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Consumer control of oak demography in a Mediterranean-climate savanna

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Abstract. Tree recruitment is rare and oak populations are declining in many Mediterranean-climate oak savannas. Factors affecting acorn production, seedling establishment and initial seedling growth have been much studied in short-term experiments. However, fecundity and early survival rates have not been placed in a demographic framework that also considers sapling survival and growth and adult tree mortality. We use matrix models and life table response experiments to analyze long-term experimental and observation data on California valley oak (*Quercus lobata* Neé) near its southern range limit in Santa Barbara County to answer three questions: (1) How sensitive is oak population growth rate to variation in acorn production and initial seedling establishment vs. sapling survivorship and growth? (2) How do mammalian consumers—specifically, cattle, deer and rodents—impact valley oak seedling establishment and sapling survival and growth? (3) Can vertebrate consumers account for the observed population decline of valley oak in savannas in its southern range? We find that population growth is far more sensitive to consumer-mediated variation in sapling survivorship and growth than to variation in fecundity or seedling establishment and that consumers exert strong influence on the demography of the species. Deterministic, finite population growth rate (λ) is <1 for unprotected plants and for plants that are protected from cattle but still exposed to mule deer and rodents. Population growth rate increases to 1.03 with protection from both cattle and deer, mainly because plants are able to quickly reach the tree layer when they are protected from ungulate browsing. Population growth rate jumps to 1.15 for plants protected from both ungulates and rodents as a result of increased survivorship and height growth of established individuals and because of increased seedling establishment during the first year. Our experimental findings are consistent with observed patterns in natural populations in Santa Barbara County, where tree recruitment is rare in both grazed and non-grazed savannas but more common in areas such as roadsides that are refuges from cattle and deer.

Key words: acorn; browsing; cattle; deer; herbivory; matrix model; recruitment; sapling; savanna; seedling; tree demography.

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INTRODUCTION

Seedlings and saplings are often rare in oak populations of Mediterranean-climate woodland and savanna ecosystems, despite the fact that mature oaks dominate the tree canopy layer (Plieninger et al. 2003, Pons and Pausas 2006, Tyler et al. 2006, Acacio et al. 2007, Zavaleta et al. 2007). This population size structure suggests recruitment-limited population decline, but connecting observed seedling and sapling densities to population trends is exceedingly difficult (Crawley and Long 1995, Clark et al. 1999). Oaks can live for several centuries, so even rare recruitment of new trees could be enough to offset adult mortality.

Because ecologists cannot directly observe variation in age-specific recruitment and mortality rates over the multi-century life spans of long-lived trees, we must rely on weaker evidence such as size and age structures in extant populations, reconstruction of past populations from sparse historical data, and model-based extrapolation of short term experimental and observational studies. Matrix population models are increasingly applied by plant ecologists to integrate such evidence to evaluate tree population viability and the demographic influences of environmental variation, disturbances such as hurricanes or fire (Batista et al. 1998, Hoffmann 1999), biological agents such as nurse plants (Siles et al. 2008), herbivores or disease (van Mantgem et al. 2004), and the interaction of habitat and herbivory (Allcock and Hik 2004). Oaks have rarely been analyzed using matrix models, despite intense scientific and management interest in oak regeneration (Alfonso-Corrado et al. 2007). In this study we combine evidence from a decade-long field experiment, a 60-year record of archival air photos, and matrix population models to examine the relative importance of acorn, seedling and sapling growth and survival, and the associated influence of vertebrate consumers, on the present day demography of valley oak (*Quercus lobata* Née) near its southern range limit in California.

The valley oak is among the largest and longest lived of the North American oaks, attaining trunk diameters up to 4 m, heights of 12 to 25 m, and ages of 300 years or more (Pavlik et al. 1993). Endemic to California, the valley oak

has also been more impacted by human activities than any other oak in the state. In remnant populations, adult mortality exceeds recent recruitment of new trees (Brown and Davis 1991, Sork et al. 2002, Kelly et al. 2005, Whipple et al. 2011). This population decline, combined with conversion of valley oak habitats to agricultural and residential uses, has motivated many public and private conservation and restoration projects (Giusti et al. 2004, Alagona 2008).

Extensive research on Mediterranean-climate oaks has elucidated the factors responsible for high mortality at the acorn and seedling life stages, notably acorn overheating and desiccation, acorn predation by insects, mammals and birds (Borchert et al. 1989, Gomez et al. 2003, Leiva and Fernandez-Ales 2003), seedling desiccation, and seedling herbivory by mammals and insects (Davis et al. 1991, Gomez et al. 2003, Gomez 2004, Acacio et al. 2007). Far less is known about sapling survival rates or the relative contributions of fecundity, seedling establishment, and sapling survivorship and growth in regulating population growth rates (Tyler et al. 2006).

Here we synthesize experimentally obtained estimates of seedling and sapling survivorship under different herbivore treatments using retrospective analysis of matrix population models and life table response experiments (Caswell 1996, 2000) to answer three questions: (1) How sensitive is oak population growth rate to variation in acorn production and initial seedling establishment compared to variation in sapling survivorship and growth? (2) How do mammalian consumers impact rates of valley oak seedling establishment and sapling survival and growth? (3) Can vertebrate consumers account for the observed population decline of valley oak in savannas of southern California?

STUDY AREA AND METHODS

Experimental and observational data were collected at Sedgwick Reserve, a 2372-ha ranch managed by the University of California Natural Reserve System that is located in the foothills of the San Rafael Mountains, central Santa Barbara County, California (Fig. 1). The three main study sites include the floor of a gently sloping, narrow valley of recent Quaternary alluvium, and two

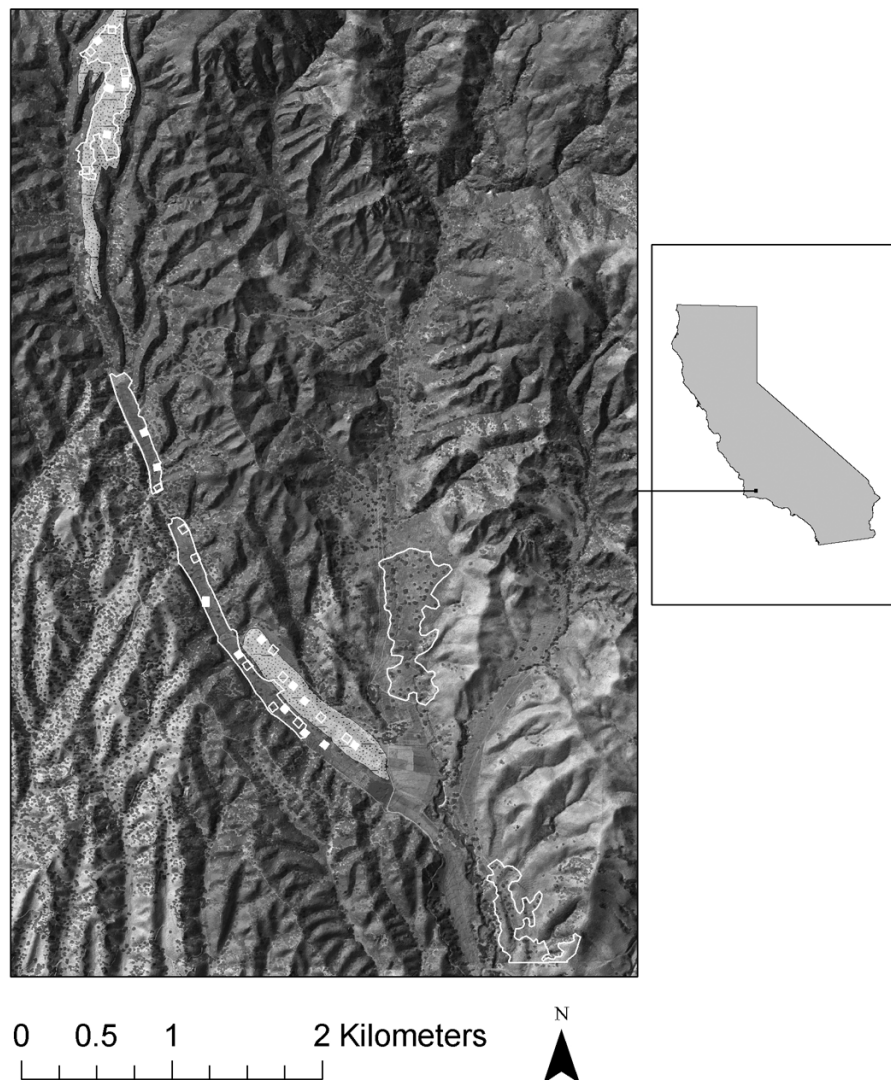


Fig. 1. Air photo of the Sedgwick Reserve and adjacent landscape. Terrace sites are identified by light gray polygons. Areas encompassed by white lines are oak savannas that were analyzed with archival photography to estimate adult survivorship. Open and filled white squares are locations of 50×50 m grazed and non-grazed experimental plots, respectively.

uplifted Pleistocene alluvial terraces adjacent to the valley floor site and raised roughly 40 m above the modern alluvial surface. Study sites range in elevation from 300m to 500m above mean sea level. All sites are level (slopes $< 3^\circ$) and underlain by deep clay loams, fine sandy loams, or gravelly fine sandy loams. Trees were removed from one terrace site roughly 60 years ago and the site now supports annual grassland. The other terrace site and the valley floor site support mixed oak savanna co-dominated by

valley oak and coast live oak (*Q. agrifolia*), with occasional blue oak (*Q. douglasii*) (see Tyler et al. (2008) for details).

