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Complex demographic responses of a common small mammal to a plant invasion

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Abstract

Context. Invasions by non-native plants can alter the abundance and distribution of resources that can affect habitat quality for native animals.

Aims. We sought to understand the demographic consequences of a plant invasion on a functionally and numerically important rodent in a grassland ecosystem. Specifically, we evaluated how abundance, survival, reproductive activity and population structure of Arizona cotton rats (*Sigmodon arizonae*) varied across a gradient of invasion by *Eragrostis lehmanniana* (Lehmann lovegrass), a bunchgrass native to Africa that has invaded grasslands in North America.

Methods. Over a four-year period, we used capture–recapture methods to survey small mammals on 54 1-ha plots between 10 and 13 times. We used vegetation data collected each autumn to quantify biomass of non-native grass, total biomass and vegetation heterogeneity to characterise vegetation structure on each plot.

Key results. We captured 1344 individual cotton rats during 106 560 trap-nights across all sampling periods. In areas dominated by non-native grass, abundance of cotton rats increased 7- to 10-fold and survival increased by 117% relative to areas dominated by native grasses. In contrast, reproductive activity of adults decreased by 62% for females and 28% for males, and the proportion of adults in the population decreased by 20% in these same areas.

Conclusions. Demography of Arizona cotton rats differed markedly in areas invaded by a non-native plant relative to native grasslands, supporting the long-held idea that life histories can reflect local environmental conditions. Because distributions of many non-native plants are predicted to increase in response to future changes in natural and anthropogenic drivers, the potential breadth of these complex effects on communities of native animal is immense.

Implications. The complex variation in demographic responses across the invasion gradient suggests that it may be necessary to evaluate a suite of vital rates to fully understand the consequences of plant invasions on animals. This is especially important for species of conservation concern because single demographic parameters, which are used frequently as targets to gauge the success of conservation and management activities, could be misleading.

Additional keywords: *Eragrostis lehmanniana*, grasslands, habitat quality, life-history strategy, non-native plants, *Sigmodon arizonae*.

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Introduction

Animals rely on vegetation directly for cover and food and indirectly for cues to the presence and abundance of resources they require for growth, survival and reproduction (Morrison *et al*. 2006). In seasonal environments, animals often use these vegetation-based cues to predict the availability of key resources before levels of those resources become apparent (Tinbergen 2005). For example, some birds use leaf cover, flower cover or leaf damage to indicate current or anticipate future abundance of insect prey (Heinrich and Collins 1983; Marshall and Cooper 2004; McGrath *et al*. 2009). Consequently, vegetation provides cues that many species use to identify areas to settle and fulfil their life histories.

Because vegetation composition of nearly all ecosystems has changed in response to human activities (Vitousek *et al*. 1996), both the resources and cues available to animals also have likely changed. Introductions of non-native plants are especially consequential because they alter vegetation structure, floristics and the physical and biological conditions of an area (Pearson 2009; Orrock *et al*. 2010; Vilà *et al*. 2011). Plant invasions, therefore, can alter the abundance and distribution of key resources, the quantity and quality of habitat and productivity and persistence of animal populations (Ferdinands *et al*. 2005; Rodriguez 2006; Litt and Steidl 2010*b*; Litt and Steidl 2011; Vilà *et al*. 2011). In some circumstances, non-native plants alter vegetation composition and structure to such a degree that invaded areas no longer provide habitat for some animal species, reducing regional abundance and altering distributions (Litt and Steidl 2010*b*; Litt and Steidl 2011; Vilà *et al*. 2011). In other circumstances, however, non-native plants can function equivalently to the native plant species they replace (Sogge *et al*. 2008; Litt and Steidl 2011; Vilà *et al*. 2011) by providing the cues and resources needed for survival, growth and reproduction. Southwestern willow flycatchers (*Empidonax traillii extimus*), for example, nest in non-native saltcedar (*Tamarix* spp.) and native willows (*Salix* spp.), as both trees provide the dense structure that flycatchers prefer for nesting (Sogge *et al*. 2008). Even if animals still recognise areas invaded by non-native plants as habitat, habitat quality may be altered by changes in abundance or breadth of food resources, susceptibility to predation, quality of thermal cover or other factors that can affect demography. For example, although flycatchers nest in non-native saltcedar, breeding success is lower than in native willows (Zavaleta *et al*. 2001).

