DENSITY-DEPENDENT NOT -INDEPENDENT FACTORS INFLUENCE

ROOSEVELT ELK RECRUITMENT IN THE BALD HILLS OF

REDWOOD NATIONAL PARK

by

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ABSTRACT

Density-independent and -dependent factors are known to influence population dynamics of Roosevelt elk (*Cervus elaphus roosevelti*). The strength of influence of both kinds of factors depends on abundance relative to K carrying capacity. I examined the influence of density, climatic variables, and prescribed fire on juvenile recruitment in an elk population in Redwood National Park, California, USA, from 2002 to 2015. In the Park, prescribed fire is used to reduce conifer and redwood (*Sequoia sempervirens*) encroachment into meadows and is not used to manage elk habitat. Consequently, prescribed fire might have a density-independent influence on juvenile recruitment and population dynamics because it is implemented without regard to elk population dynamics. Fire is also known to increase elk food supplies, but whether fire might have a positive influence on recruitment depends on the population size relative to K. Using a time series of elk counts conducted during winter from 2002 to 2015, abundance of elk varied from 190 to 279. Output from a Gompertz state-space model and expectation from the standard logistic model estimated K to be between 275 and 340 over the course of the study period. An Akaike Information Criterion model selection analysis of 36 linear regressions estimating juvenile recruitment considered abundance, prescribed fire, and climatic influences. Population abundance alone had the strongest influence on juvenile recruitment. My findings may be affected by the population being below K carrying capacity during most of the time series analyzed. Furthermore, prescribed fire might not have influenced recruitment because of inconsistent burning.

CHAPTER I

DENSITY-DEPENDENT NOT -INDEPENDENT FACTORS INFLUENCE ROOSEVELT ELK RECRUITMENT IN THE BALD HILLS OF REDWOOD NATIONAL PARK

Introduction

Determining the factors driving population dynamics of large ungulates is complex. Factors can act independently of or depend on population density. Assessing the impact of a factor also requires a range of abundances that span the spectrum from scarce to plentiful resources. Then it is possible to assess the magnitude of the effect of various factors on population dynamics and how they interact (Saether 1997). Rarely, however, do studies assess population abundance with regard to whether resources are scarce or abundant (Bowyer et al. 2014).

Many different forms of disturbance can occur in an ecosystem that alter resource availability for consumers (Sousa 1984). Stochastic climatic disturbances such as precipitation and temperature are classic examples of density-independent factors that influence populations (Singer 1989, Gaillard et al. 1997). These abiotic factors act on populations regardless of abundance (Sæther 1997, Gaillard et al. 1998, 2000, Tyler 2010). Direct effects from density-independent factors, such as extreme winter conditions, occur when animals cannot escape these conditions and subsequently die (Bartmann and Bowden 1984, Singer 1989). Yet, indirect effects from density-independent factors are more commonly observed in large mammal populations. Unusual weather conditions in a growing season, for example, affect production of vegetation and,

by extension, demography of animals in the population (Gaillard et al. 1997). However, other stochastic disturbances like fire can also modify resources available to herbivores. The presence of fire can increase resource abundance following the disturbance which, in turn, affect population dynamics (Bowyer et al. 2014, Sittler et al. 2014).

Density-dependent factors are biotic influences associated with the size of a population. Competition, predation, disease and abundance are examples of density-dependent factors. Unlike density-independent factors, density-dependent factors can regulate population growth (Stewart et al. 2005, Bowyer et al. 2014). For example, with an increasing population, the food supply becomes more limited as does competition for resources (Skogland 1985). The increase in competition negatively affects population growth by reducing an animal's physiological condition which negatively impacts survival and production (Stewart et al. 2005).

Density-dependent and -independent influences used to be thought of as mutually exclusive, but are now viewed as interacting factors (Sæther 1997, Wolcott et al. 2014). The effect of density-independent factors are often stronger with increased abundance. At low abundance, resources are more plentiful and competition for resources is relaxed. Animals are more likely to possess fat and protein stores that buffer them from stochastic climatic events that can negatively impact food availability and abundance. At high abundance resources are more limited and competition for resources is intense. Animal reserves are reduced which makes animals more susceptible to stochastic climatic events (Churkina and Running 1998, Gillard et al. 1998, Gilbert and Raedeke 2004).

The magnitude of the interaction between density-independent and -dependent factors is dictated by *K* carrying capacity of the population. *K* carrying capacity is defined as the number of animals that an environment can support and still be in equilibrium with the food supply (Caughley 1979, McCullough 1979, Bowyer et al. 2014). When population abundance is near *K* carrying capacity, density-independent and -dependent factors interact more strongly and exert greater influence on population growth (McCullough 1999, Gaillard et al. 2000, Sinclair 2003, Wolcott et al. 2014). When a population is below *K* carrying capacity, resources are more abundant and consequently, population growth is less likely to be influenced by density-independent and -dependent factors. Therefore, knowledge of *K* carrying capacity should help to clarify the strength of influences of density-independent and -dependent factors on population dynamics.

Differences in survival rates between juvenile and adult large herbivores has consequences for population dynamics as well. Adults usually have a higher survival rate and less temporal variation in survival than do juveniles (Giallard et al. 1998). Large body size of adults is associated with low mass-specific food intake and longer retention of forage for fermentation (Barboza and Bowyer 2000, Mysterud 2000, Müller et al. 2012). Adults are better able to withstand periods when nutritional resources are scarce making them less vulnerable to predation and inclement weather (Molvar and Bowyer 1994, Giallard et al. 1998). Conversely, juveniles have high mass-specific nutritional requirements for body development and are more vulnerable to predation and stochastic environmental events. This means that juvenile recruitment is usually more strongly related to density-independent and -dependent factors than is adult survivorship (Gaillard et al. 1998, 2000).

Prescribed fire was once used by indigenous people to maintain and increase forage habitat for big game species like Roosevelt elk (*Cervus elaphus roosevelti*) in Redwood National Park (Mandel and Kitchen 1979, National Park Service [NPS] 2013). However, cessation of prescribed fire since the early 1900s has facilitated conifer-redwood (*Sequoia sempervirens*) encroachment into existing meadow habitat in the Bald Hills area of the Park (Mandel and Kitchen 1979, Grenier 1991, Fritschle 2008). Consequently, in the 1980s the Park implemented a prescribed fire program to restore cultural processes and reduce conifer-redwood encroachment into meadows (NPS 2013). Prescribed fire is a disturbance (though not necessarily stochastic) that results in plant communities transitioning to an earlier successional state that stimulates perennial and annual grass and forb productivity (Biswell 1999, Johnson and Matchett 2001, Anderson et al. 2007, Holdo et al. 2007). As such, prescribed fire can provide nutritious forage to large mammalian herbivores for up to 3 years after a burn (Hobbs and Spowart 1984, Dyke and Darragh 2007). The increase in food supply can then be used by individuals to increase reproductive output (White et al. 1983). Because the prescribed fire program in the Bald Hills was not designed to manipulate forage habitat for elk or manage population growth, burning of meadows should affect elk population growth independently of density by indirectly altering the food supply.

