ELK POPULATION DYNAMICS WHEN CARRYING CAPACITIES VARY

WITHIN AND AMONG HERDS

by

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DEDICATION

For Lucinda, my madrone walking stick. She supported me through it all.

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ABSTRACT

Population and land management relies on understanding population regulation and growth, which may be impacted by variation in carrying capacity (K) within and among populations. I fit linear Ricker growth models using Bayesian statistics to seven time series of population survey data of elk (*Cervus elaphus*). I explored the effects of variation in K among herds (i.e., populations) on temporal variation in the maximum intrinsic population growth rate (r_{max}) and strength of density dependence (β) within herds in a small part of the geographic range of the species. I also estimated stochastic fluctuations in abundance around K for each herd. My results indicate that r_{max} was similar among herds due to similar life history traits, while K and β varied among herds. Also, r_{max} and β varied temporally within herds. Variation in r_{max} is traditionally viewed as being generated from density-independent factors such as climatic variables, but the variation might also be generated from individual movement. I also found that herds with smaller K will have stronger density dependence (i.e., smaller β), higher temporal variation in β within herds, and less fluctuation in abundances around K. Population regulation and the rate of return to the equilibrium abundance is often understood in terms of β, but ecological populations are dynamic systems, and temporal variation in population growth parameters such as K and r_{max} may also influence regulation. Population growth models which accommodate variation both within and among herds in population growth parameters are necessary, even in mild climates, to fully understand population dynamics and manage populations.

I. ELK POPULATION DYNAMICS WHEN CARRYING CAPACITIES VARY

WITHIN AND AMONG HERDS

Introduction

Population regulation is a central concept in population dynamics and is often used in population management and conservation. Regulation of populations is driven by density-dependent factors, the strength of which should impact the time to return to an equilibrium abundance around which the population fluctuates (Lande et al. 2002). This results in a carrying capacity (K) which can be defined as a long-term stationary probability distribution of population abundance (May 1973, Chesson 1982, Dennis and Taper 1994, Turchin 1995). The effects of variation in K within and among populations on regulation have not been fully explored. For example, the factors influencing the dynamics of a population, such as the population growth rate, strength of density dependence (β), and stochastic temporal variation in population abundance, may vary depending on K (Lande et al. 2003). Consequently, estimating K, temporal variation in K, and fluctuations in abundances around K is critical for understanding population dynamics and regulation (Lande et al. 2003, Ahrestani et al. 2016).

A Ricker model is commonly used to approximate population dynamics and estimate population growth parameters for species with slow life histories (Ricker 1954, Fowler 1981, Ferguson and Ponciano 2015). This model predicts a linear growth response such that the intrinsic population growth rate (r) will decrease in a linear fashion as abundance increases. The Ricker model can be written as the following discrete equation (Ricker 1954, Cook 1965):

$$N_{t+1} = \alpha N_t e^{-\beta N_t}, \qquad [1]$$

where N is the population abundance, t is time, and α is the maximum potential population growth rate when the population is not food limited. Although time series of population survey data from free ranging populations might indicate a non-linear relationship between abundance and growth rate (McCullough 1979, Fowler 1981), the simplicity and parsimony of the Ricker model make it an insightful approximating model (Polansky et al. 2009, Clark et al. 2010, Delean et al. 2013).

The implications of using the Ricker model to understand process variance, or actual fluctuations in population abundance, have not been evaluated fully. Process variance is influenced by both demographic and environmental stochasticity, as per the following equation (Lande et al. 2003, Sæther et al. 2008):

$$\sigma_p^2 = \sigma_{e_{DD}}^2 + \sigma_{e_{DI}}^2 + \frac{\sigma_d^2}{N}, \qquad [2]$$

where σ_p^2 is process variance, $\sigma_{e_{DD}}^2$ is density-dependent environmental variance, $\sigma_{e_{DI}}^2$ is density-independent environmental variance, and σ_d^2 is demographic variance. Environmental variance stems from heterogeneous environmental changes. It includes density-dependent effects, which are biotic effects where the population growth rate depends on past or present abundance, and density-independent effects, which capture resource variation and abiotic conditions (Ahrestani et al. 2016). Demographic variance is random changes in demographic rates such as survival and fecundity.

Most current applications of the Ricker model assume that density-independent effects, such as climatic variation, act on the maximum potential intrinsic growth rate ($r_{max} = \ln(\alpha)$) and N simultaneously (Ferguson and Ponciano 2015). As such, density-

independent effects are often assumed to have an additive relationship between r_{max} and

N, which can be expressed as a linear regression:

$$\ln \left(\frac{N_{t+1}}{N_t}\right) = r_t = \ln(\alpha) + \beta N_t + \gamma_1 x_{1,t} + \cdots + \gamma_Z x_{Z,t} + \varepsilon, \qquad [3]$$

where r is the intrinsic population growth rate, $\ln(\alpha)$ is the y-intercept (i.e., r_{max}), β is the

slope, x_1 and x_Z are values of density-independent explanatory variables that induce

temporal variation in r_{max}, whose influence is estimated by γ_1 and γ_Z, and $\mathcal{E}$ is the

residual variance, which is normally distributed. Thus, the additive model captures the

effects of density-independent environmental factors through temporal variation in r_{max},

or changes in the y-intercept, but assumes no variation in β.

The multiplicative model, on the other hand, incorporates density-dependent

effects while assuming little to no influence of density-independent factors on population

abundances. The multiplicative model approximates density-dependent effects by

assuming a multiplicative relationship between r_{max} and N, which can be written as the

following linear regression:

$$\ln \left(\frac{N_{t+1}}{N_t}\right) = r_t = \ln(\alpha) + \beta N_t + \delta_1 x_{1,t} : N_t + \cdots + \delta_Z x_{Z,t} : N_t + \varepsilon, \qquad [4]$$

where the interaction between N and density-independent explanatory variables (i.e.,

$x_{1,t} : N_t$ and $x_{Z,t} : N_t$) indicate density-independent effects augment β (i.e., the slope).

Thus, the multiplicative model assumes that r_{max} will remain constant when K varies, and

as such, the slope of the growth response, which estimates β, will vary when K varies.

In populations where density dependence can be detected, most have been

explained by either the additive (i.e., temporal variation in r_{max}) or multiplicative (i.e.,

temporal variation in β) model (Ferguson and Ponciano 2015). However, it should be

noted that natural population do not necessarily follow either framework. Indeed, it is

possible that population dynamics can be explained by no temporal variation in either parameter or by a combination of temporal variation in both parameters (Bell 1990, Underwood 2007).

The effect of variation in K among populations and temporal variation in K within populations on fluctuations in abundance around K have not been explored. The population dynamics of a species may vary spatially with resource quality and availability, but the population growth parameters are often estimated over a substantial part of a species' geographic range (Turchin and Hanski 1997, Sæther et al. 2008, Street et al. 2015). Across the geographic range of a species, environmental heterogeneity tends to be large, and so is variation in K. Two studies, however, indicate considerable variation in K within a small part of the geographic range (Iijima and Ueno 2016, Weckerly 2017), so variation in β and process variance at this spatial scale seems plausible. Thus, an understanding of population dynamics within a smaller part of the geographic range of a species is needed to fully explore the implications of the Ricker model and its parameters.

I examined seven populations of elk (*Cervus elaphus*) inhabiting northern California and south-central Washington to explore the effect of variation in K among populations within the framework of the additive and multiplicative models. Among populations, I hypothesized that r_{max} would be similar due to populations of a species having similar life history traits, and that K and β would vary among populations. Within populations, I hypothesized that temporal variation will not be detected in either r_{max} or K due to the stable composition of habitats and mild climate. I also estimated the influence of demographic and environmental stochasticity within each population. I hypothesized

that in populations with smaller K, there will be less fluctuation in abundance around K due to strong density dependence. By exploring these hypotheses, my research assesses the influence of variation in K both among and within populations on their dynamics, regulation, and stability. These are important to fully understand, especially in the face of contemporary changes in the environment (May 1973, Ahrestani et al. 2016). Thus, my findings regarding the impacts of K and β on population regulation and fluctuations in abundances around K have implications for population and land management.

Study Areas

Time series of population survey data were used from nonmigratory elk populations in three different locations along the West Coast of the USA (Fig. 1). Five of the populations were in the Prairie Creek drainage (Davison), the Lower Redwood Creek drainage (Levee Soc), the Stone Lagoon area, the Gold Bluffs region, and the Bald Hills region of Redwood National and State Parks (RNSP), Humboldt County, California (41.2132°N, 124.0046°W). These populations occupy an area of about 380 km². The climate in this region was mild, with cool summers and rainy winters. Annual precipitation was usually between 120 and 180 cm and most of the precipitation fell between October and April. Snow was rare since average winter temperatures rarely dropped below freezing and ranged from 3 to 5°C. Average summer temperatures ranged from 10 to 27°C, depending on the distance inland. Elk in RNSP were not legally hunted, and displayed strong social bonding between females, juveniles, and sub-adult males (Weckerly 2017).

An elk population in the Point Reyes National Seashore inhabited part of the Point Reyes Peninsula in Marin County, California (38.0723°N, 122.8817°W). The elk

were restricted to an area of 10.52 km^2 on the northern tip of the peninsula by a 3-m-tall fence. The climate of this study area was Mediterranean, with an average annual precipitation of 87 cm (Cobb 2010). Most of the precipitation fell from autumn to early spring. Temperatures averaged about 7°C in winter and 13°C in summer (Howell et al. 2002, Cobb 2010).

Another elk population was in the Arid Lands Ecology (ALE) Reserve and occupied a 300 km^2 area within the U.S. Department of Energy's Hanford Site, Washington (46.68778°N, 119.6292°W). The climate in this area was semi-arid with dry, hot summers and wet, moderately-cold winters. Average summer temperatures were around 20°C and average winter temperatures were around 5°C with an average annual precipitation of 16 cm, half of which fell in the winter as rain (Stone et al. 1983).

Methods

Population Surveys

In RNSP, females, juveniles, and subadult males were often in the same group and tended to use open meadow habitat more frequently than adult males (Weckerly 1998, Weckerly et al. 2001). These behavioral patterns likely explain why females, juveniles, and subadult males were sighted more frequently than adult males (Weckerly 2017). Moreover, in size-dimorphic ungulates such as elk, recruitment was strongly correlated with female abundance and weakly correlated with male abundance (McCullough 1979, 2001, Weckerly 2017). In RNSP, the abundance of groups of females, juveniles, and subadult males drove the dynamics of the group and of adult males (Weckerly 2017). Therefore, for the RNSP populations, I used herd counts where a

herd was comprised of females, juveniles, and subadult males. I also used herd counts for the Point Reyes and ALE Reserve populations to remain consistent.