Between 1996 and 2008, Dec–Jan minimum daily air temperatures at the study site averaged 4.4°C and Jul–Aug maximum daily temperatures averaged 31.2°C . Precipitation at the Santa Ynez Fire Station, which is roughly 10 km from the study site, averaged 396 mm for rain years (Oct–Sep) 1996/97 through 2006/07, close to the mean value of 401 mm for the period 1950–2007 (Fig. 2).

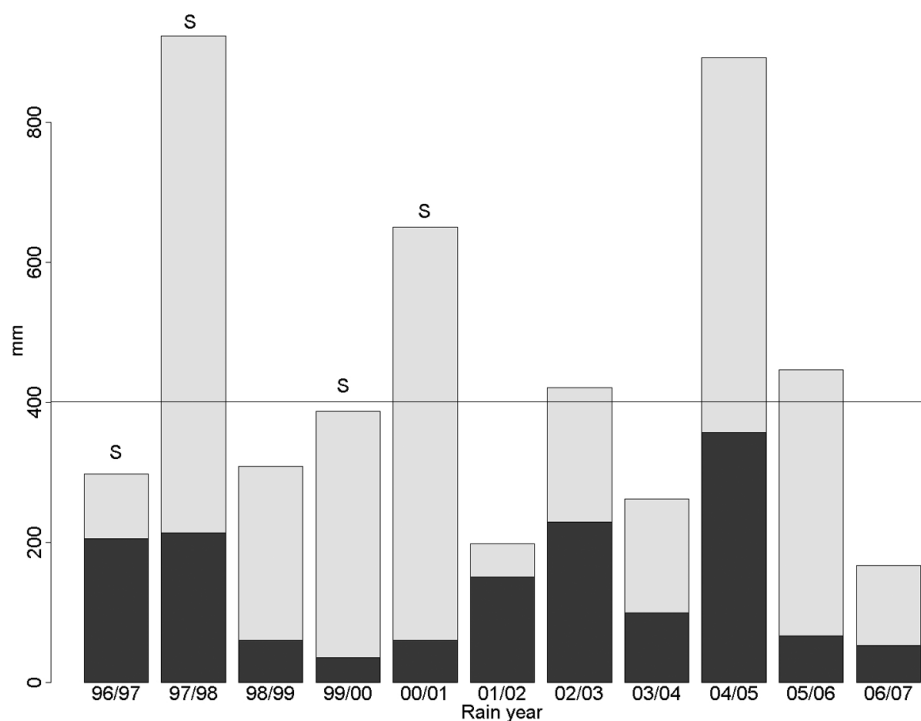


Fig. 2. Rain-year (October–September) precipitation at the Santa Ynez Fire Station between 1996/97 and 2007/08. The horizontal line indicates the mean precipitation for the period 1950–2008. The dark, lower portion of each bar is cumulative rain between October 1 and December 31, prior to acorn planting. The light, upper portion of each bar is cumulative rain between January 1 and May 31, during the period of seedling emergence. Years when acorns were experimentally sown are indicated by an “S” above the bar.

Experimental measurement of seedling and sapling survivorship and growth

Field experiments were established in 1994 to evaluate the roles of cattle, deer and rodents on seedling and sapling survival of valley oak and coast live oak. In this paper we focus solely on valley oak. As described elsewhere (Tyler et al. 2008), the design of this large-scale field experiment involved winter sowing of viable acorns in each of 4 rain years (1996/97, 1997/98, 1999/00, and 2000/01) across thirty 50 m × 50 m experimental plots (hereafter “plots”). Fifteen plot pairs were widely dispersed across the sites (7 pairs on the valley floor, 4 pairs on each of the two terraces). One member of each pair was randomly selected and fenced to exclude cattle (see below) (Fig. 1). Of the four planting years, the 1997/98 and 2000/01 rain years were wetter than average, whereas 1996/97 and 1999/00 rain years were drier than average (Fig. 2). Rainfall timing also differed considerably between planting years. In 1996/97, a large fraction of the rain

fell in early winter (Oct–Dec) before acorns were sown, whereas in the other years a large fraction of rain fell in late winter and spring during the period of seedling emergence (Fig. 2).

Nested exclosures were used to evaluate acorn, seedling and sapling survivorship and growth under 6 experimental treatments that included three levels of protection (no protection, protection from large herbivores, protection from large herbivores and rodents) in grazed vs. non-grazed plots. Within each plot, we established a 9 × 9 grid of points at 5m spacing. Level of protection and planting year were randomly assigned to grid points. Our experimental acorns were first tested for intact endosperm (by confirming that they sank in water) and then sown under a thin covering of soil at selected grid vertices. Most (88%) of our experimental acorns were sown outside the canopy drip line of trees.

Because they resulted in very similar patterns of survivorship and growth, we pooled data from grazed and non-grazed plots for the

treatment involving protection from large herbivores, as well as for the treatment involving protection from large herbivores and rodents. This produced 4 treatments for demographic analyses:

- CT—Control treatment: Unprotected acorns were sown in 15 unfenced plots open to all consumers. Plots were subjected to annual rotational grazing by cattle during winter and spring months. We planted in 8 locations per plot per planting year for a total of 828 acorns sown among four cohorts or years.
- NC—“No cattle” treatment: Acorns were sown in 15 plots, paired with the CT plots, where cattle were excluded using electric fencing. The low fences were not a deterrent to mule deer (*Odocoileus hemionus*). With the exception of one plot in one year, we found no evidence of feral pig (*Sus scrofa*) activity. We assume that cattle and deer were the only important ungulates in our experimental areas and that the effect of the NC treatment was to exclude cattle. We planted in 8–9 locations per plot per year for a total of 858 acorns among four cohorts.
- NU—“No ungulates” treatment: Acorns were sown in cylindrical cages (122 cm height, 45.7 cm diameter) in both grazed and non-grazed plots to protect plants from both deer and cattle. The 5.1 cm × 10.2 cm mesh galvanized wire allowed entry by rodents, such as gophers (*Thomomys bottae*), mice (*Peromyscus* spp.), and ground squirrels (*Spermophilus beecheyi*), as well as birds and insects. We installed 8 cages per plot per planting year in all 30 plots. For the analyses reported here we pooled data from the grazed and non-grazed plots, for a total sample size of 1564 acorns among four cohorts.
- NR—“No rodents” treatment: Nested inside the cylindrical cages that excluded ungulates, smaller, vertical cylinders (91 cm high, 15 cm diameter) constructed of hardware cloth (mesh size = 1.3 cm) were installed to exclude small mammals in addition to the ungulates. They were sealed at both ends with aviary wire. The smaller cages were set 30 cm into the ground to exclude burrowing pocket gophers and ground squirrels. Total

number of small cages per plot per year was eight and we planted in all 30 plots. Data from the grazed and non-grazed plots were pooled for the analyses reported, resulting in a sample size of 1227 acorns among four cohorts. This treatment excluded both ungulates and rodents but for brevity we refer to it as the “no rodents” treatment.

Two acorns were sown 3–7 cm apart at each planting location. Seedling survival (beginning in 1997) and height (beginning in 2000) were recorded between July and September. Survivorship rates were interpolated to end-of-calendar-year rates assuming a constant rate of mortality over the interval (Caswell 2001).

Functional stages for life table analysis

Because age and size interact to influence survival and fecundity rates in valley oak, the optimal age- or stage-based classification for life table analysis is not obvious. It is well established that mortality in Mediterranean-climate oaks is especially high in the first year during acorn germination and initial seedling establishment, so we treated the first year as a distinct stage. However, for established seedlings and saplings, size (in particular height) may be a more important determinant of survival than age, and age and height are only weakly correlated (see below). For example, an individual's height determines its competitive status for light and whether terminal growth can be reached by browsing ungulates.

To help select appropriate age- or height-based stages for life table analysis, we subjected our experimental data to classification tree analysis (Breiman et al. 1984, De'ath and Fabricius 2000). For individuals at least 1 year old, survival from year t to $t + 1$ was modeled as a function of age and height at time t . Large classification trees were constructed by recursive splitting of binary outcome data for experimental plants (died, survived) into the most homogeneous subgroups possible using a single explanatory variable at each split. Classification trees were then pruned back using 10-fold cross-validation to leave only the data splits in which the reduction in number of misclassifications produced by the split exceeded a penalty cost for the more complex tree. All procedures were con-

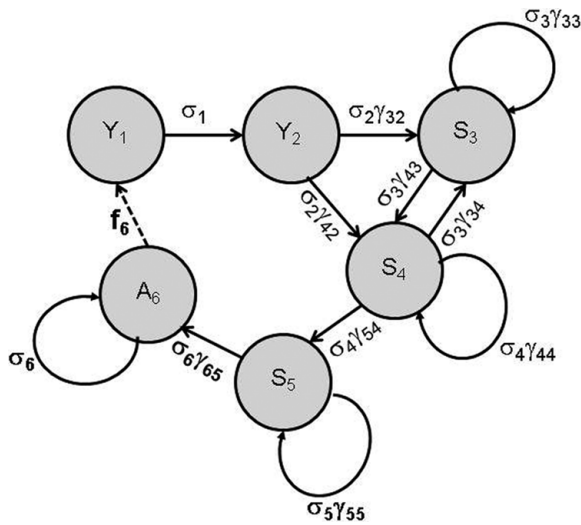


Fig. 3. Life cycle diagram for valley oak (*Quercus lobata*). Y₁ and Y₂ stages each last one year. For individuals at least 2 years in age, S₃ individuals are <20 cm in height, S₄ individuals are between 20 and 120 cm in height, S₅ individuals are >120 cm in height, and A₆ refers to reproductive adults greater than 120 cm in height. Transitions depend on survivorship at stage *i* (σ_i) and height growth (regression, stasis, or progression) to stage *i* from stage *j* (γ_{ij}). The associated transition matrices are shown in Eq. 3. Additional explanation for the stages is provided in Table 1.

ducted using the tree library in R.