Timing of density-independent and -dependent factors can also play a key role in large mammal population dynamics. Impacts from density-independent and -dependent factors might not occur immediately (Coughenour and Singer 1996, Sæther 1997, Bonenfant et al. 2002). Juvenile recruitment in north-coastal California might depend upon resources available to mothers during the growing season in early March through

June (Starns et al. 2014). During dry conditions in summer and early autumn forage is usually more difficult to digest (Gogan and Barrett 1987). Protein and fat stores deposited in spring might have to sustain lactation during the dry summer and influence whether females have sufficient protein and fat stores to conceive during the autumn mating season (Cook et al. 2004). Hence, female fecundity and juvenile survival probably depend on conditions in springs 1 to 2 years earlier.

The purpose of my study was to assess the influence of density-dependent and -independent factors on juvenile recruitment of Roosevelt elk in the Bald Hills of Redwood National Park. To determine if the population was abundant enough for the expression of density-independent factors, I estimated K carrying capacity. I also examined whether the influence of factors had a time-lag of one or two years. If the Roosevelt elk population is below K carrying capacity, I expect to find a stronger influence from density-dependent factors on population dynamics than density-independent factors. Conversely, if the population is at K carrying capacity, I expect to find a stronger influence from density-independent factors than density-dependent factors.

Methods

Study Area

The Bald Hills Meadows are located in the Redwood Creek drainage in Humboldt County, California (43°09'N, 123°53'W, Fig. 1). Meadows are in close proximity to one another and are located along a southwest facing ridge of Redwood Creek. Meadows range in size from 10 to 300 hectares and total 1010 hectares. Climate in the region is

Mediterranean with wet, cool winters, and dry, mild and foggy summers. Average yearly precipitation is approximately 180 cm and occurs mostly as rain (Starns et al. 2014). Ninety percent of this precipitation falls between October and April. Snow occurs during the winter months but rarely remains for more than a week. Summer temperatures average 24-27°C and winter temperatures average 3-5°C, respectively. Elevation of the meadows ranges from 360 to 1050 m. The landscape is comprised of mainly old- and second- growth forest (66%) dominated by coastal redwoods and Douglas fir (*Pseudotsuga menziesii*), meadows (24%), and oak woodlands (10%) which are dominated by white oak (*Quercus garryana*) and black oak (*Q. kelloggii*). Grassland meadows have a mix of perennial and annual grasses and native forbs such as California oat grass (*Danthonia californica*), sweet vernal grass (*Anthoxanthum odoratum*), trefoil (*Lotus micranthus*), and English plantain (*Plantago lanceolata*). Homesteads were established around 1850 and the Bald Hills meadows were grazed by domesticated livestock until the park purchased the area in 1978 (Mandel and Kitchen 1979, Hektner et al. 1983). Roosevelt elk were probably abundant in the Bald Hills prior to 1850 (Harper et al. 1967).

Data Collection

Population surveys to estimate elk abundance in Bald Hills were conducted in 1978, 1987, 1997, 1998, and 2002-2015. Estimates from 1978 and 1987 were acquired from surveys conducted by Mandel and Kitchen (1979) and Grenier (1991), respectfully. Abundances in 1997, 1998, and 2002-2016 were estimated from up to 10 surveys performed in January-February. Surveys consisted of driving predetermined roads within the Bald Hills and hiking into meadow areas that were not visible from vehicles.

Roosevelt elk encountered were counted and classified into age-sex categories of females, juveniles, sub-adult males and adult males. Juveniles were young of the year, sub-adult males had unbranched antlers whereas the antlers of adult males were branched (Weckerly 1996).

I defined the female segment of the population to comprise females, juveniles, and sub-adult males. These animals predominately used the meadows of the Bald Hills and occurred in the same groups (Grenier 1991, Kolbe and Weckerly 2015). The highest count of the female segment of the population within the Bald Hills from the 10 surveys was used to index abundance. Males were not included in the population estimate because of low detectability. Males tend to reside in smaller groups apart from the female segment of the population during the survey period. Furthermore, ungulate population dynamics is tied more strongly to the female segment of the population. (McCullough 1979). Juvenile recruitment was indexed as the number of juveniles in relation to strictly the number of females counted (juveniles:female).

I used data from the Redwood National Park burning program to calculate yearly hectares of meadows and oak-woodlands burned in the Bald Hills between 2003 and 2015 (J. McClelland, National Park Service, unpublished report). Prescribed fires were always conducted in September or October without regard to elk abundance. Increases in the amount of area burned each year from prescribed fires might influence the amount of vegetation available post burn, and in turn, the amount of high quality forage available for elk consumption.

I considered monthly precipitation, monthly temperatures, and hectares of

meadows burned from prescribed fire to be the most likely and readily measurable

factors influencing density-independent recruitment of juvenile Roosevelt elk (Murphy

1970; Biswell 1999; Johnson and Matchett 2001; Haldo et al. 2007, Starns et al. 2014).

Precipitation and temperature data were collected from a Remote Automated Weather

Station (RAWS) in Bald Hills (41°08'N, 123°54'W, http://www.raws.dri.edu/). Because

the climate dataset from Bald Hills was incomplete, I regressed monthly precipitation

from the Bald Hills against the same data from a weather station in Crescent City,

California (Station # 042147) to estimate data missing from the Bald Hills. The Crescent

City weather station was 68 km to the north and had no missing data (Starns et al. 2014).

Precipitation from Crescent City predicted Bald Hills precipitation (Bald Hills = 0.69 +

0.76 * Crescent City, r^2 = 0.78, n = 154, P < 0.001). The timing of precipitation might

affect juvenile recruitment. Precipitation from October through January is crucial to early

germination of annual grasses and growth of perennial grasses and influences the timing

of when green feed is available (Murphy 1970). On the other hand, rainfall across the

growing season from October through April might be more influential. When there is

more rain from October to April there might also be a longer rainy season which should

increase the time of forage growth and increase the length of time high quality feed is

available to elk. To assess the influence of timing of precipitation on juvenile elk

recruitment, accumulated precipitation from October-January and from October-April

were gathered from 2003-2015. Temperatures in the Bald Hills might affect forage

abundance as well. Extended low temperatures in January and June can hinder

germination and growth of grasses and forbs (Murphy 1970, Pitt et al. 1978, George et al.