Systematic herd surveys of elk were conducted during January from 1997 to 2019 in RNSP. Surveys in the Davison meadows, the Levee Soc area, the Stone Lagoon area, the Gold Bluffs region, and the Bald Hills region were conducted by driving specified routes 4 to 10 times on different days throughout the month of January. The time series for these five herds ranged from 19 to 23 years of data. The elk were counted and classified by age and sex as adult males, subadult males, females, and juveniles. Females could not be visually differentiated into adult and subadult age categories (Weckerly et al. 2001). The highest count of females, juveniles, and subadult males from the surveys conducted each year was used as an index of abundance of each herd since the detection probabilities were high both on an absolute basis (> 0.8) and relative to variation in detection probabilities ($CV_{sighting} = 0.05$) (Johnson 2008, Weckerly 2017). For the Bald Hills herd, which is the only herd in RNSP where harvests occurred, I added hunter harvests to the highest count of each year to account for this source of mortality. These harvests occurred only when elk from the Bald Hills herd left RNSP.

Elk population surveys were conducted at the Point Reyes National Seashore from 1982 to 2008. Weekly surveys were conducted after the mating season. Surveys were conducted on foot or horseback of female elk that were ear-tagged or had a collar containing radio telemetry (Gogan and Barrett 1987, Howell et al. 2002). Individuals counted were classified as females, juveniles, subadult males, and adult males. Data were not available for the years 1984 to 1989 and 1993, so the time series included 20 years of data. I used the highest count in each year in my analyses. This herd was not hunted.

Elk population surveys in the ALE Reserve were conducted in winters after hunting and before parturition. From 1982 to 2000, biologists used aerial telemetry studies, in which they located all collared elk during each survey. For years in which multiple surveys were conducted, I used the highest count in each year as an index of abundance for that year (McCorquodale et al. 1988, Eberhardt et al. 1996). I omitted population survey data collected in 1982 from my analysis because unusually low population counts suggest that they may be exceptionally biased by observer error. I also excluded population survey data collected in 2000 and thereafter. A wildfire occurred in the summer of 2000 and burned practically all of the available vegetation in the ALE Reserve, which likely had an immediate effect of reducing available elk forage in the reserve and caused elk to spend more time outside of the ALE Reserve (Tiller et al. 2000, Anonymous 2002). In addition, the highest recorded number of elk (about 291) were harvested that year (Tiller et al. 2000). The change in available resources and relatively high hunter harvest in 2000 might have altered K and r of the ALE Reserve elk herd. Consequently, the time series included 17 years of data. For all years of data used, I added hunter harvests to the highest count of each year to account for this source of mortality.

Ricker Growth Models

I fit Ricker growth models to each of the time series to estimate population growth parameters as well as temporal variation in r_{max} and β. I estimated K as the x-intercept of the Ricker growth model for each iteration to incorporate uncertainty associated with each model parameter. Notably, preliminary analyses showed that not accounting for observer error did not bias my results (see Appendix).

I used Bayesian statistics and Markov Chain Monte Carlo algorithms with 3 chains, 150,000 iterations, a burn-in period of 75,000, an adaptation period of 75,000, and no thinning. I conducted these analyses in the RJAGS program in RStudio (R Version 3.5.0, www.r-project.org, accessed 26 April 2018; JAGS Version 4.0.0, www.sourceforge.net, accessed 24 January 2018). Convergence among chains was determined by whether $\hat{R} < 1.01$ and visual checks of trace and density plots (Kery 2010). I used uninformative priors for the y-intercept (i.e., r_{max}) and the slope (i.e., β) (Fig. 2). The estimate of r_{max} borrowed information among herds because this parameter should be similar among populations within a species (Street et al. 2015). Therefore, I modeled r_{max} for each herd (j) as a random effect following a normal distribution with $\mu_{r_{max}} \sim Normal(0, 0.001)$ and $\sigma_{r_{max}} \sim Uniform(0, 100)$. To model temporal variation in r_{max} for each herd, I included an additive term which was also modeled following the normal distribution $\gamma_{t,j} \sim Normal(0, \sigma_{\gamma_j})$, where $\sigma_{\gamma_j} \sim Uniform(0, 100)$. The estimate of β did not borrow information among herds because this parameter can vary widely among herds (Sæther et al. 2008). I modeled β for each herd (j) following the normal distribution $\beta_j \sim Normal(0, 0.001)$. I also modeled temporal variation in β for each herd with the normal distribution $\beta_{\delta_{t,j}} \sim Normal(\mu_{\beta_{\delta_j}}, \sigma_{\beta_{\delta_j}})$, where $\mu_{\beta_{\delta_j}} \sim Normal(0, 0.001)$ and $\sigma_{\beta_{\delta_j}} \sim Uniform(0, 100)$. Thus, there were four possible Ricker growth models for each herd; no temporal variation in r_{max} or β, represented by

$$r_{t,j} = r_{max_j} + \beta_j N_{t,j} + \varepsilon_{t,j}, \tag{5}$$

temporal variation in r_{max},

$$r_{t,j} = r_{max_j} + \beta_j N_{t,j} + \gamma_{t,j} + \varepsilon_{t,j}, \tag{6}$$

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temporal variation in β,

$$r_{t,j} = r_{max\,j} + \beta_{\delta\,t,j}N_{t,j} + \varepsilon_{t,j}, \qquad [7]$$

and temporal variation in both r_{max} and β,

$$r_{t,j} = r_{max\,j} + \beta_{\delta\,t,j}N_{t,j} + \gamma_{t,j} + \varepsilon_{t,j}, \qquad [8]$$

where $N_{t,j}$ was the observed population abundance of herd j in each year t. and $\varepsilon_{t,j}$ was

modeled as $\varepsilon_{t,j} \sim Uniform(0,100)$. I fit each growth model to each time series while

modeling all other time series with no temporal variation in r_{max} or β. The model with the

lowest mean deviance by more than 2 was selected for each herd to determine if models

with more parameters provided a better fit. (Peterson and Barajas 2018).

Environmental and Demographic Stochasticity

I estimated fluctuation in abundance which can be attributed to demographic and

environmental stochasticity for herds with different K. The stochasticity model was

outlined by Ferguson and Ponciano (2015);

$$Var_j(N_{t-1,j}) = Var_{dem_j}(N_{t-1,j}) + Var_{r_{max\,j}}(N_{t-1,j}) + Var_{\beta_j}(N_{t-1,j}), \quad [9]$$

where $Var_j(N_{t-1,j})$ was total population stochasticity, $Var_{dem_j}(N_{t-1,j})$ was population

abundance fluctuation due to demographic stochasticity, $Var_{r_{max\,j}}(N_{t-1,j})$ was

population abundance fluctuation due to changes in r_{max} (i.e., density-independent

environmental stochasticity), and $Var_{\beta_j}(N_{t-1},j)$ was population abundance fluctuation

due to changes in β. The model assumes density-dependent survival following the Ricker

model. Demographic stochasticity was calculated as follows;

$$Var_{dem_j}(N_{t-1,j}) = \alpha_j N_{t-1,j} e^{-\beta_{\Delta_j}(N_{t-1,j})}\left(1 - e^{-\beta_{\Delta_j}(N_{t-1,j})}\right) +$$

$$\sigma_{dem_j}^2 N_{t-1,j} e^{-2\beta_{\Delta_j}(N_{t-1,j})}, \qquad [10]$$

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where $\sigma^2_{dem_j}$ was assumed to be equal to α (Ferguson and Ponciano 2015).

Environmental stochasticity due to changes in r_{max}, or the additive stochasticity, was calculated as follows;

$$Var_{r_{max_j}}(N_{t-1,j}) = \sigma^2_{\beta_{\Delta_j}} \alpha^2_j N^2_{t-1,j} e^{-2\beta_{\Delta_j}(N_{t-1,j})}, \qquad [11]$$

and environmental stochasticity due to changes in β, or the multiplicative stochasticity, was calculated as follows;

$$Var_{\beta_j}(N_{t-1},j) = \sigma^2_{\beta_{\Delta_j}} \alpha^2 N^2_{t-1,j} (N_{t-1,j})^2 e^{-2\beta_{\Delta_j}(N_{t-1,j})}. \qquad [12]$$

Population growth parameters from the selected Ricker growth model for each herd were used in these equations to estimate each of these sources of stochasticity for each herd across abundances ranging from five to above K. The relative total population stochasticity was expressed as the total population stochasticity at K for each herd divided by that herd's K.

Results

The growth models estimated the mean r_{max} among herds to be 0.231 (95% credible interval = [0.151, 0.345]), and the standard deviation of r_{max} among herds to be 0.045 (0.002–0.223). The growth model with temporal variation in both r_{max} and β was selected for the five herds in RNSP (Table 1, Fig. 3). The growth model with temporal variation only in β was selected for the Point Reyes herd. Using the selected growth model for the ALE Reserve herd, I did not detect density dependence, so K could not be estimated (Table 2). Consequently, I omitted this herd from subsequent analyses.

Density dependence was strongest in herds with smaller K and weakest in herds with larger K, and this relationship was non-linear (Fig. 4). Density dependence appeared to be much stronger in herds whose $K < 100$. Similarly, temporal variance in β was

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greater in herds with smaller *K* than larger *K*, and this relationship was also non-linear

(Fig. 5). Within herds, it appeared that a constant change in *K* affected temporal variation

in density dependence in herds with smaller *K* more than herds with larger *K*. A positive,

non-linear correlation was detected between *β* and the relative total stochasticity (Fig. 6),

such that herds with smaller *K* experienced less fluctuation in abundances than herds with

larger *K*. For the relative influence of demographic, density-dependent, and density-

independent sources of stochasticity, see Appendix (Fig. A2).

Discussion

Variation in *K* and *β* is an important consideration in population persistence,

especially in the face of current environmental change (May 1973, Ahrestani et al. 2016).

As I had expected, I found variation in *K* among herds within a small part of the species'

geographic range, but I also unexpectedly found variation in *K* within herds. As such, in

order to fully understand population dynamics and regulation, parameters that can

accommodate stochastic environments should be incorporated into models (May 1973,

Fowler and Pease 2010). Assuming constant *K* is probably unrealistic even when

environments seem to be mild and stable.