Guided by classification tree results (see Results, below), we defined 6 stages for life table modeling (Fig. 3) including three age-based stages (year 1 (Y₁), year 2 (Y₂), and reproductive adults (A₆)) and three height-based stages applied to non-reproductive individuals at least 2 years old: S₃, <20 cm tall; S₄, 20–120 cm tall; S₅, >120 cm tall.

In our notation, the subscript refers to life stages 1–6 and we use the letters to represent year class (Y) vs. size-based (S) or reproductive adult (A) stages. The rationale for these age- and size-based stages is summarized in Table 1.

Adult survivorship

Adult survivorship was measured using aerial photographs from 1943, 1967, 1994, and 2002, and with field surveys in February–March 2006 (Table 2). We mapped all tree-sized valley oaks in the 1943 air photo in 5 stands totaling 84 ha, excluding areas where mechanical clearing of

oaks was known to have occurred after 1950. Individuals present in 1943 were re-located in subsequent air photos and ultimately in the field in 2006. It was often possible to confirm our photointerpretation of valley oak mortality as far back as 1967 because of the long persistence of snags at the study site. At each time period, we also examined the photos for the appearance of new trees, but no recruitment was observed. Annual survivorship was assumed constant over the interval (Table 3) and calculated as:

$$\sigma_6 = (N_2/N_1)^{t^{-1}} \quad (1)$$

where σ_6 is A₆ survivorship, N_2 is the number of survivors at the end of the period, N_1 is the number of individuals at the start of the period, and t is the number of years in the period.

Age at reproduction

Many factors influence per capita acorn production, notably an individual's age and crown area (Johnson et al. 2002). We are not aware of any data relating age, size and fecundity in valley oak although the youngest reproductive individuals we have observed at Sedgwick Reserve appear to be at least 40 years old based on approximate aging using historical air photos. Open-grown eastern white oak (*Q. alba*) can begin bearing fruit at 20 yrs, although under denser conditions the species does not commence fruit production until 50–100 years of age (Rogers 1990). In our model we assume that individuals begin reproducing at 50 years of age (Table 3). This assumption attempts to balance possibly earlier age at reproduction but lower acorn production per individual for younger trees with higher acorn production per tree for older trees (Johnson et al. 2002).

Adult fecundity

Fecundity in our model is defined as the per capita production of viable dispersed acorns. This narrow definition is necessary because we monitored individuals that started as apparently sound, experimentally sown (i.e., “dispersed”) acorns, as opposed to ripe acorns selected at random from reproductive adults in the population. We estimated per capita production of dispersed, viable acorns based on the density of natural seedling recruits censused in experimental plots at the time that we censused seedling

Table 1. Valley oak (*Quercus lobata*) life history stages used for life table analysis.

Stage	Label	Explanation
Year 1	Y ₁	The population model starts with viable, dispersed acorns. Gravity- and animal-dispersed acorns germinate from late fall to early winter, producing seedlings that remain attached to and dependent on food-storing cotyledons through much of their first growing season. This stage has lowest survival probability because individuals are vulnerable to seed and seedling predation and are especially vulnerable to summer drought (Knudsen 1986, Borchert et al. 1989, Tyler et al. 2006).
Year 2	Y ₂	Y ₂ seedlings are dormant in winter months and reinitiate growth with production of new leaves during March–April of the second year. Second-year seedlings have higher survivorship than first-year individuals, presumably due to their larger size and more extensive root system, but are still vulnerable to summer drought, trampling, heavy browsing and rodent herbivory (Griffin 1971, Borchert et al. 1989, Davis et al. 1991, Mahall et al. 2009). At least some individuals are capable of resprouting after heavy browsing or dieback of above-ground tissues.
Stage 3: seedling	S ₃	These individuals have survived at least 2 growing seasons but are less than 20 cm in height. Their foliage is typically below the canopy formed by annual grasses and forbs. Such seedlings are vulnerable to browsing, trampling, and competition for light. <i>Q. lobata</i> is relatively shade-intolerant (Callaway 1992b). The short stature of these individuals is not a simple function of age, but could also be a consequence of repeated browsing as well as slow growth associated with poor microsite quality.
Stage 4: seedling/sapling	S ₄	S ₄ individuals are at least 2 years old with height between 20 cm and 120 cm. The 120 cm threshold is taken as the height required to escape ungulate browsing, based on maximum browse height measured for a sample of valley oak saplings (mean height = 123.7 ± 9.5 cm, n = 40). This browse height is lower than reported by some authors. Browsing and canopy dieback can cause regression of S ₄ individuals to S ₃ .
Stage 5: sapling/non-reproductive tree	S ₅	These are pre-reproductive individuals at least 120 cm in height. Crown development is no longer constrained by ungulate browsing. At our study site, saplings protected from browsing took at least 8 years to attain this height. Saplings protected from rodents and browsing ungulates took at least 4 years to reach this height.
Stage 6: reproductive tree	A ₆	Individuals at least 120 cm in height and at least 50 years in age.

recruits from experimentally sown acorns. We censused 4 plots in both CT and NC treatments in 1997, and two plots in each treatment in 1998. Per capita adult production of viable dispersed acorns, calibrated to our experimental plantings, was estimated as:

$$F = \frac{\text{natural seedlings at first census}}{\text{ha}} \times \frac{\text{ha}}{\text{adult tree}} \times \frac{\text{acorns}}{\text{experimental seedling at first census}}. \quad (2)$$

Adult tree density in the oak savanna stands in which experimental plots were located was measured using the 2002 air photos and field verified in 2006 by mapping all adult valley oaks using a global positioning system.

Based on visual inspection, acorn production was moderate at Sedgwick Reserve in 1996, followed by a very dry winter and spring (Fig.

2). In contrast, 1997 was a mast year for valley oaks and was followed by a wet winter and spring. Both natural and experimental seedling recruitment were relatively low in spring 1997 and were high in spring 1998, yielding adult fecundity estimates ranging from 14 to 162 viable, dispersed acorns per tree and estimated mean annual fecundity of 93 ± 62 viable, dispersed acorns per tree.

Table 2. Air photos used to reconstruct adult Valley oak survivorship rates.

Date	Air photo type	Original scale
Sept 19, 1943	Panchromatic paper prints	1:20,000
May 14, 1967	Panchromatic paper prints	1:20,000
May 29, 1994	Panchromatic digital orthophoto	1:12,000
May 2, 2002	True color digital orthophoto	1:6,000

Table 3. Assumptions made in matrix modeling of valley oak demography.

Model element	Assumption
Adult survivorship	Annual survivorship is assumed constant over the time interval between historical air photos.
Age at reproduction	Individuals begin reproducing at age 50. Age at reproduction is assumed to be 42 years after an individual's height is at least 120 cm (which takes an average of 8 years for individuals not exposed to ungulate browsing).
Per capita Fecundity	All reproductive individuals have the same fecundity, defined as annual production of viable, dispersed acorns. In calculating sensitivity and elasticity of lower level vital rates, and for life table response experiments, we assume an annual fecundity of 100 viable dispersed acorns per adult.
Stage 5 survivorship	Survivorship probability for Stage 5 individuals (>120 cm height) is constant until an individual reaches reproductive age and transitions to the reproductive adult stage. In reality, survivorship probably increases through time as individuals grow larger and more resistant to mechanical injury or extreme drought.
Stage-specific vital rates	Vital rates vary independently of one another and are constant. Associated population growth rate, sensitivities and elasticities are deterministic.
Life table response experiments (LTRE)	To calculate the contribution of the difference in matrix element between treatment (\mathbf{A}^t) and reference (\mathbf{A}^r) matrices to population growth rate, λ , we evaluate element sensitivities for the average of the two matrices, $(\mathbf{A}^t + \mathbf{A}^r)/2$ (Caswell 1996). Vital rates vary independently.

Given the uncertainty in fecundity, we experimented with values ranging from 10 to 1000 to calculate deterministic population growth rate under the different experimental treatments, as described below. We used a value of 100 acorns per adult in calculating vital rate elasticities and sensitivities, and for LTRE analyses. We assumed that all reproductive trees in the population have the same fecundity (Table 3).