1988, Starns et al. 2015). To investigate the influence of minimum temperatures on juvenile elk recruitment, I collected data on mean low temperature during January and June from 2003 to 2015.

Analyses

I used a Gompertz state-space model analyzed in RJags to summarize population dynamics and estimate K carrying capacity of the Bald Hill's elk population (R Core Team 2015). The model allows for the estimation of the intrinsic rate of growth in the absence of density-dependence (*a*) and the strength of density-dependence (*c*) (Dennis et al. 2006; Seavy et al. 2009). A density-independent population dynamic is estimated when $c = 1$, and $c < 1$ suggests a density-dependent influence on the population dynamic (Dennis et al. 2006; Seavy et al. 2009). Furthermore, the model estimates process variance (σ^2) and sampling variance (τ^2). Process variance derives from biological processes and consists of two parts: demographic and environmental variation. Demographic variation is endogenous and originates from random fluctuations in individual survival and recruitment. Environmental variation manifests from exogenous sources such as food supply, predation or any other factor that affects vital rates across individuals in a population. Sampling variance is the variation in population dynamics from imprecisions in the survey technique. Sampling variance is the variation between estimates within the time series and is centered around a normal distribution with a mean of zero. The Gompertz state-space model estimates K carrying capacity as the long-term mean and variance of a stationary distribution and requires estimates of *a*, *c*, σ^2 and τ^2.

The Gompertz state-space model was estimated with abundance estimates from 1978, 1987, 1997, 1998, and 2002-2015. The Gompertz model assumes an inverse, linear relationship between the logarithms of abundance lagged one year and the intrinsic rate of population growth rate, which is also in the log scale. The Poisson distribution was assumed for the true population size of the time series, a normal prior was assigned to a and uniform priors were given to c, σ^2 and τ^2. Three Monte Carlo, Markov Chains (MCMC) of 1,500,000 iterations were used to compare mixing across chains (Seavy et al. 2009). The first 500,000 iterations of a chain were discarded (burn-in period) to reduce the influence from autocorrelation on parameter estimates.

Recruitment of Roosevelt elk may be influenced by annual time-lags in population abundance and hectares burned in the Bald Hills (Starns et al. 2014). To assess the possibility of a time-lag, I estimated correlations between abundance and juveniles:female ratios lagged zero, one and two years. I also estimated correlations between hectares burned and juveniles:female ratios lagged one and two years. A zero year time-lag was not considered for hectares burned because prescribed fires occurred after parturition but two to three months before population surveys.

Once the appropriate annual lag was identified, I used an Akaike Information Criterion (AIC) model selection procedure to select a model to summarize juvenile recruitment (Anderson and Burnham 2002, Arnold 2010). I built 36 least-squares models to assess whether abundance, hectares burned, climatic variables or combinations of these predictors influenced juveniles:female ratios. The AIC corrected for small sample size (AIC$_c$) and the coefficient of determination (r^2) were calculated for each model (Arnold

2010, Sokal and Rohlf 2012). I used the MuMIn package in R to calculated model

selection statistics (R Core Team 2014).

Results

The number of hectares burned in a year ranged from 19 to 891. On average, the

Park burned 267 hectares or 26 percent of the Bald Hills per year between 2002 and 2015

(Fig 2). Minimum January temperature ranged from 1.5°C to 7.7°C with an average of

4°C during the time series. June had average minimum temperatures that ranged from

1.9°C to 12.2°C and averaged 8.5 °C. Precipitation accumulated from October through

January averaged 75.7 cm with a minimum of 14.9 and a maximum of 141.9.

Precipitation accumulated from October to April averaged 120.5 cm with a minimum of

81.6 and a maximum of 190.9.

The Roosevelt elk population in the Bald Hills ranged from 4 animals counted in

1978 to 279 animals in 2007 (Fig. 2). Between 1978 to 2004, the abundance counts

increased from 4 animals to 248 respectively. Following 2004 as the population began to

approach the Gompertz estimate of K, abundance counts leveled off ranging from 279 in

2007 and 223 in 2011 with a mean of 247 animals between 2004-2015. The Gompertz

State-Space model summarized the population dynamics well since there were only 3

years when the credible intervals of abundance estimates did not include the observed

counts. Moreover, process variance (σ^2) was estimated at 0.069 accounting for 70 percent

of the variation in annual counts while sampling variance (τ^2) was estimated at 0.046,

accounting for 30 percent of the variation in the counts.

For both abundance and hectares of meadow burned, a two year time-lag had the strongest association with juveniles:female ratios (Fig. 3, 4). Abundance with a two year time-lag had a statistically significant correlation with juveniles:female ratios ($F_{1,11} =$ 8.46, $P = 0.01$) whereas abundance with a one year time-lag and abundance without a time-lag did not ($F_{1,12} < 6.28$, $P > 0.03$). Burned area, however, was not significantly correlated with a one year or two year time-lag ($F_{1,12} < 2.05$, $P > 0.18$). Nonetheless, the two year time-lag displayed the strongest correlation. Because of these findings I used abundance and hectares burned that had a two year time-lag as predictors in the model selection analysis.

The model with abundance lagged two years was selected to summarize juveniles:female ratios (Table 1). The AIC_c of this model was smaller than 2 AIC_c units from any other model and also displayed the highest r^2 value. The evidence ratio between abundance lagged two years and the next top model, abundance and burned area both lagged two years, was 3.5 which provides further support for the top model. Models fit with density-independent factors of precipitation and temperature had little support in the AIC_c models selection and overall preformed worse than the intercept only model. Juveniles:female ratios were negatively correlated with abundance lagged two years (Fig. 5). Juveniles:female ratios were influenced more strongly by density-dependent than density-independent factors.

When the regression line was extended to where juveniles:female ratios were zero, abundance was projected to be 340 (Fig. 5). An abundance of 340 animals, therefore, was an estimate of K carrying capacity. From the population abundance counts, the Gompertz State-Space model also estimated a K carrying capacity of 275 Roosevelt

elk (standard deviation = 86.68). Furthermore, population abundance was affected by

density-dependence since *c* was 0.89 (credible interval; 0.78, 0.94). Like juvenile

recruitment, Bald Hills abundance was also influenced the most by density-dependence

as *c* < 1 and the credible interval not overlapping 1. Using the findings from the

abundance – juveniles:female relationship and the Gompertz State-Space model, *K*

carrying capacity in the Bald Hills was between 275 and 340 animals.