Environmental heterogeneity and variation in *K* among populations is expected

across a species' geographic range, or from the interior to the boundary of the range

(Sæther et al. 2008, Street et al. 2015). My findings, which were from herds with clear

spatial boundaries, suggest that similar variation in *K* among herds can manifest within a

small part of the species geographic range. Within RNSP, forage supply varies both

across herd home ranges and temporally, which can affect *K* (Weckerly 2017). Also,

social dynamics between herds can impact elk movement and *K*. For example, meadow

partitioning in RNSP is presumably enforced by social fences between herds, or when elk avoid interacting with unfamiliar individuals from other herds. This meadow partitioning can dictate the amount of forage available to each herd and, consequently, K and β (Weckerly 2017).

Herds with smaller K had stronger density dependence, and this relationship was non-linear. Stronger density dependence in herds with smaller K then resulted in less stochastic fluctuations in abundance than herds with larger K. Strong direct (i.e., not lagged) density dependence was also shown to increase stability in several elk populations in the northern hemisphere (Ahrestani et al. 2016). Probably due to the non-linear relationship between K and β, herds with smaller K also had higher temporal variation in β. In other words, for the same change in K over time, β will change more in a herd with smaller K than one with larger K.

These findings have implications for population and land management. For example, increasing available resources, such as forage, for a herd will increase its K and decrease β, such that the population may experience more fluctuations, which reduces population stability. Changes in resource availability can occur by several means. For example, temporal variation in K likely occurred in the Davison herd when the land area available to the herd for foraging increased when cattle were removed from a meadow (Weckerly 2017, McGuire 2018). In contrast, the area available for foraging to the Point Reyes herd could not change because of a fence that restricted the herd to a limited area. Nonetheless, annual precipitation in Point Reyes was highly variable and was correlated with calf recruitment (Cobb 2010). Thus, variation in precipitation likely resulted in variation in the amount of forage available and, therefore, temporal variation in K.

Increasing available resources or introducing a population to a new range may even lead to an irruption and overshoot of a herd's food supply (Forsyth and Caley 2006, Ricca et al. 2014, Starns et al. 2014, Weckerly 2017). My results suggest that populations with smaller K are more vulnerable to destabilizing dynamics. This is because a constant change in K should affect β and temporal variation in β more dramatically in herds with smaller K.

While K and β varied among herds, the standard deviation of r_{max} among herds was small, suggesting that herds of the same species may have similar r_{max}. This finding is further supported by the overlap in 95% credible intervals of the estimates of r_{max} for each herd. This may be influenced by the random effect parameterization, which can pull point estimates towards the mean. However, this result is also expected because herds of the same species, when not limited by forage, should have similar life history traits such as age of first reproduction, litter size, and frequency of reproduction (Weckerly 2017). On the other hand, r_{max} varied temporally within some herds, which was an unexpected result. Temporal variation in r_{max} was detected in RNSP herds, but not in the Point Reyes herd, and the amount of temporal variation in r_{max} did not appear to be related to K. The within-herd temporal variation in r_{max} in RNSP herds was surprising considering that this study area had a stable habitat composition and mild climate. Furthermore, density-dependent climatic factors did not influence juvenile recruitment in the Davison herd (Starns et al. 2014, Weckerly 2017). While density-independent factors are often described as climatic factors (Bowyer et al. 2014), they can in fact be a number of abiotic factors (Ahrestani et al. 2016), and can even include movement of individuals into or out of a population. Weckerly (2017) describes temporal variation in r_{max} due to immigration

in the Davison herd. The Davison meadows were grazed by cattle and unavailable to elk until 1991. Elk began using these meadows in 1991 when the cattle were removed, and by 1996, when population surveys began, herd abundance was such that immigration must have occurred to explain the enormously high estimate of r_{max} during that period (Weckerly 2017). In 2016, a new pasture, which had also previously been grazed by cattle and unavailable to elk, became accessible to the Davison herd (McGuire 2018). With the increase in forage, the herd grew in abundance, and r_{max} in this time period is lower than in the 1990s. These two estimates of r_{max} represents temporal variation in r_{max} in the Davison herd due to elk movement.

Temporal variation in r_{max} in the Point Reyes herd, on the other hand, was not detected. This may be because this herd also experienced a relatively stable and mild climate, and the elk were restricted on the peninsula by a well-maintained fence. Consequently, individual immigration and emigration was unlikely in this herd (Howell et al. 2002, Cobb 2010). Therefore, neither climatic factors nor elk movement generated temporal variation in r_{max} in this herd. These findings can be used in population conservation and management. Populations which are restricted by a fence or are otherwise isolated from other conspecific populations should be expected to have less temporal variation in r_{max} because of no immigration or emigration occuring. Furthermore, estimating r_{max} may be a method to determine whether net immigration into a population is occurring by comparing the r_{max} estimate for the population in question to the expected r_{max} for the species.

My interpretations depend on reliable estimates of population growth parameters. Estimates from the Ricker growth model appeared to be credible for the species and

preliminary analyses showed that not accounting for observer error in the Ricker growth

models did not bias the parameter estimates by comparing them to a Ricker state-space

model (see Appendix). Time series of population survey data almost always include

observer error, which can bias inferences of population dynamics (de Valpine and

Hastings 2002, Clark and Bjørnstad 2004, Delean et al. 2013). Bayesian state-space

models are frequently used to separate observer error from process variance (de Valpine

2003, Clark and Bjørnstad 2004, Sæther et al. 2008, Iijima and Ueno 2016, Robinson et

al. 2017). Nonetheless, the similarity in parameter estimates between my state-space

models and growth models indicate parameter estimates from the growth models might

have little bias and that there was little to moderate observer error in the time series I

analyzed. The small amount of observer error in these time series might be the result of

several features in the time series. First, data were collected by ground surveys, which

tend to have less observer error for ungulate populations than other survey methods

(Ahrestani et al. 2013). Second, the length of time series of ungulate population survey

data has been found to be negatively correlated with observer error (Ahrestani et al.

2013), and the time series used in my analyses were all relatively long (17 to 23 years).

Third, data from these time series were collected by experienced and trained observers

over decades, which can reduce observer error (Ahrestani et al. 2013). In the RNSP

herds, while there were multiple observers throughout the years, one observer was

present for all population survey data collected (Weckerly 2017), which may result in

lower observer error than data collected by multiple observers with little training (Dennis

et al. 2006). Additionally, in four of the five RNSP herds, the elk were seemingly

habituated to human presence, which decreased the distance between observers and elk,

and increased the ease of detecting elk (Weckerly 2017). Finally, the Point Reyes herd is a geographically closed population (Howell et al. 2002, Cobb 2010), and counts of geographically closed populations tend to be more precise and accurate (Ahrestani et al. 2013).

Variation in K and the consequences to population dynamics have usually been examined among populations (Sæther et al. 2008) or within populations (Fowler and Pease 2010). I simultaneously examined variation in K both within and among populations. As such, my findings add a dimension to understanding population regulation. Some of my findings reinforce what has been shown; variation in K among populations affected β and fluctuation in abundances around K. The added dimension of temporal variation in K within populations revealed that the amount of variability in β within a population is also affected by median K. Populations with small K can have greater variation in β, which has consequences for population stability. Furthermore, population regulation is often understood in terms of the rate of return to the equilibrium abundance (Lande et al. 2002), which is calculated using β. However, temporal variation in r_{max} might complicate this relationship between K, β, and regulation. Therefore, considering temporal variation in population growth parameters is necessary to understand population regulation.

Table 1. Mean deviance for each of the four possible Ricker growth models for each herd; no temporal variation in the maximum intrinsic population growth rate (r_{max}) or strength of density dependence (β), temporal variation in r_{max}, temporal variation in β, and temporal variation in both r_{max} and β. The asterisks denote the model with the lowest mean deviance by more than 2; this model was selected.

Herd	No temporal variation	r_{max} temporal variation	β temporal variation	Both temporal variation
Gold Bluffs	-139.56	-167.13	-155.15	-175.23*
Davison	-139.56	-165.47	-149.14	-172.50*
Levee Soc	-139.56	-166.68	-155.80	-161.44*
Stone Lagoon	-139.56	-161.37	-158.96	-170.60*
Bald Hills	-139.56	-167.40	-152.88	-175.84*
Point Reyes	-139.56	-165.03	-186.04*	-181.80
ALE Reserve	-139.56	-160.40*	-139.67	-160.73

Table 2. Population growth parameter estimates by the selected Ricker growth model for each herd; median and 95% credible intervals. The maximum intrinsic population growth rate is r_{max} and strength of density dependence is β. The asterisks denote 95% credible intervals that overlap 0, i.e., β and K could not be estimated.