Life table analyses

We constructed life tables based on the life cycle discussed above and illustrated in Fig. 3. The projection matrix (\mathbf{A})—and its equivalent expressed in terms of lower level vital rates of survivorship and “growth” (i.e., change in height class)—was formulated as follows:

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & \mathbf{a}_{16} \\ a_{21} & 0 & 0 & 0 & 0 & 0 \\ 0 & a_{32} & a_{33} & a_{34} & 0 & 0 \\ 0 & a_{42} & a_{43} & a_{44} & 0 & 0 \\ 0 & o & 0 & a_{54} & \mathbf{a}_{55} & 0 \\ 0 & o & 0 & 0 & \mathbf{a}_{65} & \mathbf{a}_{66} \end{bmatrix} \\
 = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & f_6 \\ \sigma_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & \sigma_2 \gamma_{32} & \sigma_3 \gamma_{33} & \sigma_4 \gamma_{34} & 0 & 0 \\ 0 & \sigma_2 \gamma_{42} & \sigma_3 \gamma_{43} & \sigma_4 \gamma_{44} & 0 & 0 \\ 0 & 0 & 0 & \sigma_4 \gamma_{54} & \sigma_5 \gamma_{55} & 0 \\ 0 & 0 & 0 & 0 & \sigma_5 \gamma_{65} & \sigma_6 \end{bmatrix} \quad (3)$$

where a_{ij} is the annual probability of an individual moving to stage i from stage j , σ_i is the annual survival probability of stage i individuals, γ_{ij} is the probability of height progression, stasis or regression to stage i from stage j , and f_6 is fecundity measured as per capita production of viable, dispersed acorns. The bold entries in the above matrices are values that were held constant across all four treatments.

We estimated annual survival and growth rates, and associated 95% confidence intervals, based on the binomial distribution and associated beta distribution for variance estimates (Kendall 1998, Morris and Doak 2002). Maximum likelihood estimates of mean survival and growth rates were used to calculate deterministic, finite population growth rate (λ), the dominant eigenvalue of \mathbf{A} . If $\lambda = 1$, population size is constant over time. If $\lambda < 1$, population size is expected to decline exponentially, and if $\lambda > 1$ population size is expected to increase exponentially.

We calculated sensitivities and elasticities of lower level vital rates per Caswell (2001). Sensitivity is the partial derivative of λ with respect to a vital rate of the projection matrix \mathbf{A} and thus measures how much the population growth rate will change for a small change in that vital rate. Elasticity measures the proportional change in λ resulting from a proportional change in a vital rate (Morris and Doak 2002).

We used Life Table Response Experiments

(LTREs) (Caswell 1996, 2001) to determine the contribution of stage specific growth and survival rates to the change in estimated population growth rate ($\Delta\lambda$) for No Cattle (NC), No Ungulates (NU) and No Rodents (NR) treatments compared to the control treatment (CT). We also used LTREs to evaluate the additive effects of rodents by comparing the NU and NR treatments. The contribution of a particular life history component was estimated based on linear decomposition of experimental effects into the additive effects of individual elements of \mathbf{A} (Table 3), assuming that elements varied independently of one another. The sensitivity of λ to a change in a matrix element was evaluated at the midpoint between the entries for \mathbf{A}^t (a treatment projection matrix) and \mathbf{A}^r (a reference projection matrix) (Caswell 1996). For each paired comparison, we modeled the difference in λ as:

$$\Delta\lambda \cong \sum_i \Delta\sigma_i \frac{\delta\lambda}{\delta\sigma_i} + \sum_{ij} \Delta\gamma_{ij} \frac{\delta\lambda}{\delta\gamma_{ij}}. \quad (4)$$

We did not include fecundity in Eq. 4, given that it was held constant among treatments. LTRE analysis considered treatment effects on λ as a function of Y_1 and Y_2 survivorship as well as the rate of progression of Y_2 , S_3 , S_4 and S_5 individuals to the next stage. Like Hoffmann (1999), we focus on overall contributions of height progression to lambda for a specific stage (the sum of the contributions of the γ_{ij} for a particular column) rather than the contributions of the individual values for γ_{ij} .

RESULTS

Survival rates varied widely among years and treatments with the highest survivorship for individuals planted in the 97/98 rain year and protected from all mammal consumers (NR). For this cohort, 33% of plants (106 from a starting sample of 317 acorns) were still alive after 10 years (Fig. 4). In contrast, no individuals survived more than 4 years from 150 acorns planted in the control treatment in the 96/97 rain year. Survival rates increased over the first 3 years, providing support for our life history classification, and exceeded 90% after year 4–6 with the exception of the control treatment, where mortality continued (Fig. 4). Mortality was rare among the few individuals older than 7 years

(Fig. 4).

Classification tree models of survivorship

After the first year, plant height was better than plant age at predicting probability of survival. Pruned classification trees for predicting survival of individuals older than 1 year were short and none explained more than 34% of the deviance, but for all 4 treatments an individual's height was selected over age as the primary splitting variable (Fig. 5). The first split distinguished individuals still in the herb layer (8–24 cm in height) from taller individuals. This split was the basis for distinguishing S_3 from S_4 individuals. Subsequent splits were based on additional height criteria with one exception; in the NC treatment, a level 3 split was based on whether an individual was a year old or was older. This level 3 split was consistent with distinguishing Y_1 and Y_2 individuals.

Stage-specific vital rates

Maximum likelihood estimates of beta-binomial survival rates ranged from 0.10 for unprotected Y_1 individuals to around 0.9 for S_4 individuals in the NC, NU and NR treatments (Fig. 6A). Broad confidence intervals reflect the large inter-annual variation in survivorship within treatments and, in the case of the control treatment, the small number of observations of S_4 individuals. Survival rates were very similar for Y_2 and S_3 stages and were considerably higher for individuals in the S_4 stage. No S_5 individuals were produced in CT and NC treatments and were rare in the NU treatment, so mean S_5 survivorship rates are not included in Fig. 6A.

For surviving individuals, the annual rates of progression or regression between height stages varied widely among treatments. In the control treatment, the annual rate at which surviving S_3 (<20 cm) individuals progressed to the S_4 stage (20–120 cm) averaged only 0.09 (Fig. 6B). By comparison, the rates were 0.5 or 0.57 in the treatments that excluded ungulates (NU) or ungulates and rodents (NR), respectively. In the control treatment, S_4 individuals regressed to the shorter S_3 stage at a high rate of 0.60, compared to 0.07 in the NU treatment and 0.04 in the NR treatment.

The transition from S_4 to S_5 stages was particularly noteworthy. Of special significance

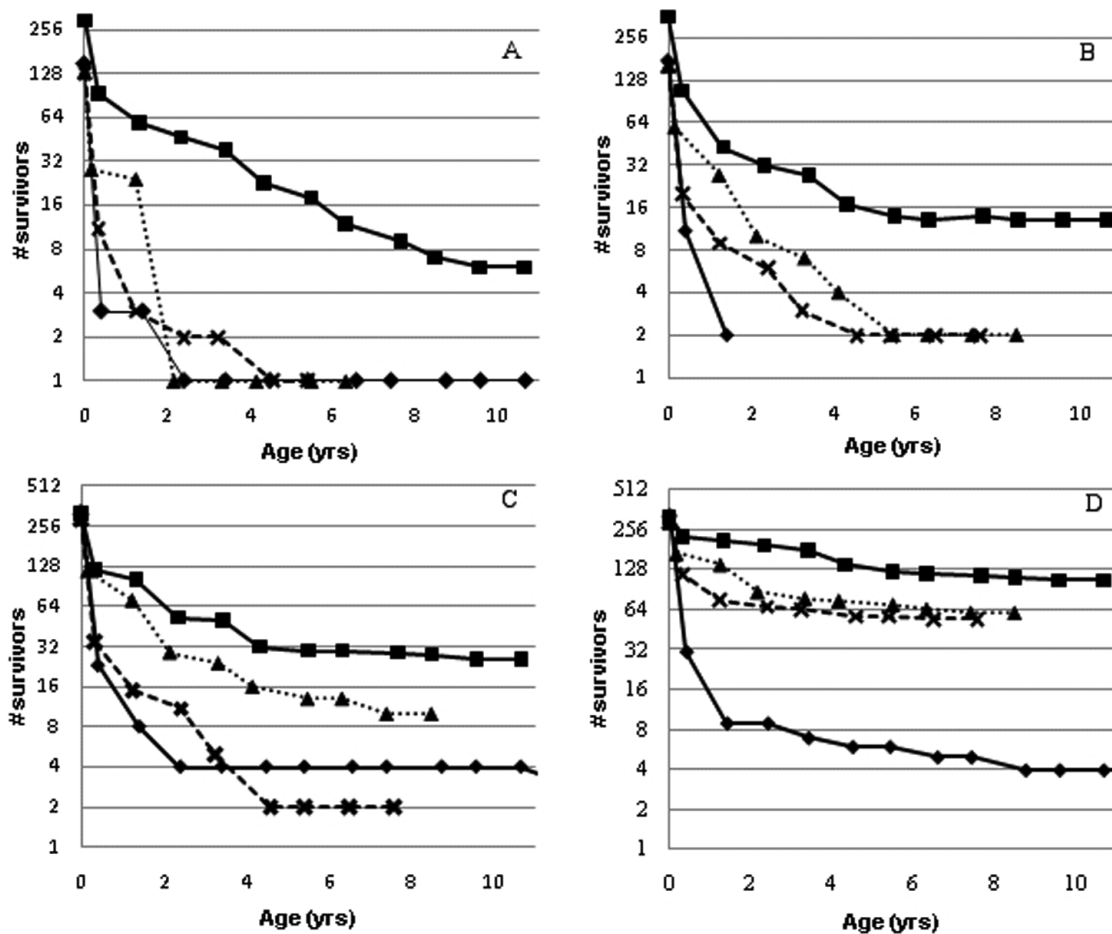


Fig. 4. Survivorship curves for *Quercus lobata* under herbivore treatments including (A) control (CT treatment), (B) no cattle (NC treatment), (C) no ungulates (NU treatment), (D) and no ungulates plus no rodents (NR treatment). Acorns were sown in winter of rain year 1996/97 (diamonds), 1997/98 (squares), 2000/01 (triangles), and 2001/02 (crosses). Y axis is log₂ scaled.

is the absence of any progression of S_4 individuals exposed to ungulates (CT, NC) to S_5 (>120 cm). None of the established seedlings in these treatments attained sufficient height to escape ungulate browsing. In contrast, such progression was observed after 7 years in NU and after 4 years in NR treatments. The fraction of S_4 individuals that transitioned out of the browse layer in the NU and NR treatments was low overall (0.01–0.04), but this small increase had large demographic consequences (see *Life table analyses*, below).