Discussion

Untangling the influence of density-dependent and -independent influences on

juvenile recruitment was needed to assess whether prescribed fire influenced elk

recruitment in the Bald Hills elk population. Past studies have examined the response of

ungulates to prescribed and natural fire on resource use (Seip and Bunnell 1985, Dyke

and Darragh 2006, 2007, Allred et al. 2011, Greene et al. 2012, Sittler et al. 2014). My

study is one of the few to examine whether there was a demographic response to fire in

the elk population (Taber and Gogan 2002). I found that density-dependent factors had a

stronger influence on population dynamics of Roosevelt elk than density-independent

factors. Understanding the influence of density-independent factors such as precipitation,

temperature, and fire on population dynamics is not possible without considering density-

dependence and –independent factors in relation to *K* carrying capacity.

Our results are surprising given that elk use of meadow areas increases post-fire.

Elk generally use habitats more frequently within two years after a burn. Sittler et al.

(2014) found that elk (*Cervus elaphus*) as well as stone sheep (*Ovis dalli stonei*)

inhabiting the Canadian Rocky Mountains used burned areas, compared to unburned

area, more frequently one to two years after fire. Increased elk use was attributed to an increase in summer food supply and forage digestibility. Similar findings were reported by Dyke and Darragh (2007) who observed an increase in elk use of burned sagebrush in south-central Montana 1-2 years after prescribed fire. Approximately 15 km from Bald Hills in another part of the Park. Elk use of meadows in January increased the January after prescribed fires were applied to a 51 ha meadow the prior September and October (Bliss and Weckerly 2016). Across a wide variety of environmental settings the pattern is consistent, elk increase use of burned areas because of an increase in the palatable food supply and its nutritional rewards.

Given that prescribed fire increases the production and digestibility of elk food supplies, juvenile recruitment should also increase up to two years after a prescribed fire. One reason why I did not detect an increase in juvenile recruitment might simply be due to the sporadic and inconsistent application of prescribed fires in the Bald Hills. Prescribed fire is used to reduce conifer encroachment and senescent growth in meadows. Because of this, the meadow area of Bald Hills burned from year-to-year can vary considerably. On average, only 26 percent of the Bald Hills meadows were burned. From 2010 to 2014 when the population was near *K*, only 34 percent of Bald Hills was burned with a maximum of 12 percent occurring in 2014 and a minimum of 3 percent in 2010. This level of burning might not have resulted in a substantial boost in per capita elk forage. Consequently, the small increase in food supplies from burning did not allow females to increase protein and fat reserves so that, in turn, juvenile recruitment would increase.

Another possible explanation for why prescribed fire had little influence on juvenile recruitment was the abundances of the population in relation to K carrying capacity (Bowyer et al. 2014, Pierce et al. 2012). Density-dependence influenced juvenile recruitment and abundance. Apparently food was more limited when the population was more abundant. Nonetheless, the abundance of the population might not have been close enough to K for prescribed fire to exert an influence on juvenile recruitment. From 2002 to 2015 there was sufficient data to accommodate the two year time-lag in the juvenile recruitment response to abundance. Across these years population size ranged from 190 to 276. If K was closer to 340 than 275 then abundances ranged from about 56 to 81 percent of K. These abundances might not have been high enough to exert extensive restrictions in the food supply that could be alleviated by an increase in forage due to the limited amount of burning of the Bald Hills. On the other hand, if K was closer to 275 than 340 then abundances ranges from about 69 to 100 percent of K. These abundances should be high enough to exert restrictions on food supply which could be alleviated from increased forage from burning. Inconsistent and small number of hectares burned during the study period may not have allowed forage abundance to increased and have an influence on juvenile recruitment.

The Gompertz state-space model provided additional evidence of density-dependent regulation on population dynamics of elk in the Bald Hills. The influence of density-dependence on demography and abundance of *C. elaphus* is pervasive (Sauer and Boyce 1983, Singer et al. 1997, Forchhammer et al. 1998, Taper and Gogan 2002, Stewart et al. 2005). My results indicating that density-independent climatic factors did not influence juvenile recruitment concurs with findings from another population in the

park (Starns et al. 2014). Similarly, Imperio et al. (2012) found a weak climatic effect on population dynamics of ungulates in Mediterranean climates. The climate of the Bald Hills is consistent and shows little variation in precipitation accumulation and minimum temperatures during the study period. The mild climate in this part of the geographic range of elk probably has little influence on population processes. Perhaps the only climatic setting that could influence elk population dynamics in the parks in a density-independent manner would be prolonged drought.

Another useful finding from the Gompertz state-space model was that population dynamics were much more affected by process variance than sample variance. The small estimate of sampling variance suggested that population counts reflected actual changes in population abundance during the study period from demographic and environmental stochasticity rather than imprecise sampling of population abundance (Dennis et al. 2006).

The usefulness of the Gompertz state-space model for estimating population dynamics, the processes that drive population change and whether count data are a reliable signal of actual abundance depends on whether this model can actually capture population processes in long-lived species (Dennis et al. 2006). The standard density-dependent model used with long-lived species is the Ricker or the standard logistic model (McCullough 1979). Both the Gompertz and Ricker model assume an inverse, linear relationship between the logarithms of abundance with a one year time-lag and the intrinsic rate of population growth rate. However, neither abundance or population growth is log transformed in the Ricker model. The Gompertz model also assumes density-dependence is strongest at low abundance whereas the Ricker model assumes

density-dependence is strongest near *K* (McCullough 1979, Dennis et al. 2006). In long-lived species such as elk, density-dependence has been observed nearer *K* (Boyce 1989, Taber and Gogan 2002, Coulson et al. 2004). Nonetheless, in comparing Gompertz and Ricker models to observed population dynamics of northern Yellowstone elk, neither model fit the data markedly better than the other (Taber and Gogan 2002). For my time series, the Gompertz model seems to fit my data well as all but three population estimates were within their credible intervals (Fig. 2.).

The continuous 14 year time series between 2002 and 2015 in the Bald Hills was rather limited for estimating a time-lag between abundance and juvenile recruitment. Because of this limitation we only considered one and two year time-lags. A longer time series would have allowed for longer time-lags to be considered. Our findings were consistent with what Starns et al. (2014) reported for another elk population in the Park. The strongest influence on juvenile recruitment was a two year, rather than a one year, time-lag in abundance. Juvenile recruitment in north-coastal California might depend upon resources available to mothers during the growing season in early March through June (Starns et al. 2014). Protein and fat stores deposited in spring probably have an influence on milk production for lactation during the dry summer and influence whether females have sufficient protein and fat stores to conceive during the autumn mating season (Cook et al. 2004).