Herd	r_{max}	r_{max} temporal variation	β	β temporal variation	K
Gold Bluffs	0.235 [0.114, 0.418]	0.128 [0.006, 0.282]	-0.01110 [-0.01934, -0.00407]	0.00483 [0.00026, 0.01198]	22 [14, 39]
Davison	0.219 [0.054, 0.349]	0.120 [0.009, 0.235]	-0.00538 [-0.00943, -0.00083]	0.00161 [0.00008, 0.00562]	40 [24, 82]
Levee Soc	0.237 [0.114, 0.459]	0.082 [0.003, 0.171]	-0.00479 [-0.00933, -0.00188]	0.00108 [0.00003, 0.00328]	50 [38, 74]
Stone Lagoon	0.246 [0.142, 0.494]	0.059 [0.003, 0.138]	-0.00474 [-0.00895, -0.00262]	0.00096 [0.00005, 0.00234]	53 [42, 67]
Bald Hills	0.235 [0.144, 0.354]	0.072 [0.004, 0.163]	-0.00089 [-0.00147, -0.00038]	0.00035 [0.00002, 0.00076]	268 [198, 453]
Point Reyes	0.221 [0.162, 0.305]	-	-0.00058 [-0.00097, 0.00021]	0.00047 [0.00004, 0.00078]	386 [262, 883]
ALE Reserve	0.212 [0.121, 0.290]	0.088 [0.005, 0.173]	-0.00007* [-0.00043, 0.00029]	-	942* [-17181, 18106]
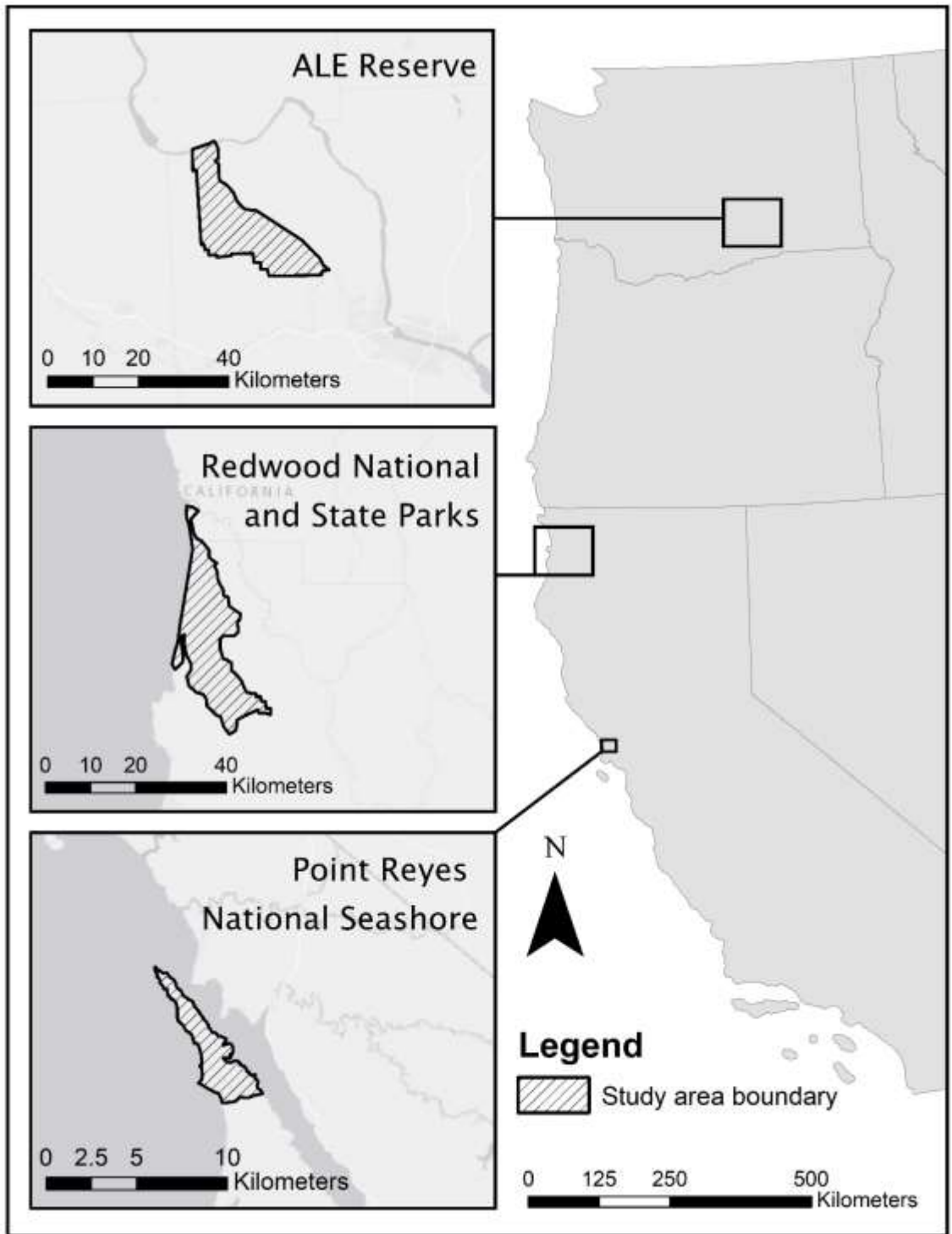
Figure 1. Map of study areas; Arid Lands Ecology (ALE) Reserve, southern part of Redwood National and State Parks, and Tomales Point Elk Reserve in Point Reyes National Seashore.
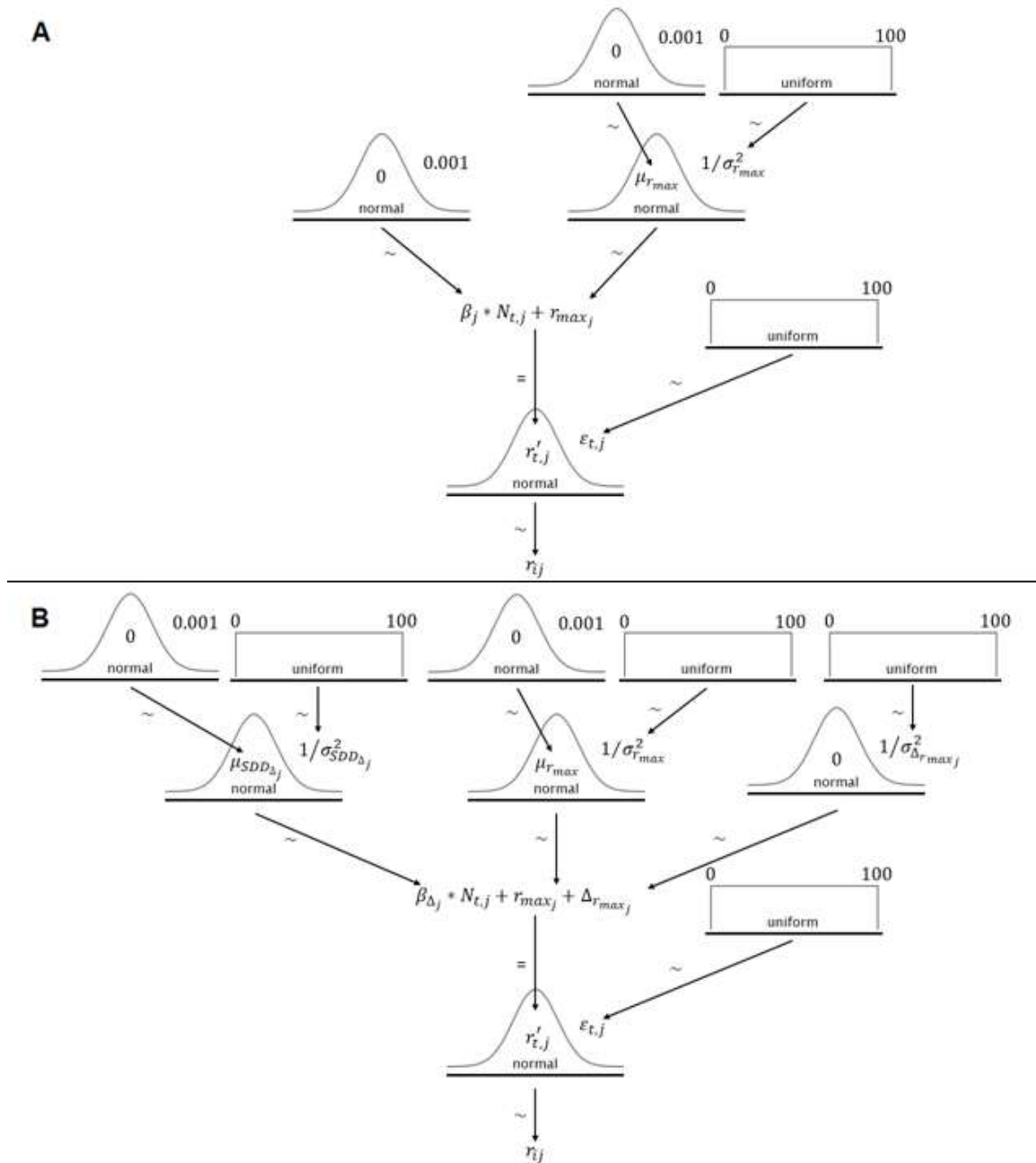
Figure 2. Diagram of parameters and priors for the Ricker growth models; with no temporal variation in either maximum intrinsic population growth rate (r_{max}) or strength of density dependence (β) (A), and with temporal variation in both r_{max} and strength of density dependence (B).