Fig. 7 provides a more detailed picture of height development for individuals between 1 and 9 years of age. In the control treatment, the

tallest of three plants that survived 9 years was only 58 cm high (Fig. 7A). The mean annual height increment for individuals after they entered the S_4 class was 0 cm/yr ($n_{\text{obs}} = 4$). Height gain after nine years was only slightly greater for seedlings protected from cattle but exposed to deer and rodents: the tallest of 13 plants was 45 cm and the median height was 29 cm (Fig. 7B). The mean annual height increment for S_4 individuals was –1.1 cm/yr ($n_{\text{obs}} = 66$). In contrast, the median heights of individuals in NU and NR treatments after nine years were 60 cm and 76 cm, respectively (Fig. 7C, D). The mean annual height increment was 3.7 cm for plants in the NU treatment ($n_{\text{obs}} = 268$) and 5.7 cm for

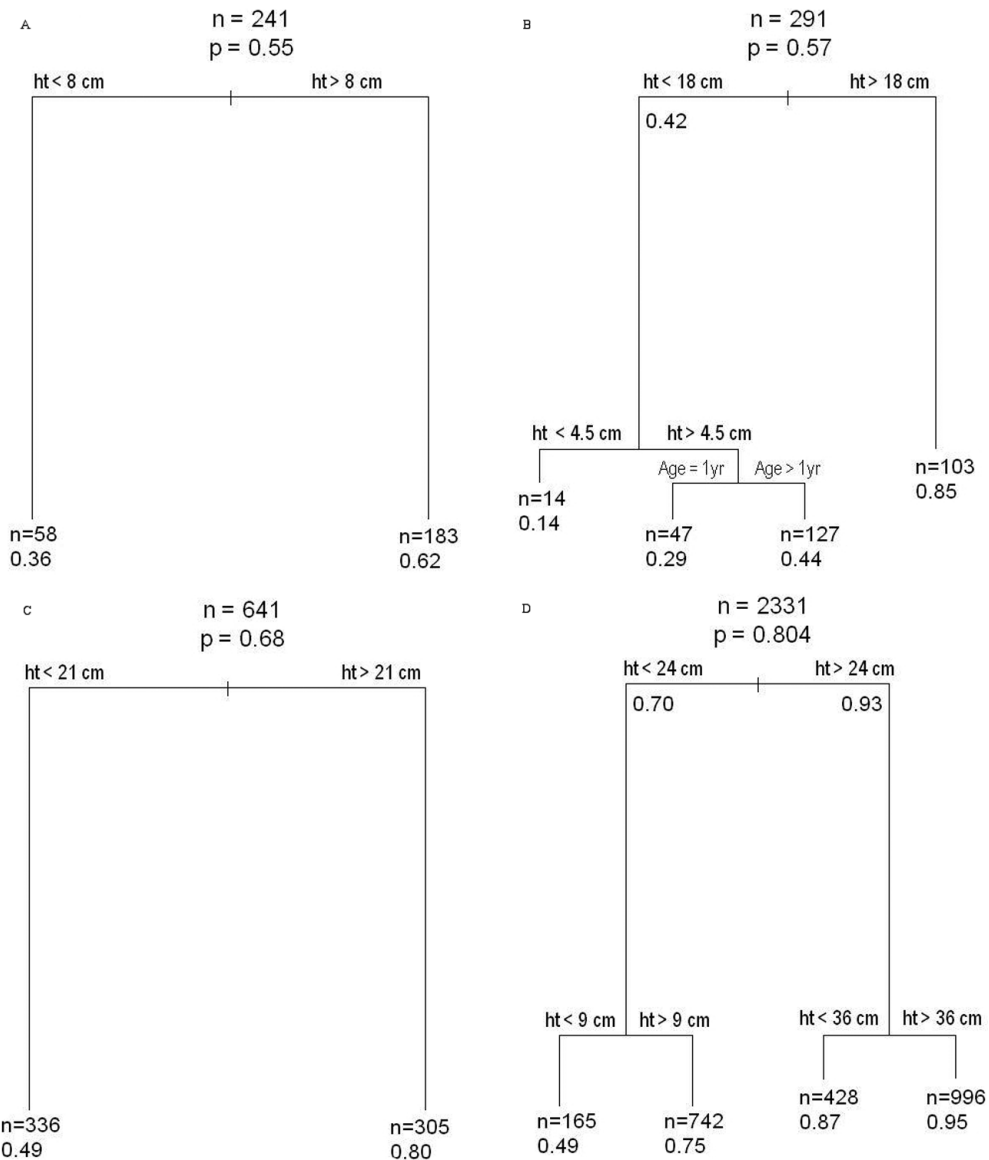


Fig. 5. Classification trees fitted to survival data for experimental valley oak seedlings and saplings at least 1 yr in age. At each branch of the trees, the samples are split into two groups based on either the height (ht) or age of the individuals. Associated sample sizes (n) and survival probabilities are indicated. Treatments include: (A) no protection from vertebrate consumers (CT treatment); (B) protection from cattle (NC treatment), (C) protection from all ungulates (NU treatment), and (D) protection from both ungulates and rodents (NR treatment). Classification trees were pruned to the most parsimonious size based on deviance explained vs. the size of the tree. Total deviance explained by the models is as follows: CT = 34%, NC = 18%, NU = 17%, NR = 24%.

those in the NR treatment ($n_{\text{obs}} = 1352$).

Adult survivorship

No new trees appeared in the census areas between 1943 and 2006. Annual per capita survivorship increased slightly over the period

of observation and was 0.996 for the period 1943–2006 (Table 4). Because no new trees were recruited into the censused area, the annual survival rate (σ_6) is identical to the estimated annual population growth rate over the 63-year period (i.e., $\lambda = 0.996$).

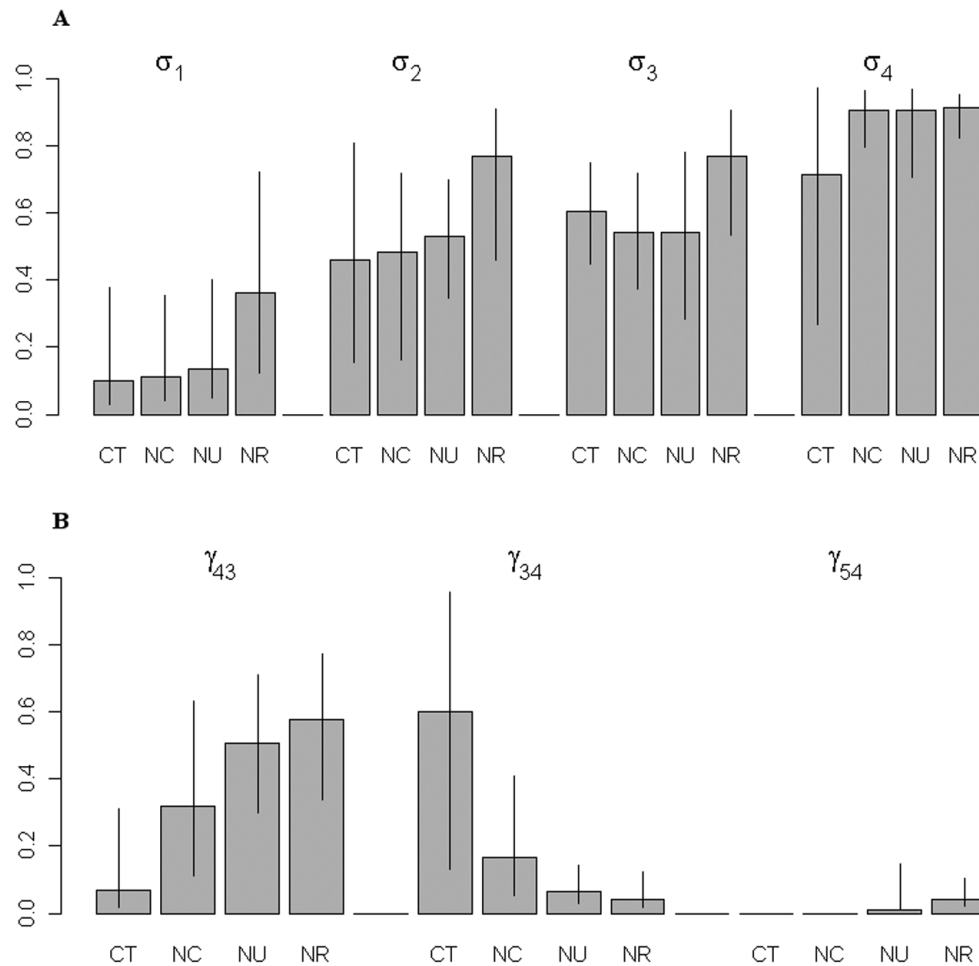


Fig. 6. Maximum likelihood estimates of beta-binomial vital rates and associated 95% confidence intervals (vertical lines) for (A) survivorship (σ) of Y_1 , Y_2 , S_3 and S_4 stages and (B) height growth including rate of progression from S_3 to S_4 (γ_{43}), regression from S_4 to S_3 (γ_{34}) and progression from S_4 to S_5 (γ_{54}). Experimental treatments include no protection (CT), no cattle (NC), no ungulates (NU), and no ungulates and no rodents (NR). Y axes are vital rate values.