Life-history strategies have evolved to reflect a series of tradeoffs that animals must make with regards to allocating energy and resources to reproduction, survival and growth in ways that maximise fitness (Wilbur *et al*. 1974; Roff 1992; Stearns 1992; Cox and Calsbeek 2010). Environmental conditions play a key role in mediating these compromises (Wilbur *et al*. 1974; McNamara and Houston 1996), although this idea has been supported by data infrequently (e.g. Leggett and Carscadden 1978; Ellers and van Alphen 1997; Vadell *et al*. 2014). If the optimal life-history tradeoff for individuals under one set of environmental conditions varies from the optimal tradeoff under another set of conditions, we expect systematic variation in the expression of life-history characteristics, such as age of first reproduction and number of offspring produced (McNamara and Houston 1996; Ellers and Van Alphen 1997). Further, if resource availability and other environmental conditions change in response to invasions by non-native plants, organisms may change the way they allocate resources, which in turn may affect demography and their life histories (Leggett and Carscadden 1978; McNamara and Houston 1996). Developing conservation strategies to maintain viable populations of animals in areas invaded by non-native plants requires that we understand thoroughly the effects of changes in habitat quality on demography and fitness-related tradeoffs.

To assess the consequences of a non-native-plant invasion on habitat quality and life-history strategies, we evaluated how demography of the Arizona cotton rat (*Sigmodon arizonae*) varied across a gradient of invasion by *Eragrostis lehmanniana* (Lehmann lovegrass). The Arizona cotton rat, a rodent in a genus common in grasslands across North, Central and South America, inhabits areas dominated by dense grasses and feeds on plants and insects (Cameron and Spencer 1981). *Eragrostis lehmanniana* is a perennial bunchgrass native to southern Africa that has become dominant after being introduced to semi-desert grasslands of the south-western United States and northern Mexico (Anable *et al*. 1992). Like many non-native grasses, *E. lehmanniana* produces much more biomass, cover and litter than native grasses, and reduces heterogeneity in vegetation structure in areas where it is dominant (Cox *et al*. 1990; Anable *et al*. 1992; Geiger 2006). Because vegetation structure is a strong determinant of the composition and structure of many small mammal communities (Brown and Harney 1993), changes in vegetation structure are likely to be an important mechanism explaining demographic responses of animals to plant invasions and influencing life-history tradeoffs. In addition, when a species is abundant and sampling is thorough, many aspects of demography can be characterised reliably, allowing population processes to be explored that might otherwise be challenging to detect. Finally, grasslands are among the most endangered ecosystems worldwide (Noss *et al*. 1995; Olson and Dinerstein 1998) and the distribution and abundance of many grassland organisms also have decreased substantially (e.g. Samson and Knopf 1994), requiring that we understand the consequences of plant invasions on patterns and processes affecting biodiversity in these ecosystems.

Material and methods

Study area

We studied semi-desert grasslands in south-eastern Arizona between elevations of 1420 and 1645 m on Fort Huachuca Military Reservation (31° N, 110° W). Annual precipitation averaged 391 mm (s.e. = 17 mm, $n = 39$ years, 1955–98, Air Force Combat Climatology Center), with two-thirds typically falling during a monsoonal period between July and October. Common native grasses included cane bluestem (*Bothriochloa barbinodis*), grama grasses (*Bouteloua* spp.), Arizona cottontop (*Digitaria californica*), plains lovegrass (*Eragrostis intermedia*), panicgrasses (*Panicum* spp.), and *Aristida* spp. Common shrubs included yerba de pasmo (*Baccharis pteronioides*), desertbroom (*Baccharis sarothroides*), desert spoon (*Dasylirion wheeleri*), burroweed (*Isocoma tenuisecta*), catclaw mimosa (*Mimosa culeaticarpa*), and velvetpod mimosa (*Mimosa dysocarpa*).

