JRC and JRH differed qualitatively, despite sharing many historical and environmental characteristics. In addition, our results support the warnings of Ariño and Pimm (1995) about removing trends in data prior to analysis. When population trends are known to result from environmental changes, detrending may be warranted (Turchin and Taylor 1992). Otherwise, removing a trend may exclude the primary dynamical pattern (e.g. random walk of JRC). When the cause of a trend is unknown, we recommend Royama's (1992) protocol for diagnosing properties in data. If the resulting diagnosis is inconclusive, we suggest developing models with both original and detrended data, using model prediction accuracy (Eq. 3) to determine whether detrending is appropriate. Here, low prediction accuracy with detrended JRH data rejected trend removal for JRH.

Uncertainty in exogenous variables can reduce model performance. Although many factors affect the dynamics of most populations, long-term data rarely are available for relevant variables. With the endogenous component, the problem of unknown variables can be addressed by reconstructing the multidimensional system using time-lagged population data (Schaffer 1985; Ellner et al. 1991; Turchin and Taylor 1992). With the exogenous component, reconstruction in time-delay coordinates may not work well because exogenous variables often are poorly correlated with each other or act in current time. This problem is acute for annual species like *E. e. bayensis*. In our models, rainfall variables represent direct effects and serve as surrogates for other exogenous factors, such as host plant phenology. Uncertainty in surrogate relationships reduce model fit, however.

The length of population time series limits understanding of population dynamics, including the ability to detect population regulation (Turchin 1995). Although the JRBP population data are celebrated for their length, they are not long enough to fit models containing more than three variables. More complex models reserve insufficient degrees of freedom for error (Perry et al. 1993). Kendall et al. (1999) reached parallel conclusions about identifying mechanisms that drive fluctuations in cyclic populations.

A final limitation of our models is the tendency for prediction errors to propagate during simulations (Fig. 1). Correlated errors result when prediction errors are not corrected during simulations (Lewellen and Vessey 1998). Prediction errors may decay over time in endogenous simulations, but not in exogenous simulations. This limitation is compounded by uncertainty in weather forecasts. Hence, Lewellen and Vessey (1998) warn that “even when population fluctuations can be explained, accurately predicting future densities may be impossible when fluctuations are driven by weather.”

Conclusions

Four main conclusions emerge from this work. First, full understanding of population dynamics requires explicit consideration of both endogenous and exogenous components. It is difficult to determine the relative importance of one component if analyses do not include both. Second, dynamics in *E. e. bayensis* populations at JRBP appear to have been driven by exogenous factors, although their effects differed between JRC and JRH. These results support the emerging consensus that population persistence requires either immigration or endogenous limitation of population fluctuations (Murdoch 1994; Middleton and Nisbet 1997). Without immigration or much endogenous regulation, both populations went extinct. Third, topographic diversity buffers *E. e. bayensis* populations from climatic variability. Field study of annual population changes documented the mechanistic basis for this conclusion. Analyses reported here show that the mechanism also explains *E. e. bayensis* population dynamics on the scale of decades. Fourth, this work illustrates the value of combining long-term population sampling, model analysis, and field study of mechanisms causing population fluctuations. All three components have been essential to understanding the dynamics of *E. e. bayensis* populations at JRBP. This approach requires more research effort than most populations will receive, but it promises to resolve the protracted debate over population regulation if it can be applied to enough species (Murdoch 1994; Turchin 1995, 1999).

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