Life table analyses

Treatment-specific transition matrices are provided in the Appendix. To estimate a finite population growth rate (λ) for CT and NC treatments and to conduct life table response experiments, we replaced the observed probability that a surviving S_4 individual would attain 120 cm height ($\gamma_{54} = 0$) with $\gamma_{54} = 0.001$. Even at this artificially high rate, calculated λ was <1 for the control treatment across annual adult fecundity values ranging from 10 to 1000 (Fig. 8). Calculated λ was less than 1 in the NC treatment for $\gamma_{54} = 0.001$ and fecundity values less than 600,

increasing to 1.002 at a fecundity value of 1000 (Fig. 8). In contrast, with both cattle and deer excluded, deterministic population growth rate exceeded replacement rate, with λ ranging from 1.002 at $f_6 = 10$ to as high as 1.11 for $f_6 = 1000$. With the exclusion of both ungulates and rodents, λ ranged from 1.05 to 1.33 (Fig. 8).

Fig. 9 presents sensitivity and elasticity values for lower level vital rates assuming $f_6 = 100$. In the control treatment, population growth rate is sensitive to height growth of S_4 individuals (γ_{54}) but dominated by adult survivorship (i.e., σ_6 in Eq. 3, Fig. 9A). If cattle are excluded, finite

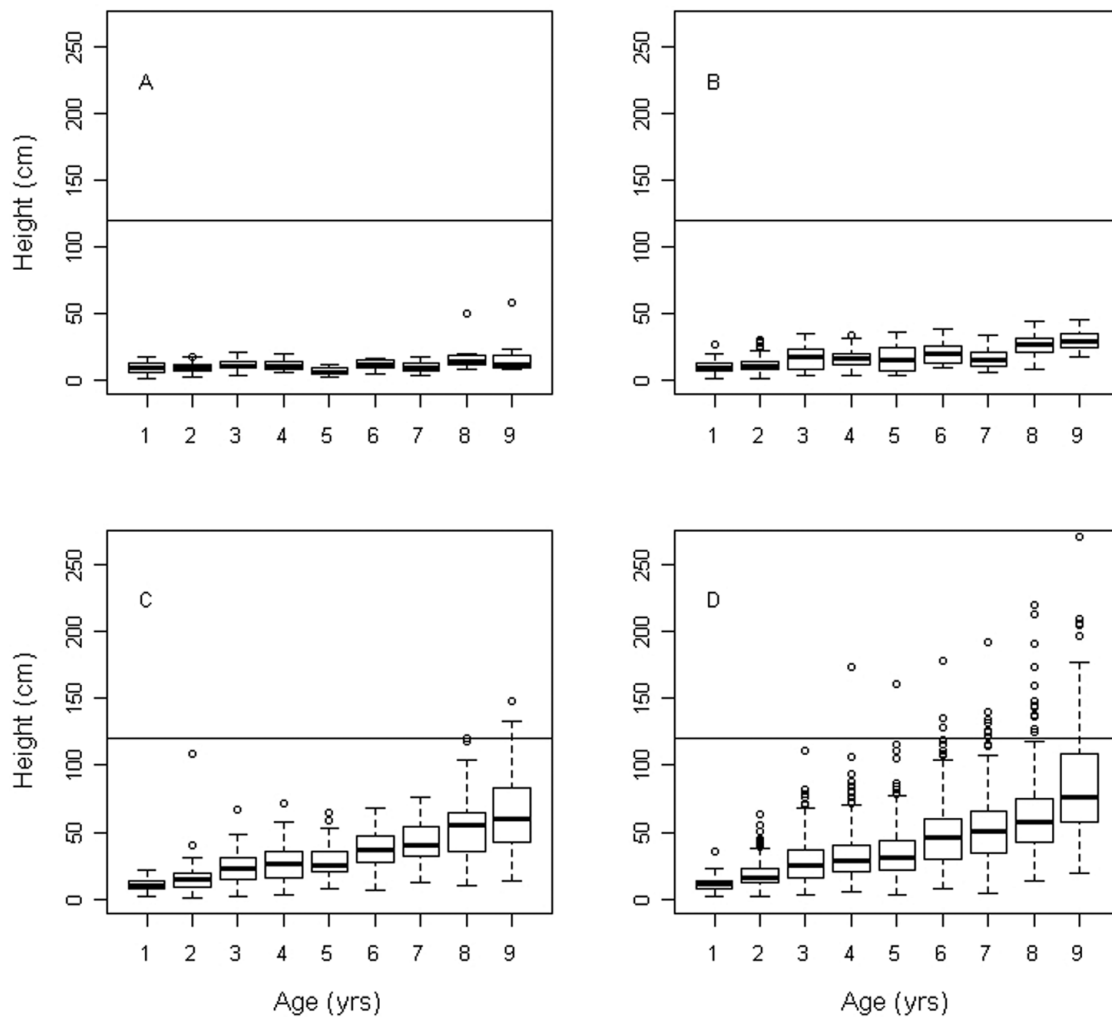


Fig. 7. Boxplots of age class (years) vs. height (cm) for experimental valley oaks under four consumer protection treatments including (A) no protection (CT treatment), (B) no cattle (NC treatment), (C) no ungulates (NU treatment), and (D) no ungulates and no rodents (NR treatment). Boxes display the sample median, upper and lower quartiles; whiskers indicate the data range, and open circles display individual outliers. In all plots, the horizontal line at 120 cm is the observed browse line for cattle and deer browsing in the study area and the height used to distinguish S_4 from S_5 stages in life table analyses.

population growth remains <1 and is most sensitive to the rate of height progression from S_4 to S_5 stages and the rate of adult survivorship (Fig. 9B). The effect of excluding cattle on population growth rate is negligibly small ($\Delta\lambda = 0.0003$) and, as revealed by LTRE analysis, due mainly to slight increases in S_3 growth and S_4 survivorship and growth (Fig. 10A).

With cattle and deer excluded, λ increases to 1.03 (Fig. 8). Roughly 55% of this increase is due to greater height growth of S_4 individuals (γ_4)

(Fig. 10B). The increased rate of transition from S_4 to S_5 is small in absolute terms (see Fig. 6B)—rising from one in a thousand to 1 in one hundred individuals—but the impact is large because attaining 120 cm height most limits population growth rate in the NC treatment (Fig. 9B). In both NC and NU treatments, population growth rate is mainly sensitive to changes in vital rates of later life stages (S_4 , S_5 and A_6). Variations in fecundity, first- and second year survivorship, and S_1 height growth have

Table 4. Survival of tree-sized valley oaks in mixed oak savannas, 1943–2006, based on analysis of archival air photos and 2006 field reconnaissance. Total area monitored was 83 ha (see Fig. 1). N_1 and N_2 are the number of individuals at the start and end of the period, respectively.

Time period	N_1	N_2	Annual per capita survivorship (Eq. 1)
1943–1967	347	306	0.9948
1967–1993	306	275	0.9959
1993–2006	275	267	0.9977
1943–2006	347	267	0.9958

little influence on λ .

With exclusion of ungulates and rodents, λ jumps to 1.15 (Fig. 8). Increased height growth of S_4 individuals (γ_4) and their transition to S_5 accounts for 39% of the increase in λ over the control treatment (Fig. 10C). Increased Y_1 survivorship accounts for 17% of the increase and increased height growth of S_3 individuals (γ_3) contributes another 16% (Figs. 6A, 10C). The LTRE analysis comparing NR vs. NU treatments indicates that the additional increase in population growth rate accompanying rodent exclusion is due mainly to increased height growth of S_4 individuals (42%) and increased Y_1 survivorship (29%) (Fig. 10D).