Study design and sampling

We established 54 1-ha plots (100 m × 100 m) across the invasion gradient where biomass of *E. lehmanniana* ranged from 0 to 466 g m^{-2} and comprised 0–91% (mean = 44.2%, s.e. = 2.8) of total biomass of all live vegetation; plots were separated by ≥100 m. On each plot, we established an 8 × 8 grid of Sherman live traps spaced 12.5 m apart to capture small mammals. At dusk, we set and baited traps with wild bird seed, mainly millet and sunflower seeds, and a mixture of peanut butter and oats, then checked traps at dawn every day for five consecutive days.

We surveyed small mammals from spring 2000 through spring 2004, trapping once each spring (May–June), summer (July–August), and winter (February–March); we trapped for 5-day periods on all plots during a 3 to 4-week interval that we defined as a sampling period. We sampled 27 plots from spring 2000 through spring 2004 for 13 consecutive sampling periods and 27 additional plots from spring 2001 through spring 2004 for 10 consecutive sampling periods. Given the staggered initiation of surveys and because 36 plots burned at various times during the study (after which we excluded them from analysis), the number of plots trapped per sampling period ranged from 18 to 45 (mean = 25.6 plots/period, s.e. = 2.5, total plot samples = 333).

For each individual captured, we measured body mass and total length (nose to last caudal vertebra), and classified sex, age (juvenile or adult, based on morphology and size) and whether females (pregnant or lactating) and males (testes descended) were reproductively active (Kunz *et al*. 1996). Animals were double-marked uniquely with a numbered ear tag (Monel tag 1005–1, National Band and Tag, Newport, KY) and ink from permanent felt-tipped markers. We made every effort to minimise handling time and released animals at the point of capture. Our trapping and data-collection protocol followed guidelines provided by the American Society of Mammalogists (Sikes and Gannon 2011) and was approved by the University of Arizona Institutional Animal Care and Use Committee (protocols 99-121, 02-109).

We quantified dominance of non-native grass on each plot based on biomass (g m^{-2}) of *E. lehmanniana*, which was almost exclusively the only non-native plant present; all other non-native plants combined constituted <1% of total biomass per plot (Geiger 2006). Because *E. lehmanniana* grows mainly during summer (Cox *et al*. 1990), we characterised vegetation during fall when biomass was at its peak (Geiger 2006). Each September, all vegetation was clipped on 25 0.5-m^2 quadrats (established at random on each plot) and then oven-dried; dry weights were recorded by species (Geiger 2006). We used biomass of *E. lehmanniana* estimated each fall to characterise vegetation conditions present on each plot from summer of the sampling year through winter and spring of the subsequent year (e.g. we used vegetation data from fall 2001 to characterise vegetation for the summer 2001, winter 2002, and spring 2002 sampling periods). We characterised vegetation structure on each plot based on total biomass and characterised vegetation heterogeneity as the coefficient of variation (%) in total vegetation biomass for the 25 quadrats sampled on each plot.

Data analyses

We used Huggins closed-capture models in Program MARK (White and Burnham 1999) to estimate abundance of Arizona cotton rats on each plot for each sampling period while accounting for imperfect detection. To model detection probabilities, we aggregated data across plots and years for each season separately (spring, summer, winter) (Litt and Steidl 2010*a*), and developed a set of candidate models for detection probability (p) that included additive effects of age class (adult or juvenile), survey year and degree of non-native-grass dominance. We used Akaike's information criterion adjusted for small sample bias (AICc) to compare models, and generated model-averaged estimates of abundance for each plot for each sampling period.

We used generalised-linear mixed models to assess changes in abundance, reproductive activity (proportion of reproductively active adult females and males during spring and summer only), age (proportion of adults), sex (proportion of females) and weight : length ratios across the gradient of non-native grass, specifying the appropriate distribution and link function for each response variable and accounting for repeated sampling of plots. For analyses of abundance (log-transformed) and weight : length ratios, we specified a normal distribution and identity link, given that the estimated abundance values were continuous. We modelled proportions of reproductively active females and males as well as sex and age ratios as counted proportions, and specified a binomial distribution and logit link. We included sampling season (spring, summer, winter) in models to examine the influence of seasonal variation on all demographic parameters except reproductive rates, where we excluded winter because animals were not reproductively active; we included season in final models only if $P < 0.10$. We treated plots as subjects to account for repeated measurements taken on the same plots over time, and for each analysis we evaluated four possible covariance structures (compound symmetric, first-order autoregressive, first-order autoregressive moving average and toeplitz), and selected one based on values of Akaike's information criterion adjusted for small sample bias (AICc) and the Bayesian information criterion (BIC; Littell *et al*. 2006).