Although prescribed fire has repeatedly been shown to increase forage availability and by large herbivores (Seip and Bunnell 1985, Dyke and Darragh 2006, 2007, Allred et al. 2011, Greene et al. 2012, Sittler et al. 2014), its influence on Roosevelt elk recruitment in the Bald Hills was not detected. Variability in number of hectares burned

per year and the elk population being below K carrying capacity resulted in density-dependence influencing juvenile recruitment much more so than density-independent influence from climatic factors or prescribed fire. Continued and consistent prescribed fire application by the Redwood National Park may influence the population dynamics of Roosevelt elk if the population continues to increase and approaches K carrying capacity.

Figure Legend

Figure 1. Map of the Bald Hills in Redwood National Park, California.

Figure 2. Observed abundance (x) of Roosevelt elk (*C. e. roosevelti*), estimated population abundance (open diamond) with their associated upper and lower bounds of 95 percent credible intervals, and hectares burned from 1978 to 2015 in the Bald Hills Meadows, California.

Figure 3. Scatter plot illustrating the relationship between abundance and juveniles:female ratios of Roosevelt elk (*C. e. roosevelti*) from 2003-2015 in Bald Hills, Redwood National Park, California. Subscripts denote time-lags of 1 or 2 years. The correlation coefficient (*r*) is reported to show strength of relationship.

Figure 4. Scatter plot illustrating the relationship between hectares burned and juveniles:female ratios of Roosevelt elk (*C. e. roosevelti*) from 2003-2015 in Bald Hills Meadows, Humboldt County, California. Subscripts denote time-lags of 1 or 2 years. The correlation coefficient (*r*) is reported to show strength of relationship.

Figure 5. Abundance with a time-lag of two years and juveniles:female data with regression and the upper and lower bound confidence envelope for Roosevelt elk (*C. e. roosevelti*) in Bald Hills Meadows, Humboldt County, California. Dotted line extending estimates *K* carrying capacity of 340 elk by the logistic model.

Table 1. Model selection summary of 36 linear regression models estimating juveniles:female ratios of Roosevelt elk (*C. e. roosevelti*) considering abundance, hectares burned, and climatic variables. Subscripts denote a time-lag of 2 years. Fit of models were assessed with Akaike information criterion corrected for small sample size (AIC$_c$). The summary consists of delta (Δ, difference in AIC$_c$ between model and model with smallest AIC$_c$), number of parameters estimated in models (*n*Par), log-likelihood (LL), coefficient of determination (r^2), and the Akaike weight of each model. The adjusted r^2 is presented for models with >1 predictors.

Models	Δ	*n*Par	LL	r^2	Weight
N_{t-2}	0.00	3	16.666	0.46	0.369
N_{t-2} + Burned$_{t-2}$	2.48	4	17.786	0.45	0.104
N_{t-2} + OctAprPrec$_{t-2}$	2.58	4	17.734	0.44	0.099
N_{t-2} + OctJanPrec$_{t-2}$	2.59	4	17.730	0.44	0.099
1 (Null Model)	3.70	2	17.132	0.41	0.054
N_{t-2} + JanMinTemp$_{t-2}$	3.78	4	14.588	0.39	0.054
JanMinTemp$_{t-2}$	4.16	3	16.876	0.23	0.045
N_{t-2} + JunMinTemp$_{t-2}$	4.30	4	14.106	0.36	0.042
Burned$_{t-2}$	5.12	3	13.980	0.17	0.028
OctAprPrec$_{t-2}$	5.37	3	13.946	0.15	0.024
OctJanPrec$_{t-2}$	5.44	3	13.760	0.15	0.024
JunMinTemp$_{t-2}$	5.81	3	15.775	0.12	0.020
JunMinTemp$_{t-2}$ + OctJanPrec$_{t-2}$	6.50	4	18.461	0.23	0.014
N_{t-2} + JunMinTemp$_{t-2}$ + OctJanPrec$_{t-2}$	7.41	5	15.281	0.44	0.009
JunMinTemp$_{t-2}$ + OctAprPrec$_{t-2}$	7.48	4	15.246	0.16	0.009
Burned$_{t-2}$ + JunMinTemp$_{t-2}$	7.55	4	18.287	0.16	0.008
N_{t-2} + Burned$_{t-2}$ + OctAprPrec$_{t-2}$	7.76	5	15.038	0.43	0.007
Burned$_{t-2}$ + JanMinTemp$_{t-2}$	7.97	4	17.902	0.13	0.007
N_{t-2} + Burned$_{t-2}$ + JanMinTemp$_{t-2}$	8.53	5	14.738	0.39	0.005
JanMinTemp$_{t-2}$ + OctJanPrec$_{t-2}$	8.57	4	17.838	0.08	0.005
N_{t-2} + Burned$_{t-2}$ + JunMinTemp$_{t-2}$	8.66	5	14.668	0.38	0.005
Burned$_{t-2}$ + OctJanPrec$_{t-2}$	8.71	4	14.629	0.07	0.005
JanMinTemp$_{t-2}$ + OctAprPrec$_{t-2}$	8.79	4	17.761	0.07	0.004
N_{t-2} + JunMinTemp$_{t-2}$ + OctAprPrec$_{t-2}$	8.81	5	17.753	0.37	0.004
N_{t-2} + JanMinTemp$_{t-2}$ + OctJanPrec$_{t-2}$	8.83	5	17.739	0.37	0.004
N_{t-2} + JanMinTemp$_{t-2}$ + OctAprPrec$_{t-2}$	8.85	5	17.732	0.37	0.004
N_{t-2} + JunMinTemp$_{t-2}$ + OctJanPrec$_{t-2}$	8.87	5	14.534	0.37	0.004
Burned$_{t-2}$ + OctAprPrec$_{t-2}$	8.98	4	16.735	0.05	0.004
Burned$_{t-2}$ + JunMinTemp$_{t-2}$ + OctJanPrec$_{t-2}$	10.86	5	16.011	0.26	0.002
Burned$_{t-2}$ + JunMinTemp$_{t-2}$ + OctAprPrec$_{t-2}$	12.31	5	15.151	0.16	0.001
Burned$_{t-2}$ + JanMinTemp$_{t-2}$ + OctJanPrec$_{t-2}$	14.03	5	15.042	0.04	0.000
Burned$_{t-2}$ + JanMinTemp$_{t-2}$ + OctAprPrec$_{t-2}$	14.25	5	18.487	0.02	0.000
N_{t-2} + Burned$_{t-2}$ + JunMinTemp$_{t-2}$ + OctJanPrec$_{t-2}$	16.16	6	18.468	0.37	0.000
N_{t-2} + Burned$_{t-2}$ + JanMinTemp$_{t-2}$ + OctJanPrec$_{t-2}$	16.20	6	18.319	0.36	0.000
N_{t-2} + Burned$_{t-2}$ + JanMinTemp$_{t-2}$ + OctAprPrec$_{t-2}$	16.50	6	18.291	0.35	0.000
N_{t-2} + Burned$_{t-2}$ + JunMinTemp$_{t-2}$ + OctAprPrec$_{t-2}$	16.55	6	0.899	0.35	0.000