DISCUSSION

The “regeneration problem” has motivated extensive research on factors limiting oak recruitment in Mediterranean-climate ecosystems. Most experimental research has consisted of short-term and small-scale studies of acorn and seedling ecology (Tyler et al. 2006, Brudvig 2008). All studies report high rates of acorn and seedling mortality (Borchert et al. 1989, Gordon et al. 1989, Davis et al. 1991, Callaway 1992a, Leiva and Fernandez-Ales 2003, Gomez 2004, Acacio et al. 2007) but none has quantified the impact of early mortality in relation to the complete life cycle and demography of the species (Tyler et al. 2006). The combination of a large, long term field experiment to estimate seedling and sapling vital rates plus archival air photos to estimate adult survival rates has allowed us, for the first time, to retrospectively model valley oak demography and to provide tentative answers to the three questions posed in

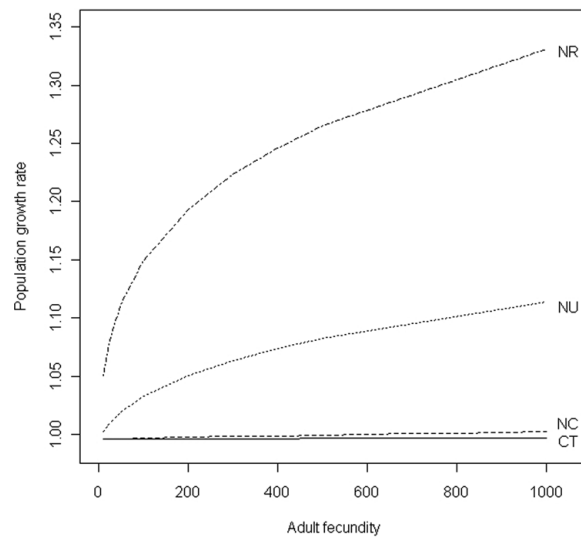


Fig. 8. Deterministic population growth rate (λ) as a function of adult fecundity for four experiment treatments: no protection (CT), no cattle (NC), no ungulates (NU), and no ungulates and no rodents (NR).

the Introduction. For valley oak at our study site, it appears that population growth rate is currently not limited by fecundity, acorn survival, or seedling establishment in the first two years. Instead, population growth is primarily limited by survivorship and growth of established seedlings and saplings, which are in turn strongly regulated by ungulate browsing and rodent damage by herbivory and digging. Our findings are consistent with observed population trends in Santa Barbara County and imply that cattle grazing and deer browsing suffice to explain declining populations of valley oak in savannas of our region.

Demographic sensitivity to variation in acorn and seedling production

We did not measure fecundity directly but life table analysis indicates that in the presence of ungulates and rodents, population growth is relatively insensitive to changes in average acorn production. Griffin (1976) estimated viable acorn production for valley oak as 40 ± 52 acorns/m² of tree canopy. Given the crown sizes of valley oaks at our site (290 ± 129 m², Pluess et al. (2009)), our back-calculated estimate of per capita annual production of 93 viable dispersed acorns (Eq. 2)

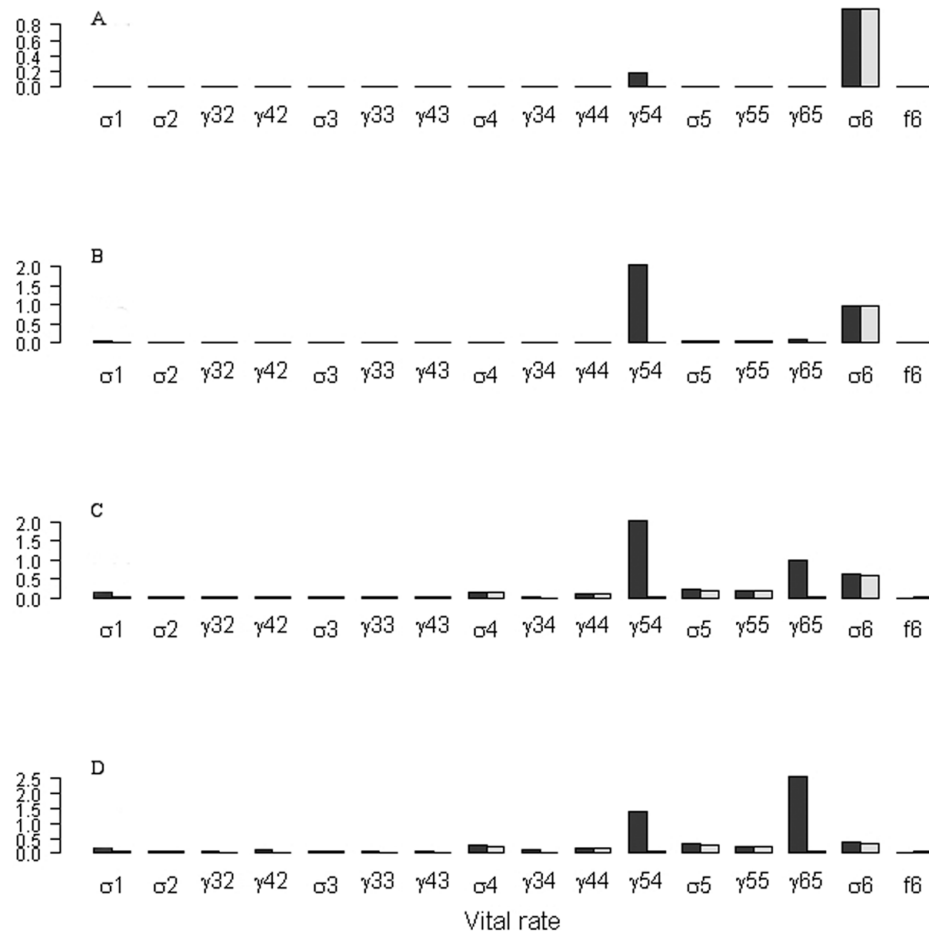


Fig. 9. Vital rate sensitivities (dark gray bars) and elasticities (light gray bars) for four experimental treatments: (A) no protection (CT treatment), (B) no cattle (NC treatment), (C) no ungulates (NU treatment), and (D) no ungulates and no rodents (NR treatment). See Fig. 3 and Eq. 3 for explanation of survivorship (σ) and growth (γ) rates. For better visibility, subscripts in Eq. 3 are printed in normal position in the plot labels (e.g., σ_{ij} is printed as σ_{ij}).

represents roughly 1% of Griffin's estimated annual acorn fall. This production could be increased by a factor of at least 5–10 in areas grazed by cattle or with cattle excluded without appreciably increasing population growth rate (Fig. 8). Consistent with previous studies, we recorded fairly low survivorship of unprotected valley oak acorns and seedlings through the first two years. However, 10% of individuals planted as acorns in the extremely wet 1997/98 rain year survived at least 2 years in the control treatment and 14% survived 2 years in areas protected from cattle. Given the longevity of valley oaks and high interannual variation in rainfall amount and

timing, wet years almost certainly occur with sufficient frequency to allow episodic seedling recruitment events. Highest seedling recruitment rates probably occur when mast years are followed by wet winter and spring conditions (Griffin 1971), as was observed in natural populations at our study site in 1998. Based on gauge data from the Santa Ynez Fire Station, rain years in which precipitation exceeded 100 mm (160% of normal) occurred 11 times since 1950 (roughly 1 in 5 years). Given a masting cycle of 2–3 years, episodes of high seedling recruitment could occur many times over the lifespan of a valley oak—perhaps 1 in 15–20 years in our

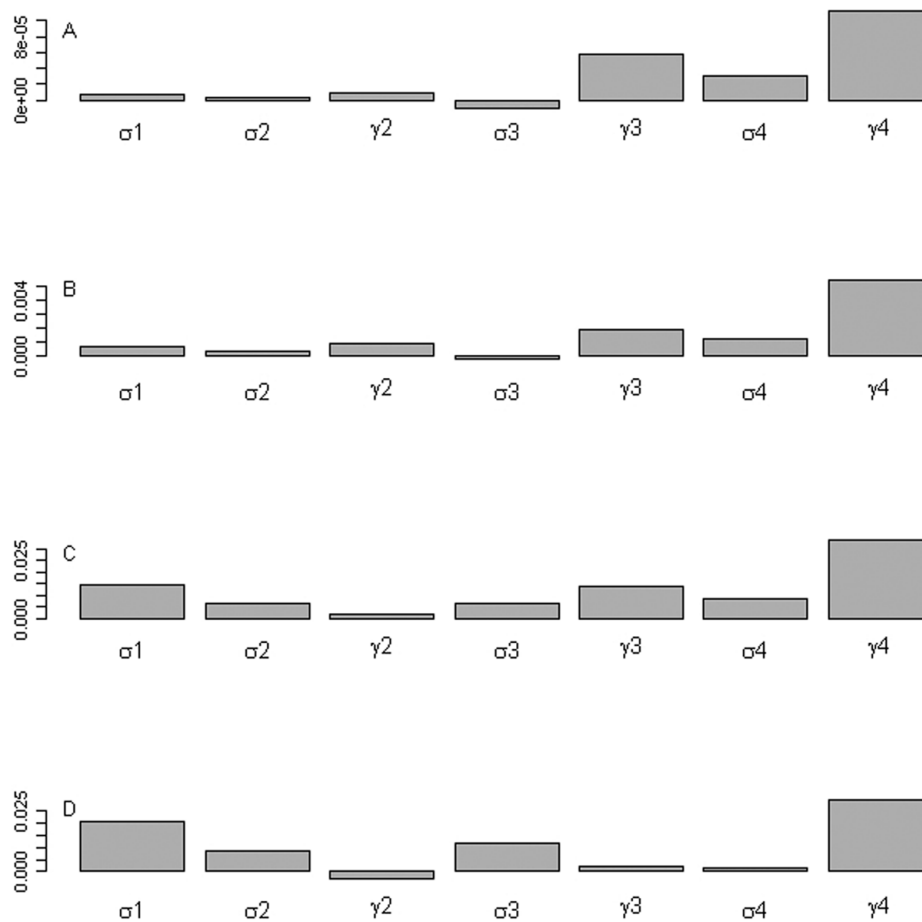


Fig. 10. Life Table Response Experiment (LTRE) estimates of experimental treatment effects expressed as the contribution of lower vital rates to changes in population growth rate (λ) for (A) no cattle (NC) vs. no protection (CT), (B) no ungulates (NU) vs. no protection (CT) and (C) no rodents and no ungulates (NR) vs. no protection (CT), and (D) no rodents and no ungulates (NR) vs. no ungulates (NU). See Fig. 3 and Eq. 3 for explanation of survivorship (σ) and growth (γ) rates. For better visibility, subscripts in Eq. 3 are printed in normal position in the plot labels (e.g., σ_j is printed as σ_j).

region—assuming independence of mast years and ensuing wet years (Koenig et al. 1994, Koenig et al. 2010).