To assess variation in survival across the gradient of non-native grass, we used Cormack–Jolly–Seber models in Program MARK (White and Burnham 1999) to estimate monthly apparent survival of cotton rats (hereafter, survival). We specified the amount of time between sampling periods to account for unequal intervals and to make survival rates for each interval comparable. We evaluated 36 candidate models where we constrained survival (phi, φ) to be constant or allowed it to vary additively with all combinations of degree of non-native-grass dominance, age class (juvenile or adult) and season (winter, spring, summer), and to vary multiplicatively between age and non-native-grass dominance; we constrained detection probability as constant or allowed it to vary additively with season and degree of non-native-grass dominance. We used AICc to compare candidate models and report model weights as a measure of support.

We report variation in demographic parameters across the gradient of non-native-grass dominance as both absolute and relative changes. We report absolute changes in each demographic parameter as the difference in model-based predictions for plots dominated by native grasses (0 g m^{-2} of *E. lehmanniana*) and plots dominated by non-native grass (466 g m^{-2} of *E. lehmanniana*). We computed relative change as the percentage change in each parameter ((non-native – native)/ native × 100) across the observed range of *E. lehmanniana* biomass, based on predictions for plots at the endpoints of the invasion gradient, which is a convenient form to compare effects of non-native-grass dominance for parameters measured on different scales.

Results

Vegetation biomass and heterogeneity varied systematically across the gradient of non-native grass invasion. Specifically, as biomass of non-native grass increased, total vegetation biomass increased (0.51 g m^{-2}, s.e. = 0.11, $t_{53} = 4.7$, $P < 0.001$). Vegetation heterogeneity changed in a curvilinear way (0.17%, s.e. = 0.05, $t_{52} = 4.2$, $P < 0.001$; quadratic: $-0.0005\%^2$, s.e. = 0.0001, $t_{52} = -4.5$, $P < 0.001$), with heterogeneity highest at low-to-intermediate levels of non-native grass.

We captured 1344 individual cotton rats during 106 560 trap-nights across all sampling periods. Overall, abundance averaged 5.8 individuals per 1-ha plot (95% CI = 4.8–6.8), but varied markedly with vegetation composition and season, ranging from 0 to 49 individuals per ha. Abundance of Arizona cotton rats increased 8-fold across the full range of the invasion gradient in winter, 10-fold in spring and 7-fold in summer, with an average of 0.9 individual per ha in areas dominated by native grasses