Bald Hills of Redwood National Park

California

Bald Hills of Redwood National Park

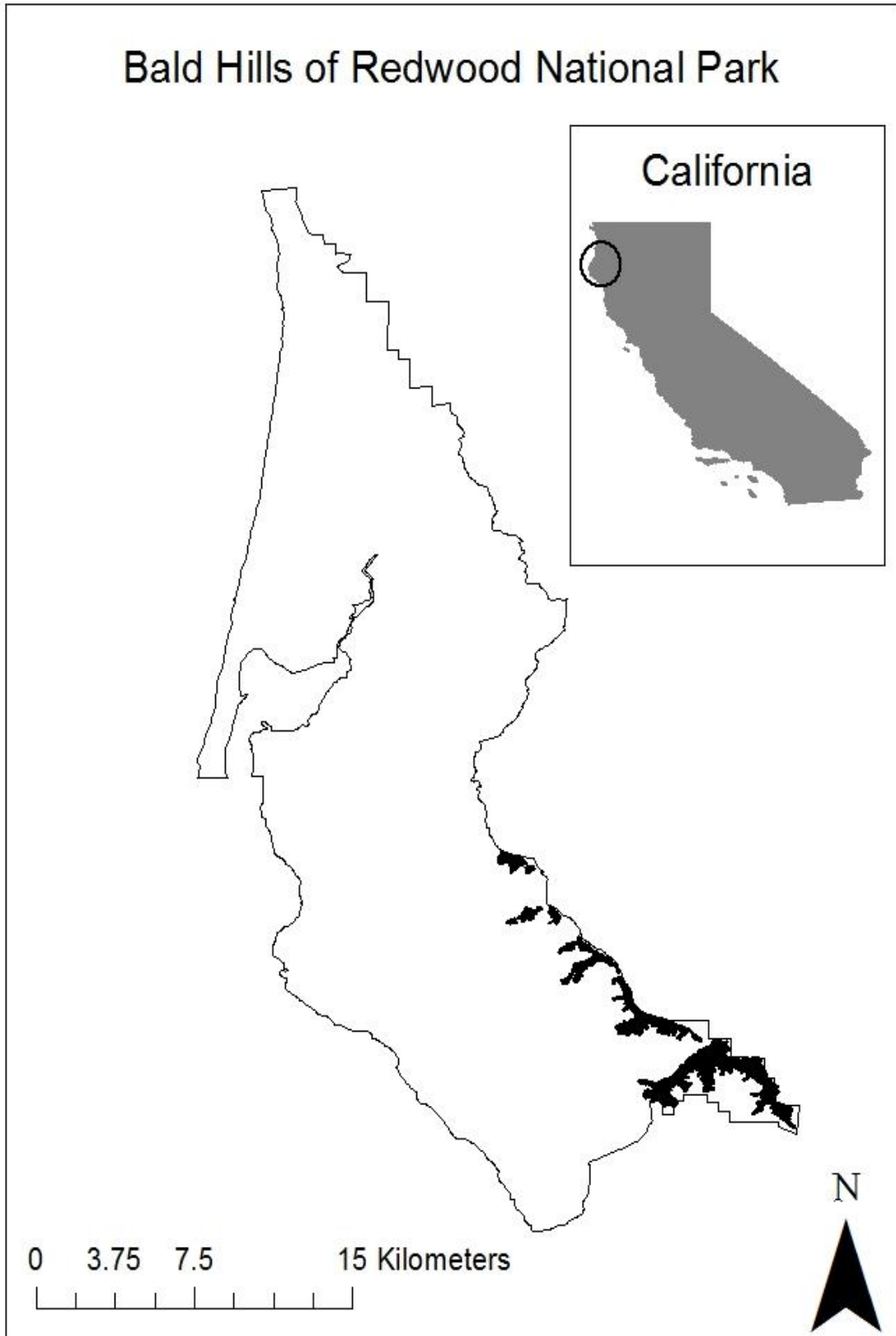0   3.75   7.5   15 Kilometers

N

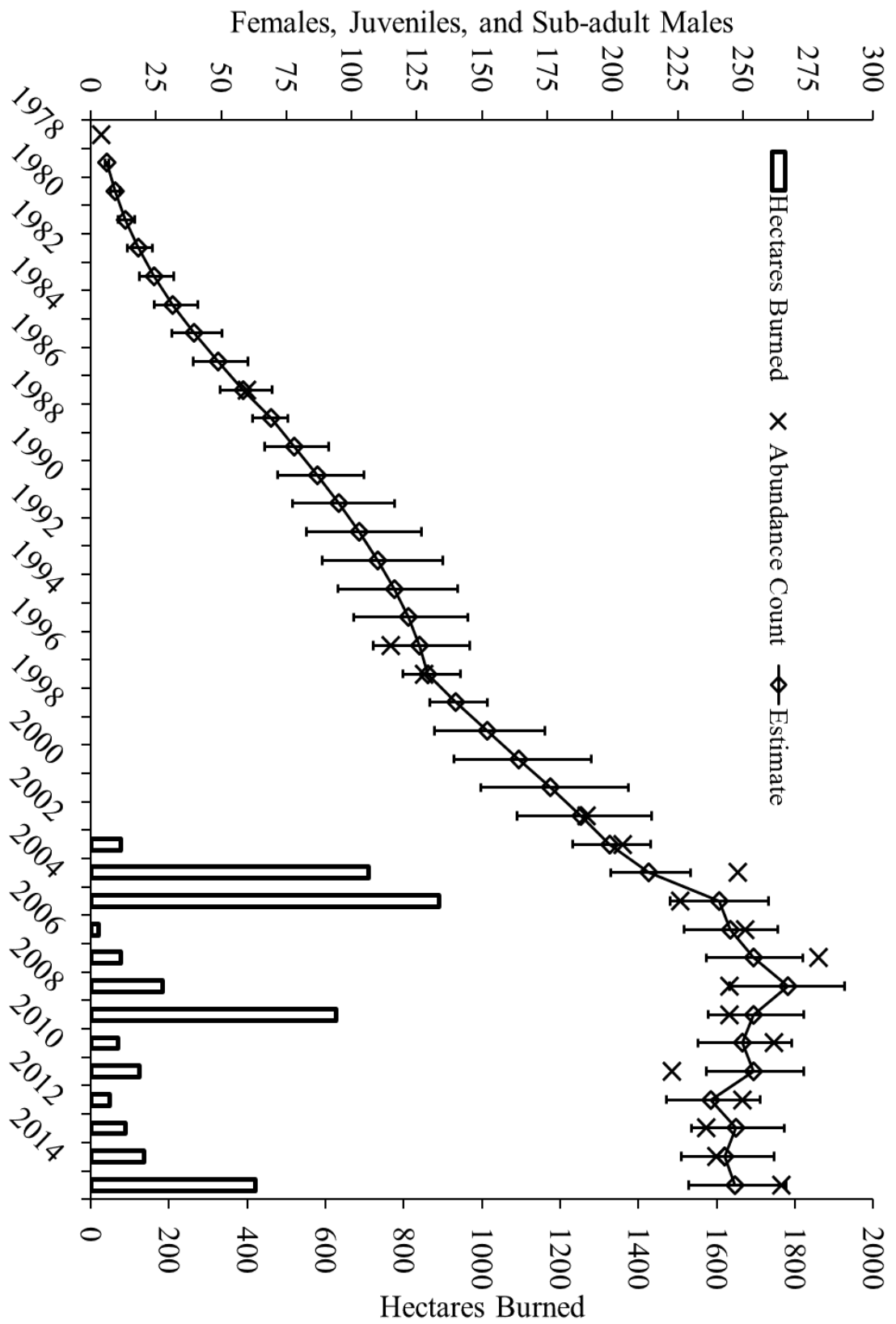Figure 1. Map of Bald Hills from the Redwood National Park, California