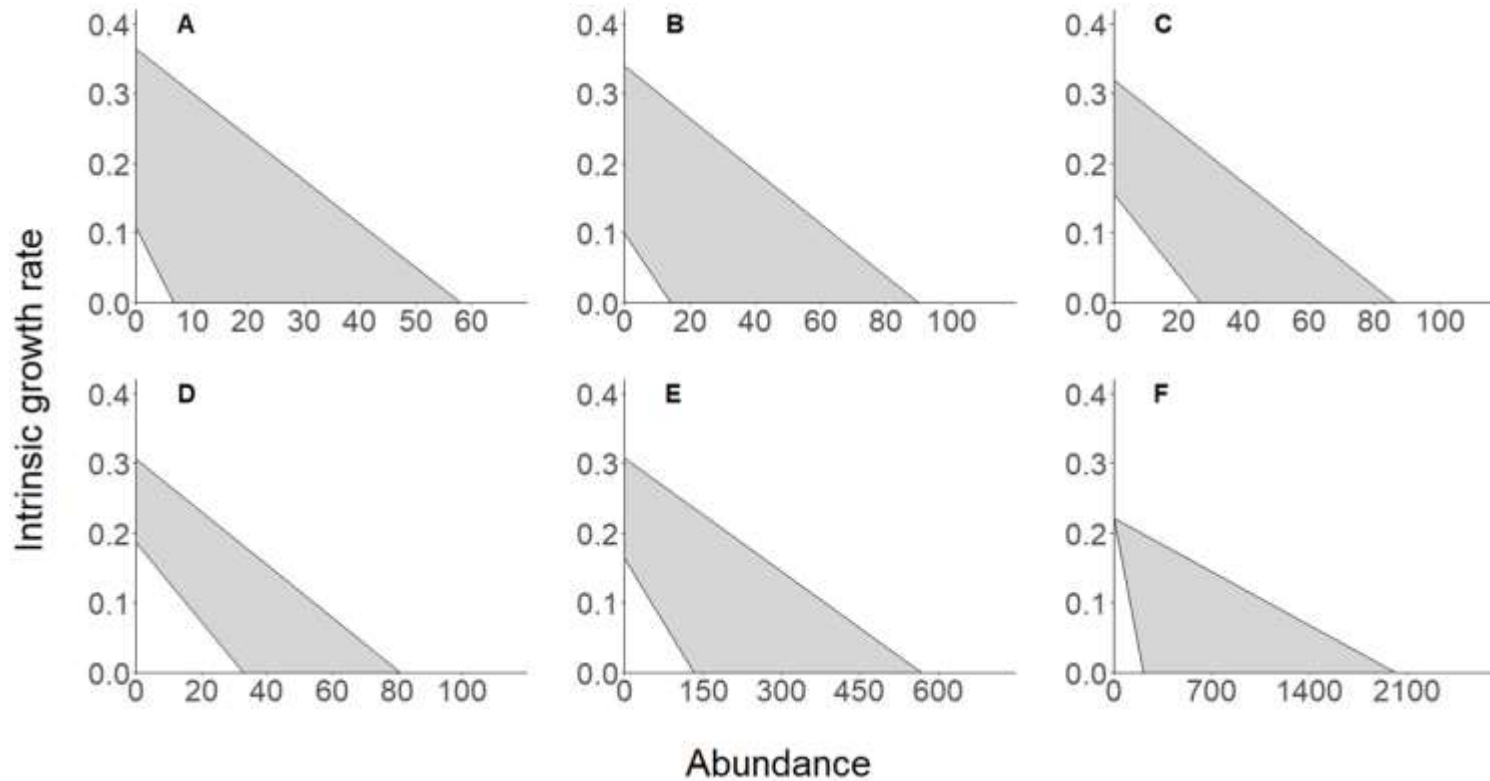
Figure 3. The fitted Ricker growth models for six elk herds; Gold Bluff (A), Davison (B), Levee Soc (C), Stone Lagoon (D), Bald Hills (E), and Point Reyes (F). The grey shaded areas represent temporal variation in the selected for each herd; in maximum intrinsic population growth rate (r_{max}) and the strength of density dependence (β) (A-E) or only in β (F). The x-intercept represents the carrying capacity (K).
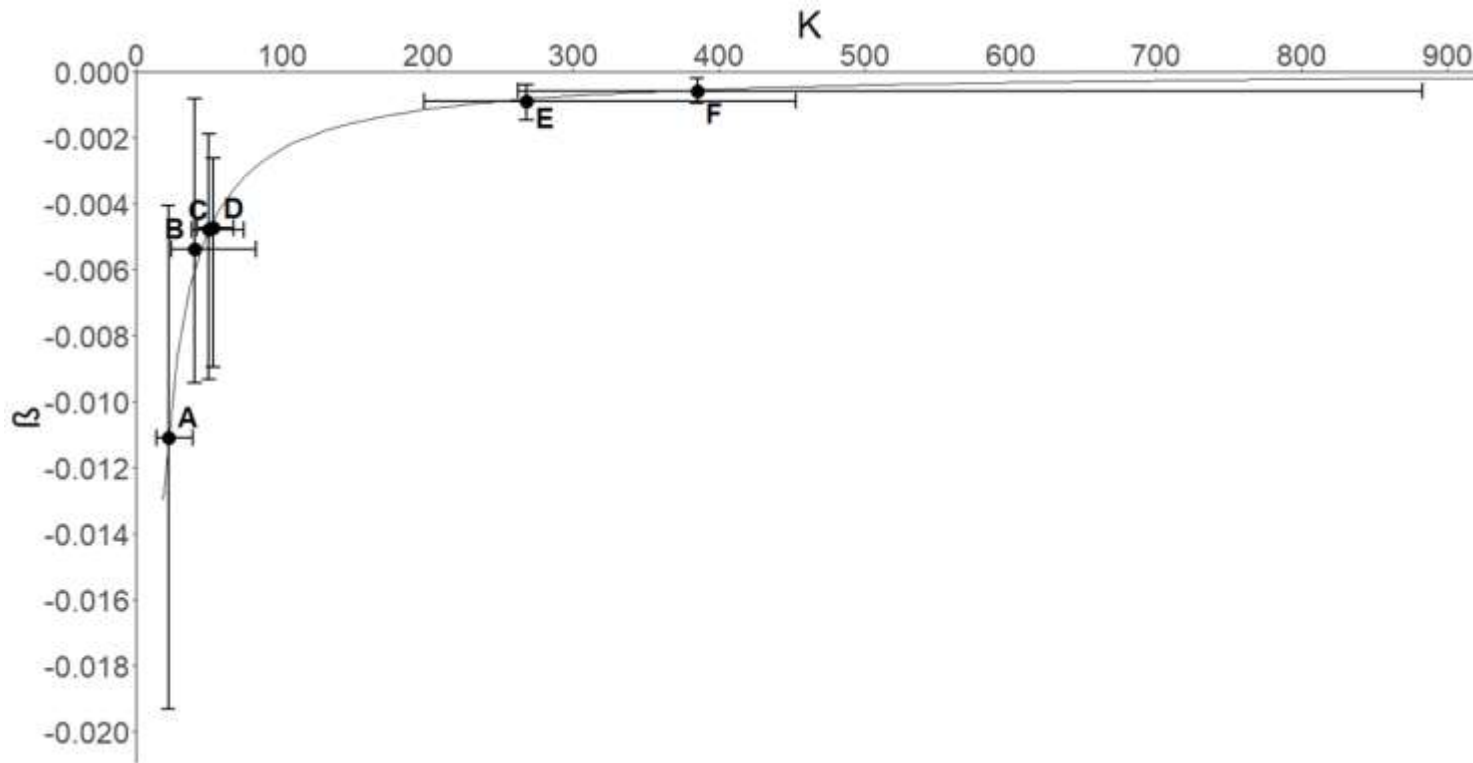
Figure 4. Strength of density dependence (β) and carrying capacity (K) for six elk herds. Letter designations are the same as in Figure 1. A smaller value of β indicates stronger density dependence. The estimated regression was $density\ dependence = \frac{-0.2417}{K} + 0.00008$ ($R^2 = 0.9938$, P < 0.001). Error bars represent 95% credible intervals for K and β.
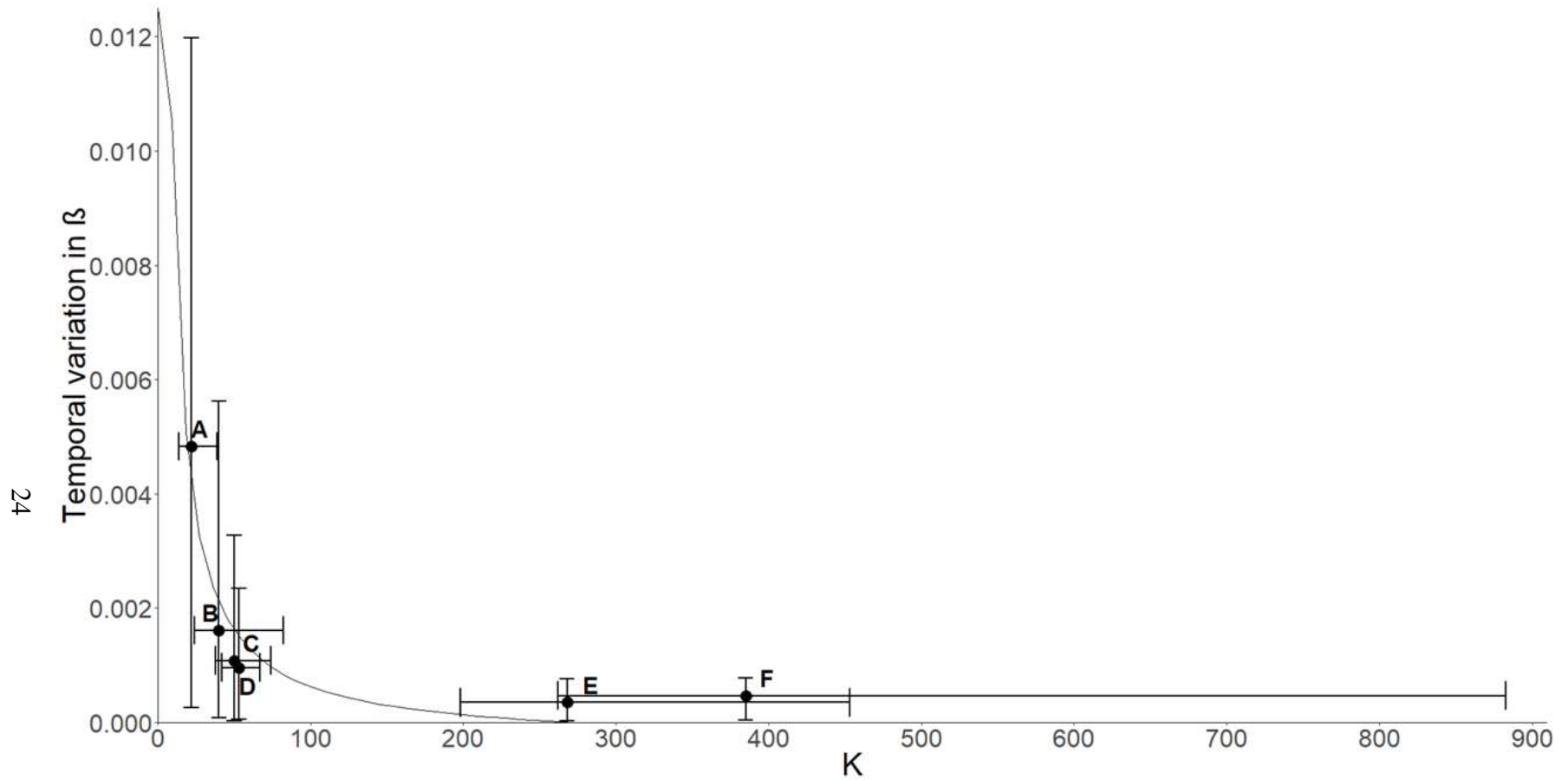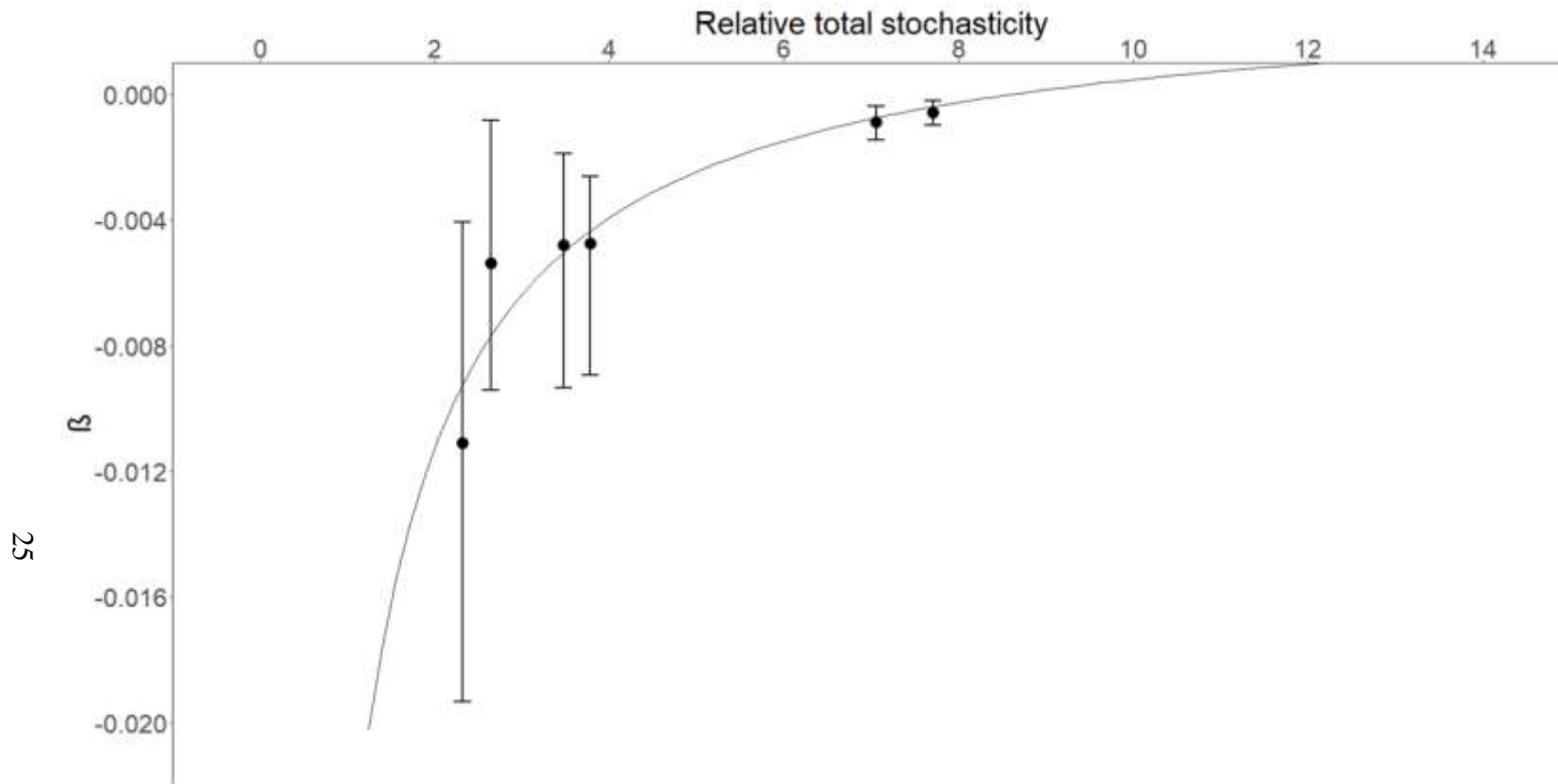
Figure 5. Temporal variation in strength of density dependence (β) and carrying capacity (K) for six elk herds. Letter designations are the same as in Figure 1. The estimated regression was $temporal\ variation\ in\ strength\ of\ density\ dependence = \frac{0.099}{K} - 0.00036$ ($R^2 = 0.8732$, P $= 0.006$). Error bars represent 95% credible intervals for K and temporal variation in β.