Consumer control on valley oak demography

Our data indicate that rodents and deer play a dominant role in regulating survival and growth rates during initial establishment as well as for established seedlings. Our results add to an already sizeable body of evidence that mice, gophers and ground squirrels have a large effect on valley oak acorn and initial seedling survivorship (reviewed in Tyler et al. 2006). From a demographic perspective, exclusion of rodents

produces a very large increase in population growth rate through the combination of increased acorn and seedling survivorship and increased growth of established seedlings. The pronounced effect of rodent exclosures on survivorship beyond two years was unexpected. It appeared that gophers were capable of killing small, and even some large saplings, presumably by cutting developing taproots. Ground squirrels killed some tall, older saplings by completely excavating the soil around the base of the plant, damaging the root system and probably accelerating drying of the topsoil. These observations indicate that plants can remain vulnerable to

rodent impacts for many years.

Over forty years ago, White (1966) and Griffin (1971) called attention to the apparent lack of regeneration of valley oak and blue oak (*Q. douglasii*) in the Carmel Valley of central coastal California. Both authors observed that the lack of regeneration persisted even after long term removal of cattle, and speculated that deer browsing of seedlings could be an important factor. Griffin (1971, p. 868) noted that none of the heavily browsed blue oak seedlings “showed any promise of becoming saplings under present deer population levels. . . . If browsing pressure were reduced for a few years, the presently established seedlings would produce saplings in many habitats.” Our experimental results support his conclusion: In the presence of either deer or cattle, top browsing (Gill and Beardall 2001) limits new tree recruitment. If ungulates are excluded, within a decade individuals can develop into small trees at a rate high enough to more than offset adult mortality. The impact of ungulates in our experiment would likely have been even greater if cattle grazing had been extended into the summer months (Hall et al. 1992). Furthermore, browsing impacts on demography would have been even more influential in our model if we had assumed a browse height of 150 cm (Bartolome et al. 2002) instead of 120 cm.

In a recent analysis of long term exclosures at Hastings Natural History Reserve in the Carmel Valley, Seabloom et al. (2009) concluded that rodents and deer had no effect on long term oak recruitment. There could be several reasons for the apparent contradiction between those findings and work by Griffin (Griffin 1971, 1976) at the same site or our findings at Sedgwick Reserve. Seabloom et al. (2009) pooled counts of *Q. agrifolia*, *Q. douglasii*, and *Q. lobata* to measure “oak recruitment,” where previous studies and our results are species-specific. They defined seedlings and saplings as all individuals less than 5 cm dbh and pooled them to measure recruitment. Thus their recruitment class combines individuals with very different survivorship and growth rates. As we have tried to show here, and as observed by Griffin (1971), the presence of seedlings and small saplings is not a good indicator of tree recruitment.

An explanation for valley oak population decline in the study region

For our experimental populations, calculated population growth rate is less than 1 and thus non-replacing for unprotected populations, and for populations protected from cattle, over a wide range of fecundity values. Only populations protected from all ungulates or ungulates and rodents are modeled as stable or increasing. These results obviously depend on the structure of our matrix model and our modeling assumptions (Table 2), notably the extrapolation of vital rates estimated from a short time series to asymptotic population growth rates and associated vital rate sensitivities (Caswell 2001, Crone et al. 2011). Nevertheless, the general results from our modeling study are consistent with demographic patterns observed in natural populations in open woodlands and savannas in our study region: While seedlings are not uncommon, saplings are extremely rare and tree densities have declined steadily for at least 70 years (Brown and Davis 1991, Sork et al. 2002). The only exceptions are the moderate numbers of naturally occurring valley oak saplings and young trees near homes and along busy roads in our study area (Kuhn 2010). Based on observational and experimental studies of physical and biological factors, Kuhn (2010) concluded that roadsides facilitated oak recruitment by providing a refuge from cattle and deer.

The important role of deer in the demography of *Q. lobata*, which has been suggested by other researchers but not quantified until this study, is consistent with observations for other oak species (Fuller and Gill 2001, Johnson et al. 2002, Cote et al. 2004, Gotmark et al. 2005, MacDougall et al. 2010). Mule deer populations in our study region have been stable or perhaps increased slightly over the past 50 years (California Department of Fish and Game 1998). Longer-term deer population trends are not well documented.

More generally, we can say little about the conditions under which the current population of adult trees established. Livestock ranching occurred on the Sedgwick Reserve site since at least 1860 and probably since the late 18th Century. Until the mid-19th century, the Chumash culture regularly burned oak woodlands in this region (Keeley 2002). Although the pre-European demography of valley oak remains obscure, the

dearth of saplings and small trees in valley oak savannas was noted by at least one early author. Bartlett (1854) recorded the following observation of oak savannas in the Napa Valley in 1852: “What is singular, and to me unaccountable in these groves of large trees is, that there are no young ones, none but the venerable and full-grown oaks, which, doubtless, for centuries have held exclusive sway over this wide-spread and beautiful domain. Nor is there any undergrowth of other trees and shrubs.”

Concluding remarks

Our results have several implications for valley oak conservation and restoration in our region. First, despite being at the southern end of the species' range, populations in our area are capable of recruitment and positive population growth under today's climate if individuals are protected from large ungulates. Second, our results indicate the need for restoration efforts to protect individuals from both rodents and ungulates for many years, perhaps up to a decade, to assure high survival and growth rates. Finally, our results underscore the demographic importance and thus conservation significance of remaining adult trees in extant savannas. For example, for the control treatment, the calculated reproductive value (or left eigenvalue of the project matrix, per Caswell (2001)) of a reproductive adult is 480,000 times that of an acorn and 2,400 times that of an established seedling.

The mammalian consumers at our site occur in savannas over most or all of the species' range and we would expect their influence to be pervasive, although perhaps not always as strong as in our study area. The demography of the species might be different in cooler, moister sites where the species is capable of faster growth. We encourage comparative studies, especially in locations such as riparian valley oak forests or in more northern savanna populations (Allcock and Hik 2004, Zavaleta et al. 2007). Comparative studies with other Mediterranean climate oak species would also be valuable, and towards that end we are currently conducting similar analyses using our experimental data on *Quercus agrifolia*.

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APPENDIX

Table A1. Population transition matrices for valley oak (*Quercus lobata*) under 4 experimental treatments: (a) control treatment, no protection from mammal consumers; (b) No cattle; (c) No ungulates; (d) No ungulates and no rodents. Matrix entries are the annual rates of transition from stage j (column) to stage i (row). See text for a description of the experimental design and Table 1 for a description of life history classes.

Stage	Y ₁	Y ₂	S ₃	S ₄	S ₅	A ₆
a) Control treatment (CT)						
Y ₁	0.000	0.000	0.000	0.000	0.000	100
Y ₂	0.099	0.000	0.000	0.000	0.000	0.000
S ₃	0.000	0.459	0.561	0.428	0.000	0.000
S ₄	0.000	0.005	0.043	0.286	0.000	0.000
S ₅	0.000	0.000	0.000	0.001	0.920	0.000
A ₆	0.000	0.000	0.000	0.000	0.021	0.996
b) No cattle (NC)						
Y ₁	0.000	0.000	0.000	0.000	0.000	100
Y ₂	0.113	0.000	0.000	0.000	0.000	0.000
S ₃	0.000	0.453	0.370	0.152	0.000	0.000
S ₄	0.000	0.030	0.173	0.753	0.000	0.000
S ₅	0.000	0.000	0.000	0.001	0.920	0.000
A ₆	0.000	0.000	0.000	0.000	0.021	0.996
c) No ungulates (NU)						
Y ₂	0.000	0.000	0.000	0.000	0.000	100
S ₃	0.136	0.000	0.000	0.000	0.000	0.000
S ₄	0.000	0.399	0.267	0.060	0.000	0.000
S ₅	0.000	0.129	0.273	0.833	0.000	0.000
A ₆	0.000	0.000	0.000	0.010	0.920	0.000
Y ₁	0.000	0.000	0.000	0.000	0.021	0.996
d) No ungulates and no rodents (NR)						
Y ₁	0.000	0.000	0.000	0.000	0.000	100
Y ₂	0.363	0.000	0.000	0.000	0.000	0.000
S ₃	0.000	0.672	0.326	0.036	0.000	0.000
S ₄	0.000	0.097	0.441	0.838	0.000	0.000
S ₅	0.000	0.000	0.000	0.038	0.920	0.000
A ₆	0.000	0.000	0.000	0.000	0.021	0.996