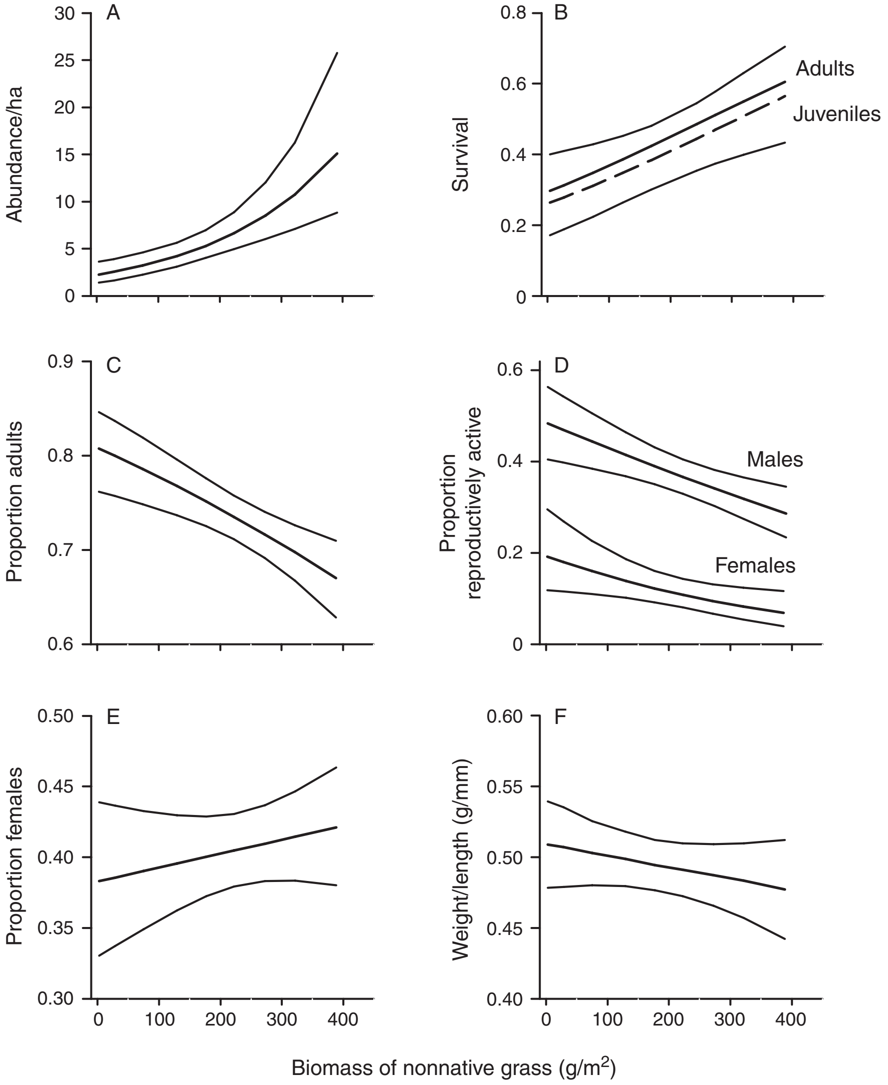

Fig. 1. Changes in demographic parameters for Arizona cotton rats (A – abundance, B – survival, C – age ratios, D – reproductive activity of males and females, E – sex ratios, F – weight : length ratios) across the gradient of dominance by the non-native grass *E. lehmanniana*. Centre lines represent model predictions, which are bounded by 95% confidence intervals.

Table 1. Estimates and standard errors of regression coefficients for changes in demographic parameters for Arizona cotton rats for every 100 g m^{-2} change in the non-native grass *E. lehmanniana*

Parameter	*n*	Estimate	s.e.	*t*	*P*
Abundance (log(no. individuals))	54	0.357	0.074	4.85	< 0.001
Weight : length (g mm^{-1})	44	–0.002	0.004	–0.62	0.54
Reproductive activity (proportion adults)					
Females	39	–0.245	0.148	–1.66	0.10
Males	44	–0.173	0.096	–1.79	0.078
Age ratio (proportion adults)	47	–0.177	0.060	–2.97	0.004
Sex ratio (proportion females)	47	0.038	0.043	0.88	0.38
Survival	54	0.314	0.116	2.71	0.009

(0 g m^{-2} of non-native grass) and 10.1 individuals per ha in areas dominated by non-native grass (466 g m^{-2}; Fig. 1A, Tables 1, 2).

As dominance of non-native grass increased, rates of reproductive activity for adult cotton rats decreased (Tables 1, 2). Relative to areas dominated by native grasses, the proportion of reproductively active females decreased by 62% and the proportion of reproductively active males decreased by 28% in areas dominated by non-native grass (Fig. 1D, Tables 1, 2). Relative to areas dominated by native grasses, the proportion of adults in the population decreased by 20% in areas dominated by non-native grass (Fig. 1C, Tables 1, 2). Neither sex ratios nor weight : length ratios varied appreciably across the invasion gradient (Fig. 1E and F, Tables 1, 2).