Figure 2. Gompertz state space model estimating abundance of Roosevelt elk and displaying hectares burned in Bald Hills.
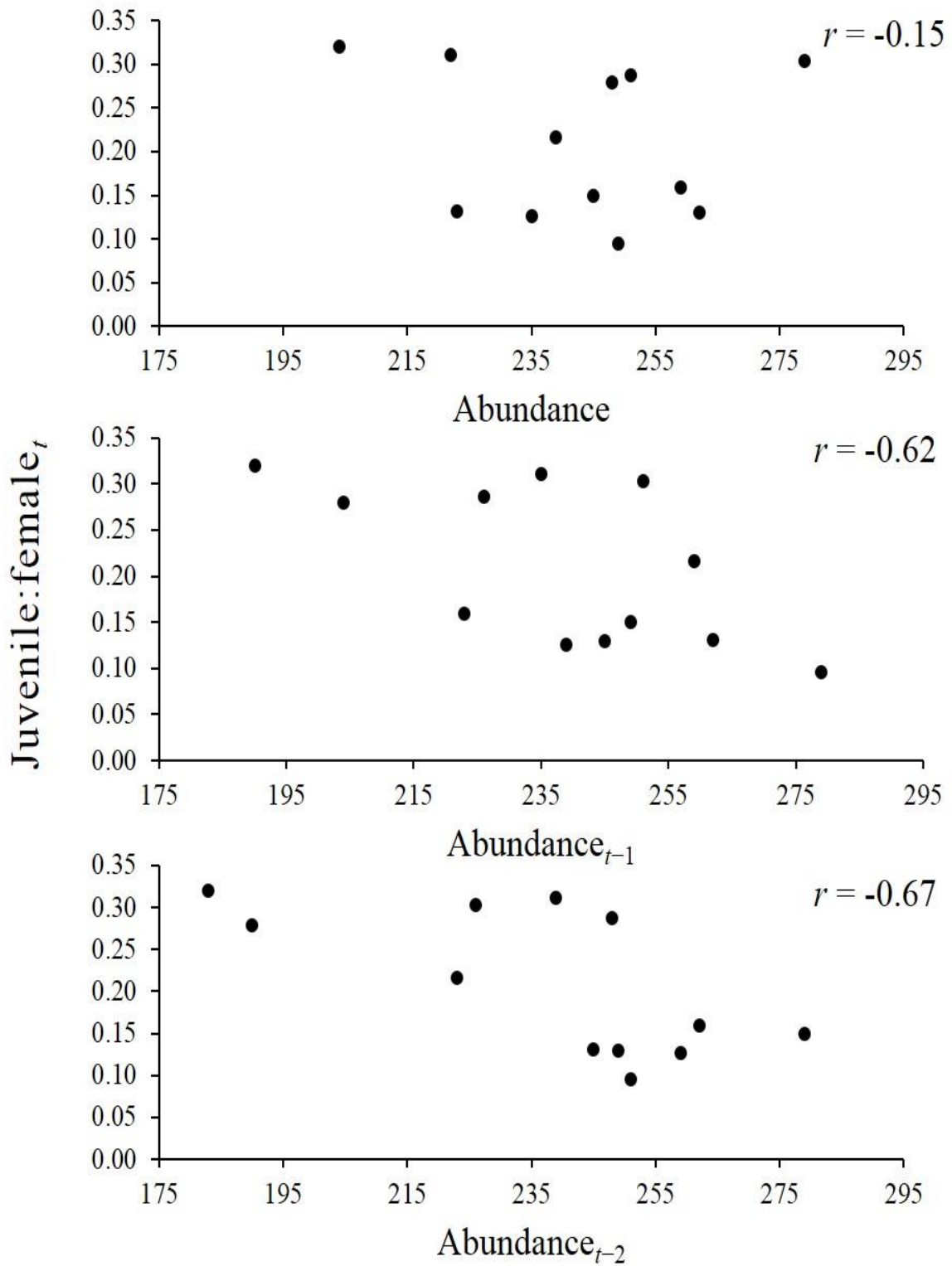
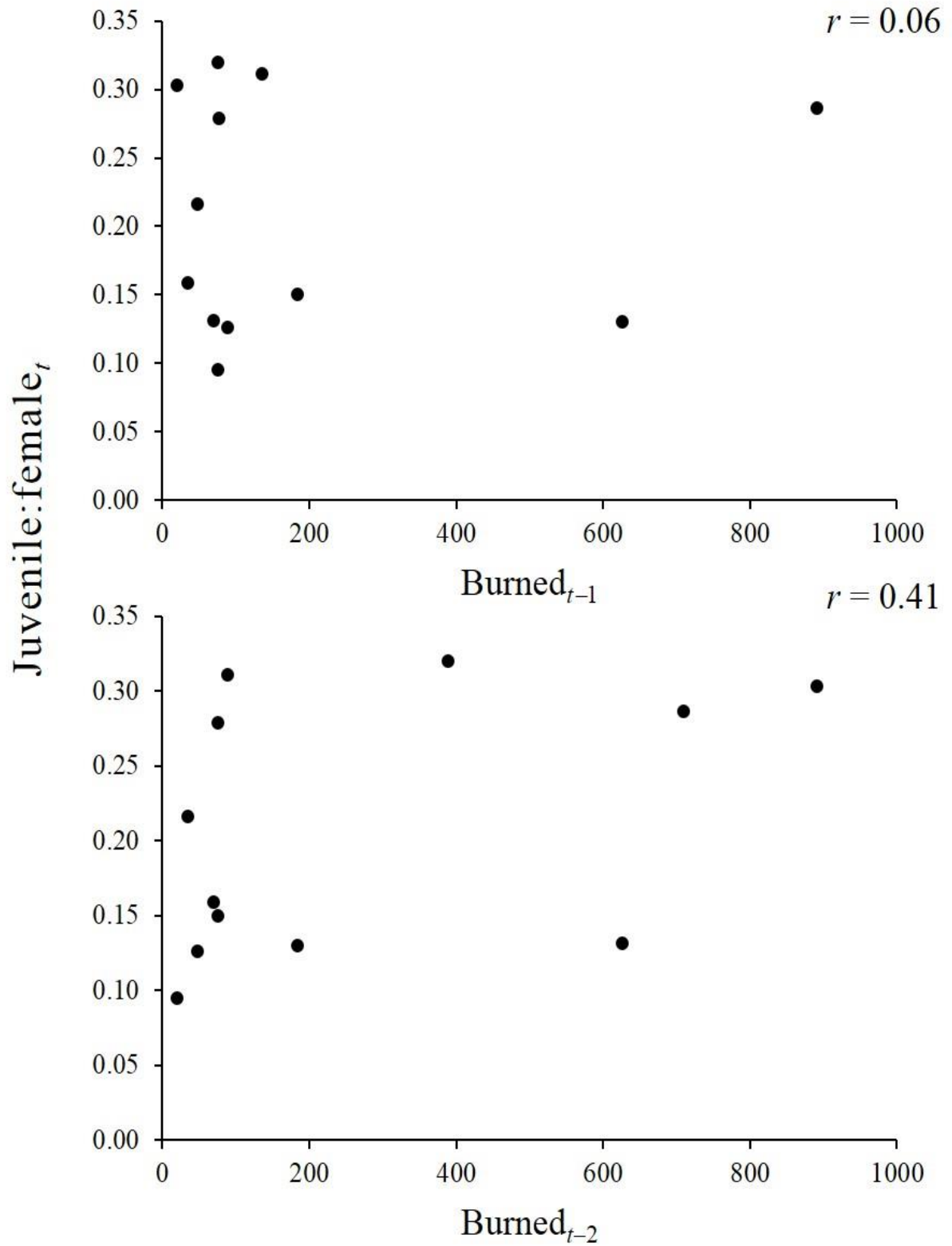Figure 3. Scatter plot illustrating relationship between abundance and juveniles:female ratios