Figure 6. Strength of density dependence (β) and relative total stochasticity for six elk herds. Letter designations are the same as in Figure 1. A value for β further from zero indicates stronger density dependence. The estimated regression was $\beta = \frac{-0.0293}{relative\ total\ variance} + 0.0034$ ($R^2 = 0.8764$, P = 0.006). Error bars represent 95% credible intervals for β. My calculation of the relative total variance did not include an estimate of variance.

APPENDIX SECTION

State-Space Model Methods

Since the Ricker growth models described in this paper do not account for

observer error, I used hierarchical models in a state-space formulation to distinguish

observer error (i.e., measurement and sampling errors) from process variance in herd

counts (de Valpine and Hastings 2002, de Valpine 2003, Clark and Bjørnstad 2004). I

then compared the results of the growth models with the state-space model to verify that

observer error was not biasing my results. I modeled observer error using a Poisson

distribution such that $N_{o_{ij}} \sim Poisson(N_{e_{ij}})$, where $N_{o_{ij}}$ is the count in year i from the

survey of herd j and $N_{e_{ij}}$ is the estimated true abundance from year i of herd j. I selected

the Poisson distribution since larger herds tend to increase the probability of double-

counting individuals or missing individuals that were obscured by other animals,

vegetation, or terrain (Weckerly 2017).

I fit the Ricker model using Bayesian statistics and Markov Chain Monte Carlo

algorithms with three chains, 150,000 iterations, a burn-in period of 75,000, an adaptation

period of 75,000, and no thinning. Convergence among chains was determined by

whether $\hat{R} < 1.01$ and visual checks of trace and density plots (Kery 2010). I used

uninformative priors for r_{max} and K. I modeled r_{max} for each herd as a random effect

following the normal distribution $r_{max} \sim Normal(\mu_{r_{max}}, \sigma_{r_{max}})$, where

$\mu_{r_{max}} \sim Normal(0, 0.001)$ and $\sigma_{r_{max}} \sim Uniform(0, 100)$. I modeled K using a gamma

distribution (shape = 0.01, rate = 0.01). When estimating the models, I drew the

population abundance in the first year from a Poisson distribution with stochasticity

included, such that $N_{e_{1j}} \sim Poisson(\lambda)$ and $\lambda = Uniform(N_{o_{1j}} - 5, N_{o_{1j}} + 5)$ where

$N_{e_{1j}}$ was the estimated abundance in the first year of herd j and $N_{o_{1j}}$ was the count for the

first year of herd j. If $N_{o_{1j}} - 5 < 1$, it was rounded to 1. I used this initial abundance of

each herd to estimate abundance in year i ($N_{e_{ij}}$) for the next n_j years, where n_j is the

number of years of population survey data for herd j, using the Ricker model.

State-Space Model Results

The state-space model estimated the mean r_{max} among herds to be 0.228 (95%

credible interval = [0.094, 0.332]), and the standard deviation of r_{max} among herds to be

0.068 (95% CI = [0.003, 0.279]). For parameter estimates, see Table A1.

The 95% credible intervals of parameters estimated by the Ricker growth models

(Table 1) and the Ricker state-space model (Appendix, Table A1) overlapped. This

finding indicates that the results of the growth models were similar to the results of fitting

the state-space models, which distinguished observer error from process variance.

Furthermore, the 95% credible intervals of each of the abundance estimates of the Ricker

state-space model overlapped the abundance survey data, except one year for the Bald

Hills herd and two years in the Point Reyes (Appendix, Fig. A1). Thus, because the state-

space model was in agreement with the data and the growth models were in agreement

with the state-space model, the growth model estimates were likely to be little biased by

observer error.

Table A1. Estimates (median) and 95% credible intervals of the maximum intrinsic population growth rate (r_{max}) and carrying capacity (K) by the state-space model for each herd.

| Herd	r_{max}	K
Gold Bluffs	0.230 [0.015, 0.425]	22 [11, 40]
Davison	0.194 [-0.025, 0.319]	44 [13, 113]
Levee Soc	0.223 [-0.007, 0.427]	51 [24, 94]
Stone Lagoon	0.242 [0.028, 0.513]	53 [33, 70]
Bald Hills	0.205 [0.122, 0.273]	266 [229, 336]
Point Reyes	0.245 [0.176, 0.320]	367 [318, 447]
ALE Reserve	0.257 [0.209, 0.311]	991 [747, 1401]