Table 2. Predicted values, 95% prediction intervals, and relative change in demographic parameters for Arizona cotton rats in areas dominated by native grass relative to areas dominated by the non-native grass *E. lehmanniana*

Parameter	Native		Non-native		Relative change (%)
	Prediction	95% PI	Prediction	95% PI	
Density (log(no. individuals ha^{-1}))					
Winter	1.1	0.6–1.9	10.1	5.6–17.7	818.2
Spring	0.7	0.2–1.2	7.8	4.2–13.7	1014.3
Summer	1.5	0.9–2.4	12.4	7.0–21.5	726.7
Weight : length (g mm^{-1})					
Winter	0.44	0.42–0.46	0.43	0.41–0.45	–2.3
Spring	0.52	0.50–0.54	0.51	0.49–0.53	–1.9
Summer	0.55	0.53–0.57	0.54	0.52–0.57	–1.8
Reproductive activity (proportion adults)					
Females	0.25	0.14–0.40	0.10	0.04–0.20	–61.6
Males	0.69	0.58–0.78	0.50	0.37–0.63	–27.8
Age ratio (proportion adults)	0.80	0.75–0.85	0.64	0.57–0.71	–20.1
Sex ratio (proportion females)	0.38	0.33–0.44	0.43	0.37–0.48	11.2
Survival	0.30	0.21–0.40	0.65	0.51–0.78	116.7

Survival of cotton rats varied strongly with dominance of non-native grass and slightly by age class (Fig. 1B, Appendix 1). Relative to areas dominated by native grasses, monthly survival of cotton rats increased by 117% in areas dominated by non-native grass; monthly survival averaged 0.30 in areas dominated by native grasses and 0.65 in areas dominated by non-native grass for both age classes combined (Table 2). In areas dominated by native grasses, monthly survival averaged 0.31 for adults and 0.27 for juveniles; in areas dominated by non-native grass, monthly survival averaged 0.66 for adults and 0.62 for juveniles (estimates from model {phi(age+non-native) p(non-native+season)}). Survival of juveniles increased slightly more than that of adults as dominance of non-native grass increased ({phi(age × non-native) p(non-native+season)}, Appendix 1). We found little evidence to indicate that survival varied appreciably by season (Appendix 1).

Discussion

Native animals can exploit environments dominated by non-native plants if the invading plants provide some or all of the resources that animals require (Rodriguez 2006). We found that abundance and survival of cotton rats increased markedly in areas invaded by a non-native grass, which indicates fitness advantages for individuals in these areas. In contrast, however, reproductive activity of adults decreased in areas dominated by non-native grass, which indicates disadvantages. Apparently, the life-history strategy of this species changed in areas invaded by a non-native plant, reflecting a state-specific shift in the balance of resources allocated to reproduction and survival (Leggett and Carscadden 1978; Stearns 1992; McNamara and Houston 1996). Increases in reproduction are often accompanied by decreases in survival (e.g. Ellers and Van Alphen 1997;Cox and Calsbeek 2010), which could result from a shift in how resources are allocated or because reproductively-active individuals suffer increased predation risk (Roff 1992; Cox and Calsbeek 2010). For example, female northern elephant seals (*Mirounga angustirostris*) that delay first reproduction are smaller but have higher survival than those that first reproduce earlier; for this species, timing of first breeding is linked strongly to population densities and colony conditions (Reiter and Le Boeuf 1991). In several species of lizards, females that are reproductively active are less mobile and subject to increased predation risk (Snell *et al*. 1988; Sinervo *et al*. 1991; Landwer 1994). When clutch sizes of lizards were reduced experimentally their survival and growth rates increased; females with clutches that were not manipulated suffered higher predation (Landwer 1994).

Invasions by non-native plants change vegetation structure frequently, especially cover, height and heterogeneity (Orrock *et al*. 2010; Litt and Steidl 2010*b*; Vilà *et al*. 2011). Increased vegetation cover and height can provide native animals with additional refugia that reduce the risk of predation (Taylor 1984; Jacob and Brown 2000; Mattos and Orrock 2010; Orrock *et al*. 2010). Increased survival of both adult and juvenile cotton rats that we observed in areas dominated by *E. lehmanniana* could be explained by reduced predation and increased protection in areas where vegetation biomass was higher. Alternatively, higher rates of survival may be a function of the higher proportion of non-reproductive individuals in these areas, who may be subject to lower predation risk than that of breeding individuals engaged in behaviours that increase their exposure to predators, such as searching for mates (Roff 1992).