Figure 4. Scatter plot illustrating relationship between burned hectares and juveniles:female ratios
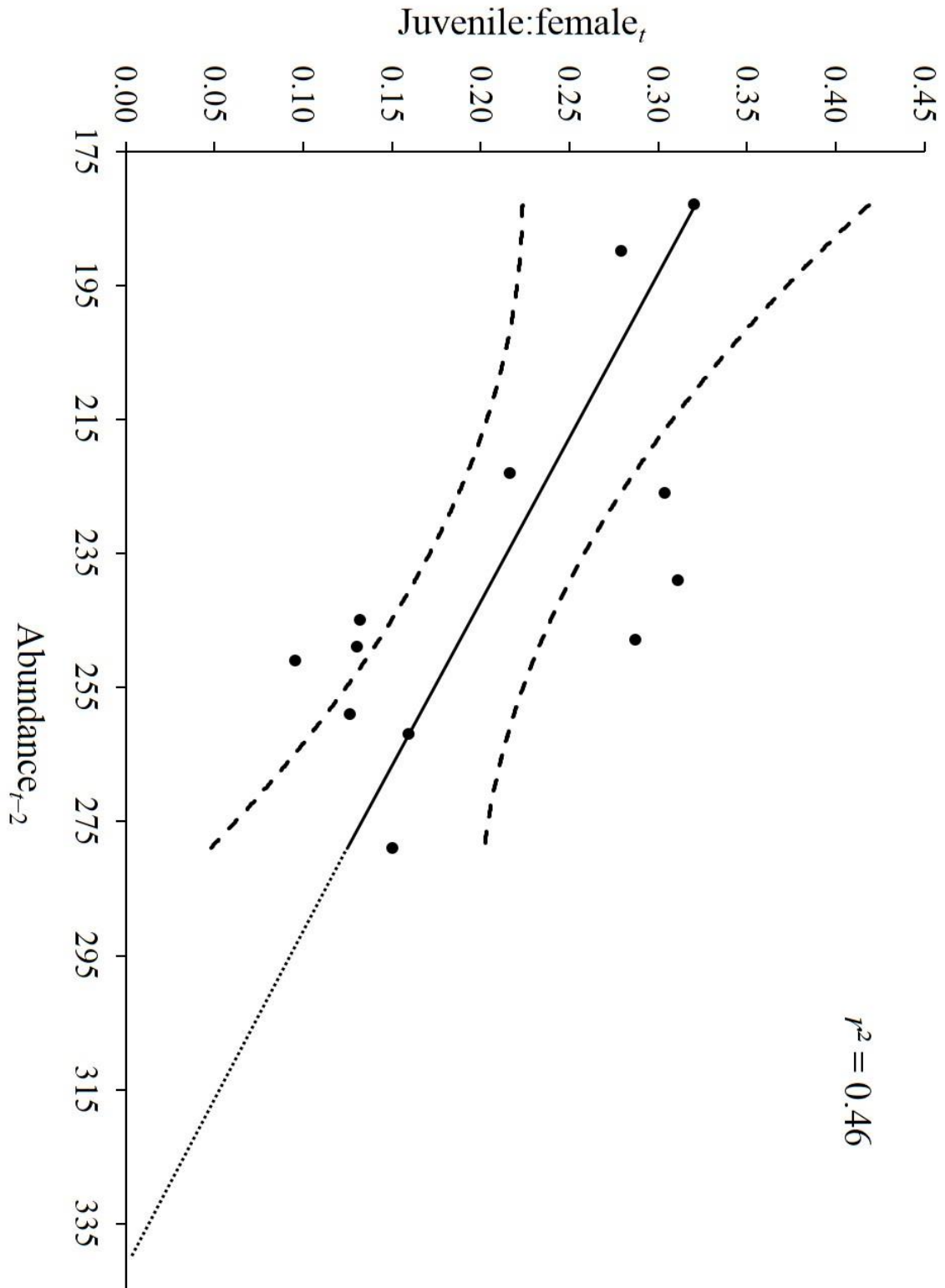
Figure 5. Carrying capacity estimate for Bald Hills, California

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