Food abundance and diet breadth are important determinants of reproductive rates in many animals, including mammals (Boutin 1990; Brown and Harney 1993; Ortega *et al*. 2006); changes in food availability and diversity can alter how individuals allocate resources (e.g. Millar 1975; Ellers and Van Alphen 1997). Food abundance and nutrient quality can affect onset and duration of breeding, age at first reproduction and litter size (Boutin 1990; Cameron and Eshelman 1996), and may be especially important for female small mammals because of their high energy demands during reproduction – lactating females can consume twice as much food as non-reproductive females (Millar 1975). Additionally, females require specific nutrients and extra dietary water during pregnancy, lactation and rearing of young that can be provided only by certain foods. Winter annuals, for example, may be especially important as a source of certain nutrients (Millar 1975; Cameron and Spencer 2008). Amino acids, which come from dietary protein, are also an important influence on rates of pregnancy and the age of first reproduction (Cameron and Eshelman 1996). Forbs contain higher levels of protein compared with grasses (Randolph *et al*. 1991) and cotton rats make extensive use of forbs to obtain sufficient protein (Cameron and Eshelman 1996; Schetter *et al*. 1998). Similarly, seeds and insects are primary sources of protein that can have strong effects on rates of reproduction of small mammals (Schetter *et al*. 1998; McAdam and Millar 1999). Cotton rats can exploit a diverse array of foods, but they concentrate on grasses and insects when available (Fleharty and Olson 1969; Cameron and Spencer 2008). In areas dominated by non-native grass, richness and abundance of native grasses, herbaceous dicots and insects decrease (Geiger 2006; Litt and Steidl 2010*b*); these changes in vegetation composition resulting from invasion by *E. lehmanniana* may have reduced the diversity, quality and availability of food resources important to Arizona cotton rats. Declines in reproductive activity of cotton rats that we observed in areas dominated by non-native grass suggest that changes in food resources may be important in explaining effects of plant invasions on generalist omnivores. The number of litters and litter sizes (i.e. reproductive output) also may vary with food resources (Boutin 1990; Cameron and Eshelman 1996), although these data are challenging to collect.

Juveniles typically are subordinate to adults, therefore the shift in age ratios towards juveniles in areas dominated by non-native grass might reflect juveniles being forced to inhabit areas of lower habitat quality (Van Horne 1983). Because increases in abundance and survival in response to changes in non-native-grass dominance were similar for juveniles and adults, it seems unlikely that these changes resulted from juveniles being excluded from areas of high-quality habitat. Areas dominated by non-native grass could be preferred by juveniles, however, as predation risk may be lower in areas of dense cover (Bowers and Smith, 1979 but see Schooley *et al*. 1996; Spencer *et al*. 2005).

Small mammals are important in structuring composition of vegetation communities through seed dispersal, seed predation and soil disturbance (Davidson 1993). If native rodents forage preferentially on native plants and if the increase in biomass resulting by invasions from non-native grasses provides increased protection from predation, small mammals may facilitate invasions by non-native plants (i.e. resource-mediated apparent competition, White *et al*. 2006; Orrock *et al*. 2010). The increases in survival and abundance of cotton rats, increased homogeneity of vegetation structure and decreases in abundance of native plants that we and others (Geiger 2006) have documented in areas dominated by *E. lehmanniana*, suggest that Arizona cotton rats could be facilitating the invasion of this non-native plant.

Implications for conservation

Life-history theory predicts that individuals should allocate proportionally more resources to reproduction when and where conditions are favourable, and more to survival when conditions are less favourable (Ellers and Van Alphen 1997). Plasticity in life-history strategies should be favoured in variable environments so individuals can respond to changes by altering how they allocate resources (Stearns 1989). Differences in reproduction and survival in Arizona cotton rats across the invasion gradient we studied may indicate that the optimal life-history tradeoffs differed appreciably in these areas, providing evidence for state-specific life-history strategies in this species. The complex variation in demographic responses across the invasion gradient also suggests that it may be necessary to evaluate a suite of vital rates to fully understand the consequences of plant invasions on animals, especially in landscapes that are changing rapidly (Wilbur *et al*. 1974; Leggett and Carscadden 1978; McNamara and Houston 1996; Ellers and Van Alphen 1997). This is especially important for species of conservation or management concern because single demographic parameters are used frequently as targets to gauge the success of conservation and management activities, which could be misleading (Tear *et al*. 2005). For example, higher abundances and survival rates in areas invaded by a non-native grass suggest these areas are ideal for the small mammal we studied, at least when considered in isolation. Only by evaluating multiple demographic parameters did we recognise that populations in areas invaded by non-native plants functioned differently than populations in native grasslands. Because millions of hectares of grasslands have been invaded by dozens of species of non-native plants (Bahre 1995; McLaughlin and Tellman 2002), the breadth of these complex effects on grassland organisms is immense. Given that distributions of many non-native plants are predicted to increase in response to anticipated changes in natural and anthropogenic drivers (Bradley *et al*. 2010), understanding the effects of these widespread changes on animal populations may require us to consider complex responses, including state-specific changes in demographic and life-history strategies (Rodriguez 2006; White *et al*. 2006).

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Appendix 1. Candidate models for survival and detection probability of Arizona cotton rats

Model	ΔAICc	No. parameters	Weight	Deviance
{phi(non-native) p(non-native+season)}	0.00	6	0.411	134.53
{phi(age+non-native) p(non-native+season)}	1.21	7	0.224	133.73
{phi(age × non-native) p(non-native+season)}	3.13	8	0.086	133.62
{phi(non-native+season) p(non-native+season)}	3.72	8	0.064	134.21
{phi(age+non-native+season) p(non-native+season)}	4.89	9	0.036	133.36
{phi(season) p(.)}	5.62	4	0.025	144.18
{phi(season) p(non-native+season)}	5.95	7	0.021	138.46
{phi(.) p(non-native+season)}	6.48	5	0.016	143.03
{phi(.) p(season)}	6.78	4	0.014	145.35
{phi(age+season) p(.)}	6.98	5	0.013	143.53
{phi(non-native+season) p(non-native)}	7.17	6	0.011	141.70
{phi(age+season) p(non-native+season)}	7.30	8	0.011	137.79
{phi(non-native+season) p(.)}	7.42	5	0.010	143.97
{phi(season) p(non-native)}	7.63	5	0.009	144.18
{phi(age) p(non-native+season)}	7.99	6	0.008	142.53
{phi(age) p(season)}	8.38	5	0.006	144.93
{phi(non-native) p(season)}	8.46	5	0.006	145.01
{phi(age+non-native+season) p(non-native)}	8.54	7	0.006	141.05
{phi(age+season) p(non-native)}	8.55	6	0.006	143.08
{phi(age+non-native+season) p(.)}	8.71	6	0.005	143.25
{phi(season) p(season)}	9.65	6	0.003	144.18
{phi(age × non-native) p(season)}	9.97	6	0.003	144.50
{phi(age+non-native) p(season)}	9.97	6	0.003	144.50
{phi(age+season) p(season)}	11.02	7	0.002	143.53
{phi(non-native+season) p(season)}	11.46	7	0.001	143.97
{phi(age+non-native+season) p(season)}	12.76	8	0.001	143.25
{phi(non-native) p(non-native}	13.53	4	0.000	152.10
{phi(age+non-native) p(non-native)}	14.76	5	0.000	151.31
{phi(.) p(.)}	15.22	2	0.000	157.81
{phi(non-native) p(.)}	16.58	3	0.000	157.16
{phi(age × non-native) p(non-native)}	16.68	6	0.000	151.21
{phi(age) p(.)}	16.78	3	0.000	157.36
{phi(.) p(non-native)}	17.18	3	0.000	157.76
{phi(age+non-native) p(.)}	18.04	4	0.000	156.60
{phi(age) p(non-native)}	18.72	4	0.000	157.29
{phi(age × non-native) p(.)}	19.99	5	0.000	156.54