Figure A1. Population survey data (stars) and estimates of abundance from the Ricker model (circles) for seven elk herds; Gold Bluff (A), Davison (B), Levee Soc (C), Stone Lagoon (D), Bald Hills (E), Point Reyes (F), and ALE Reserve (G). Error bars represent the 95% credible intervals for each abundance estimate.
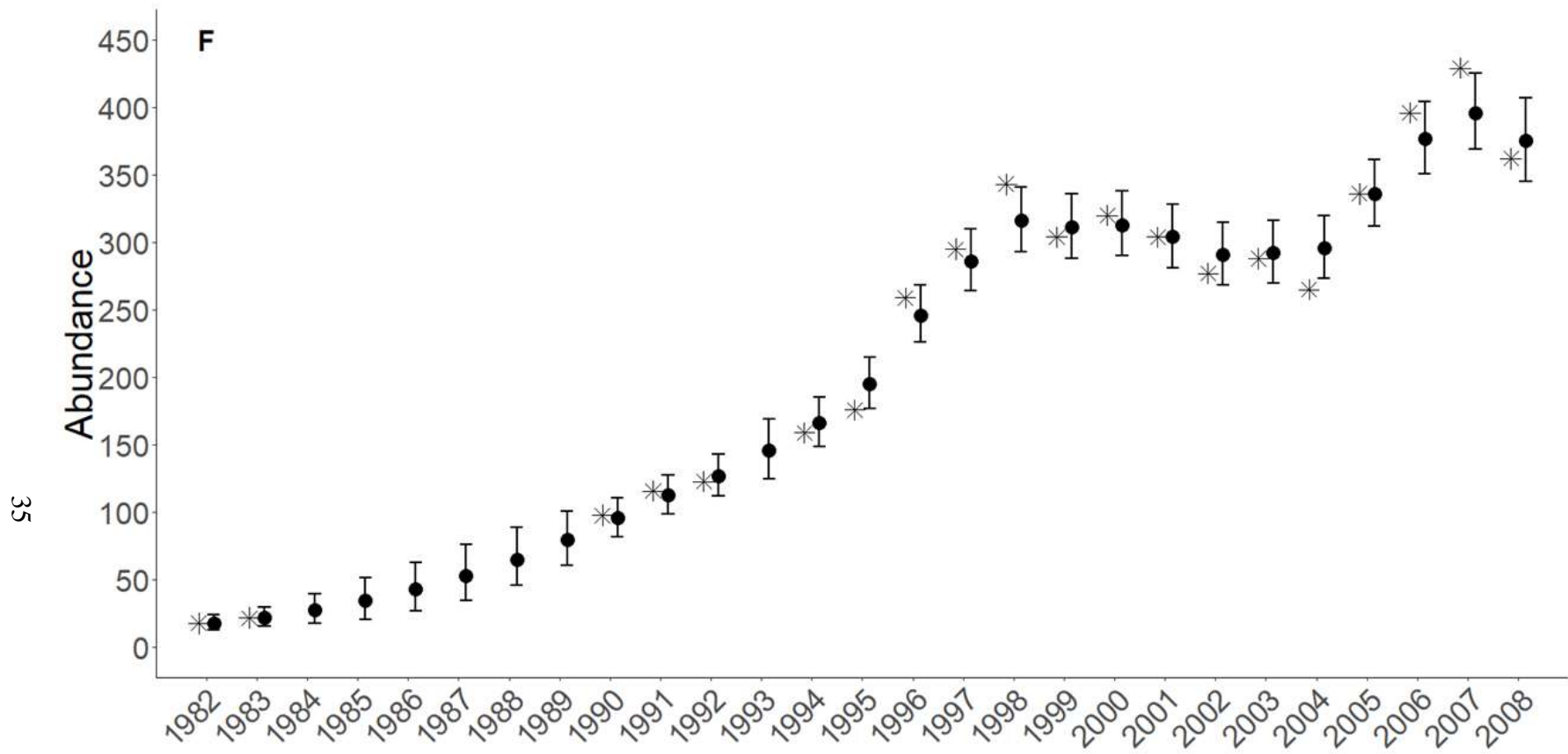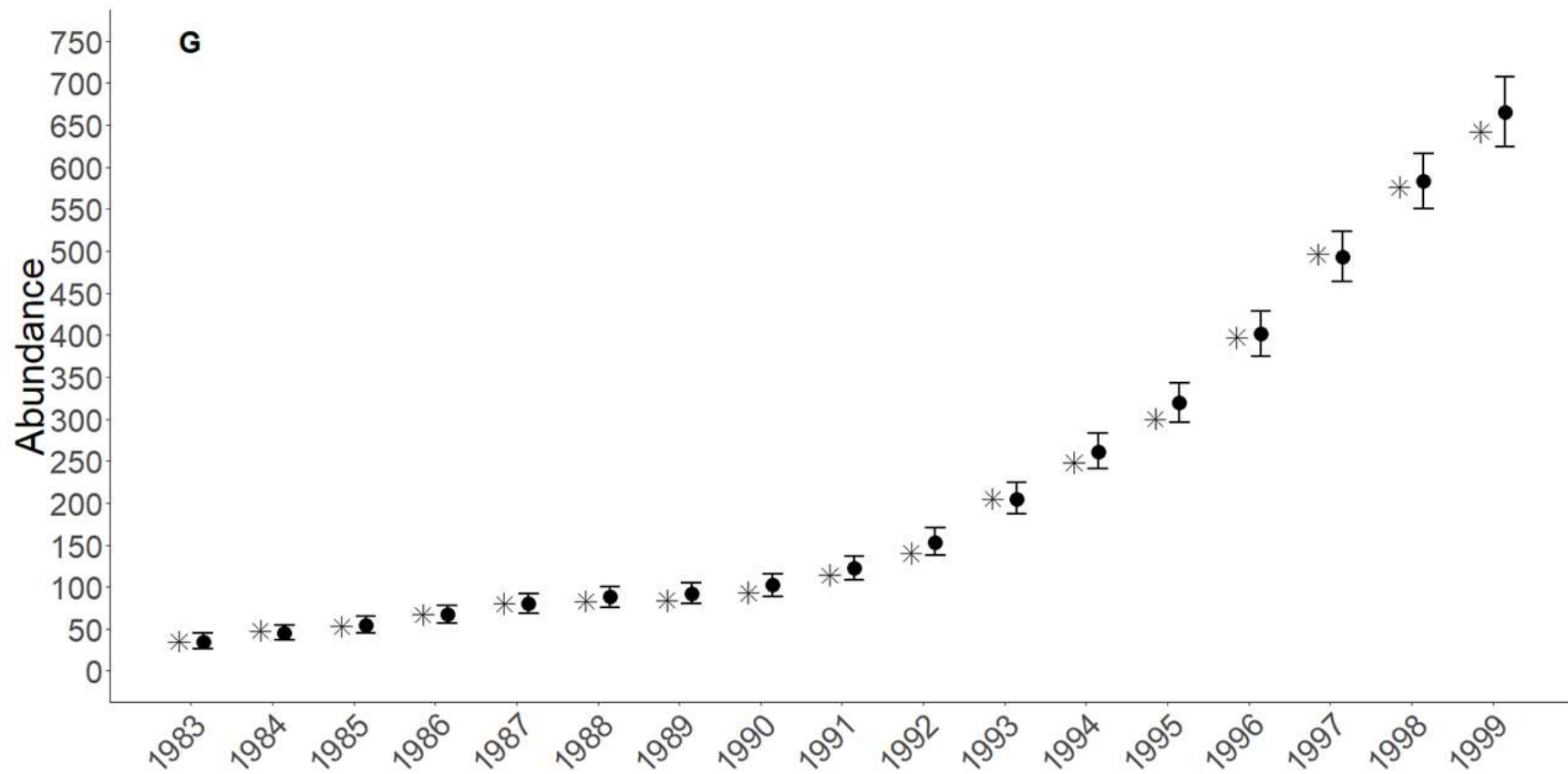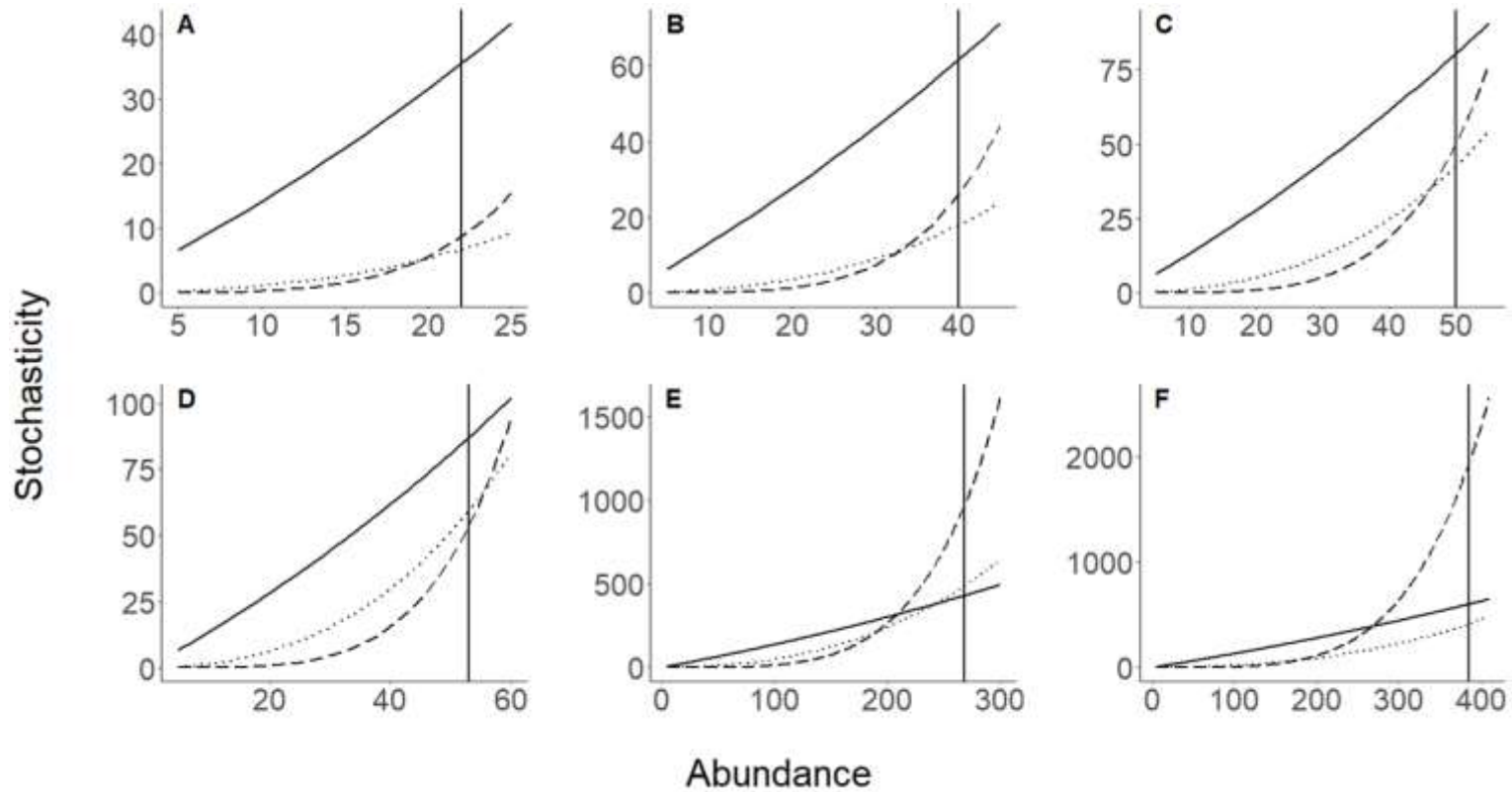
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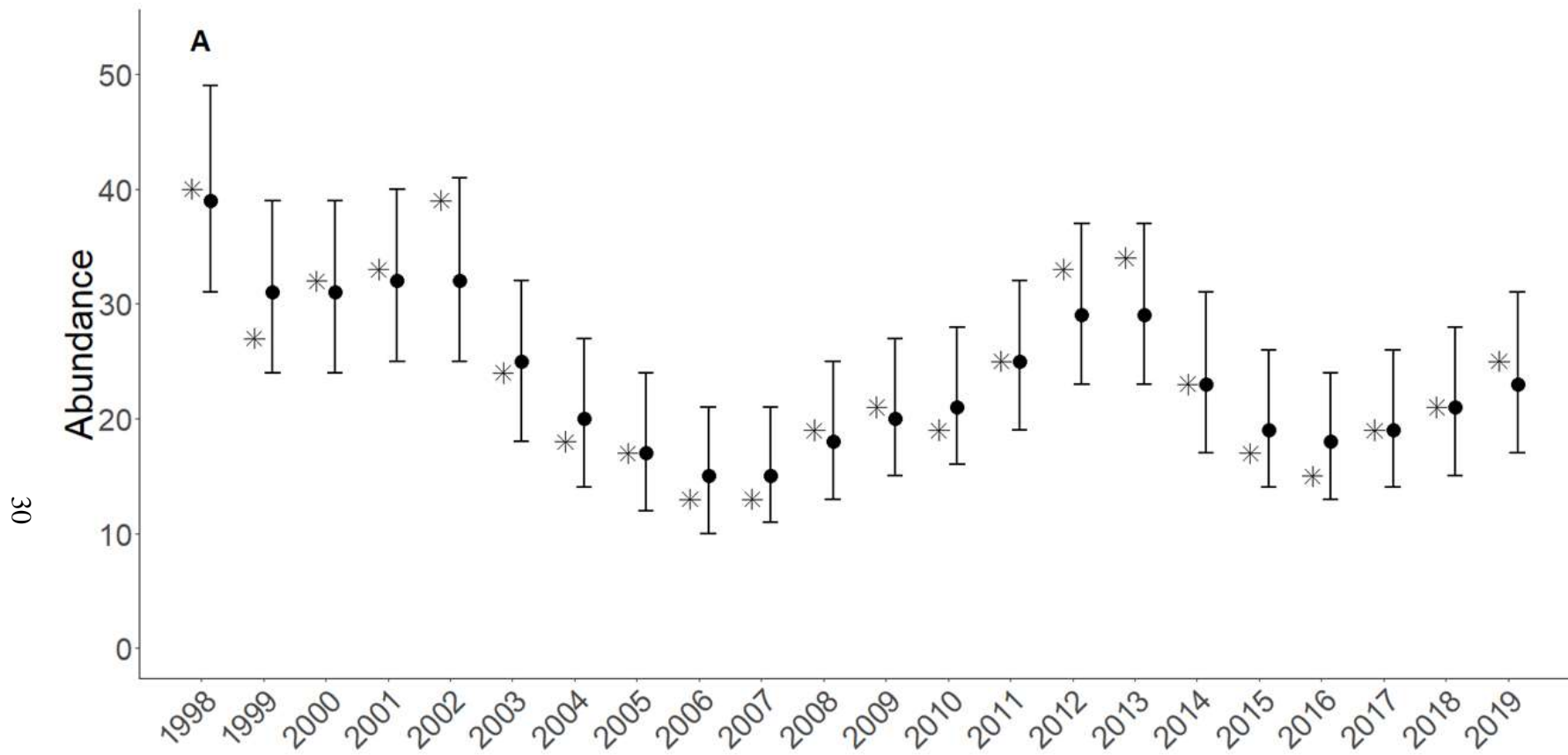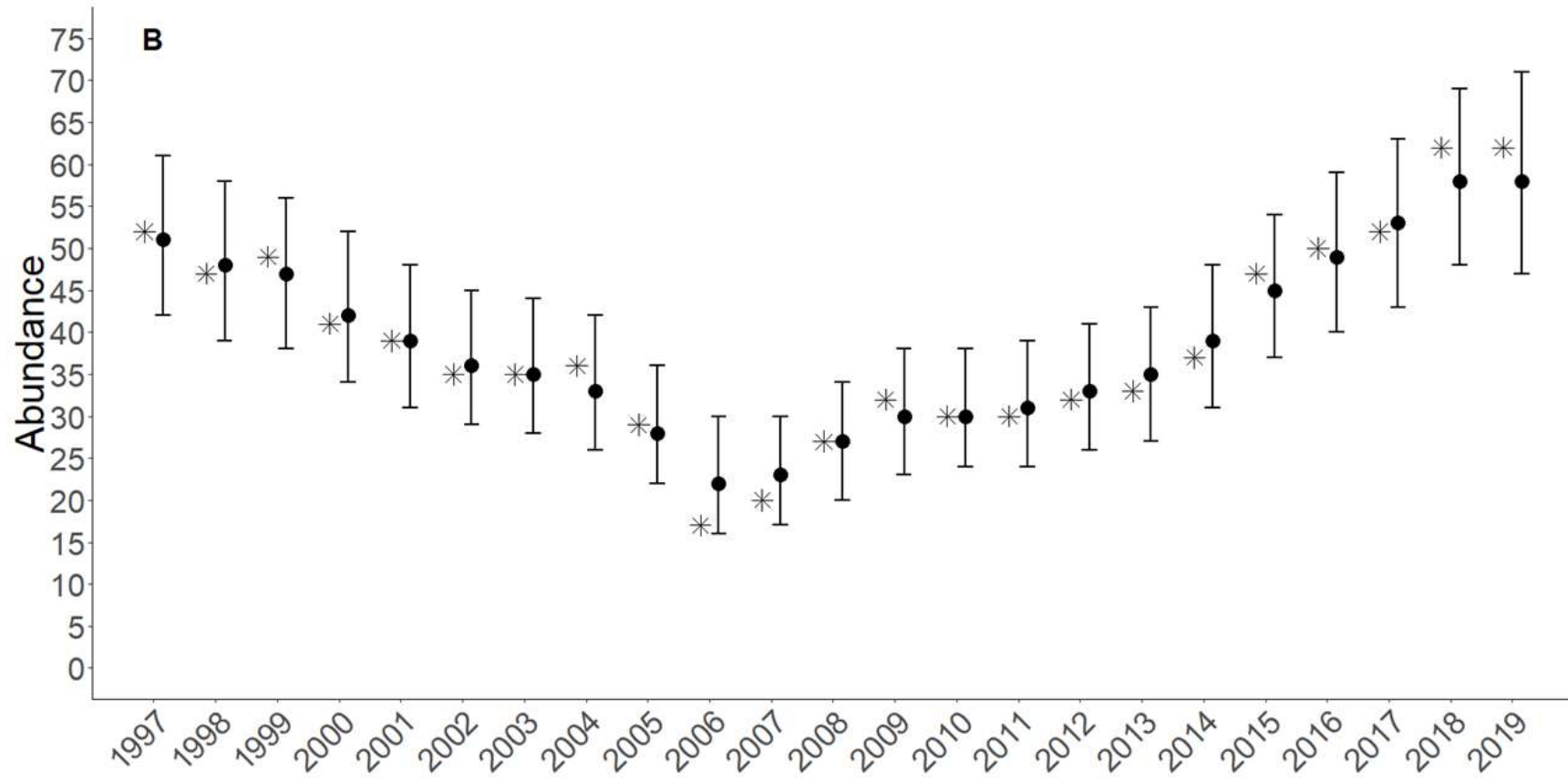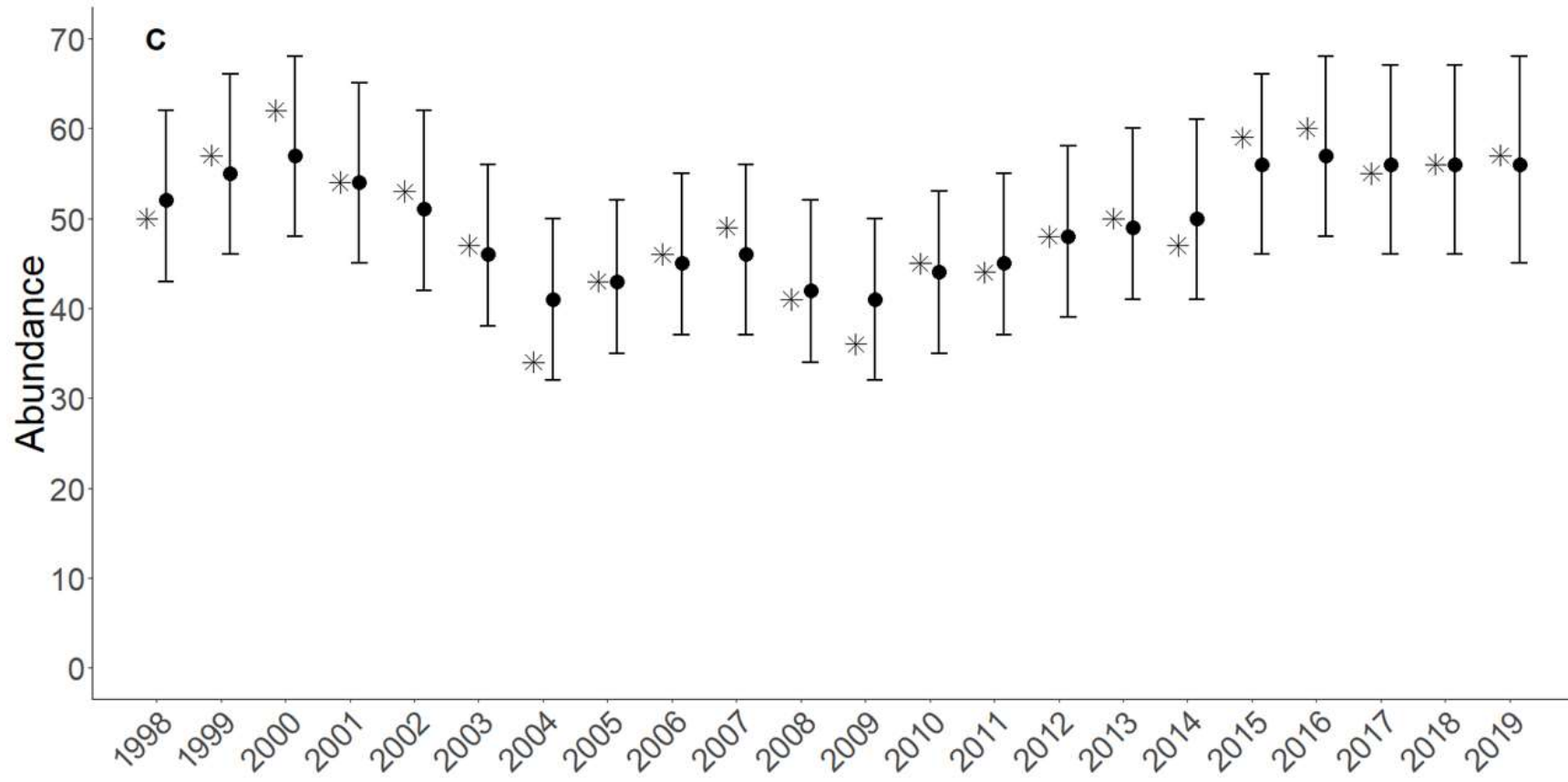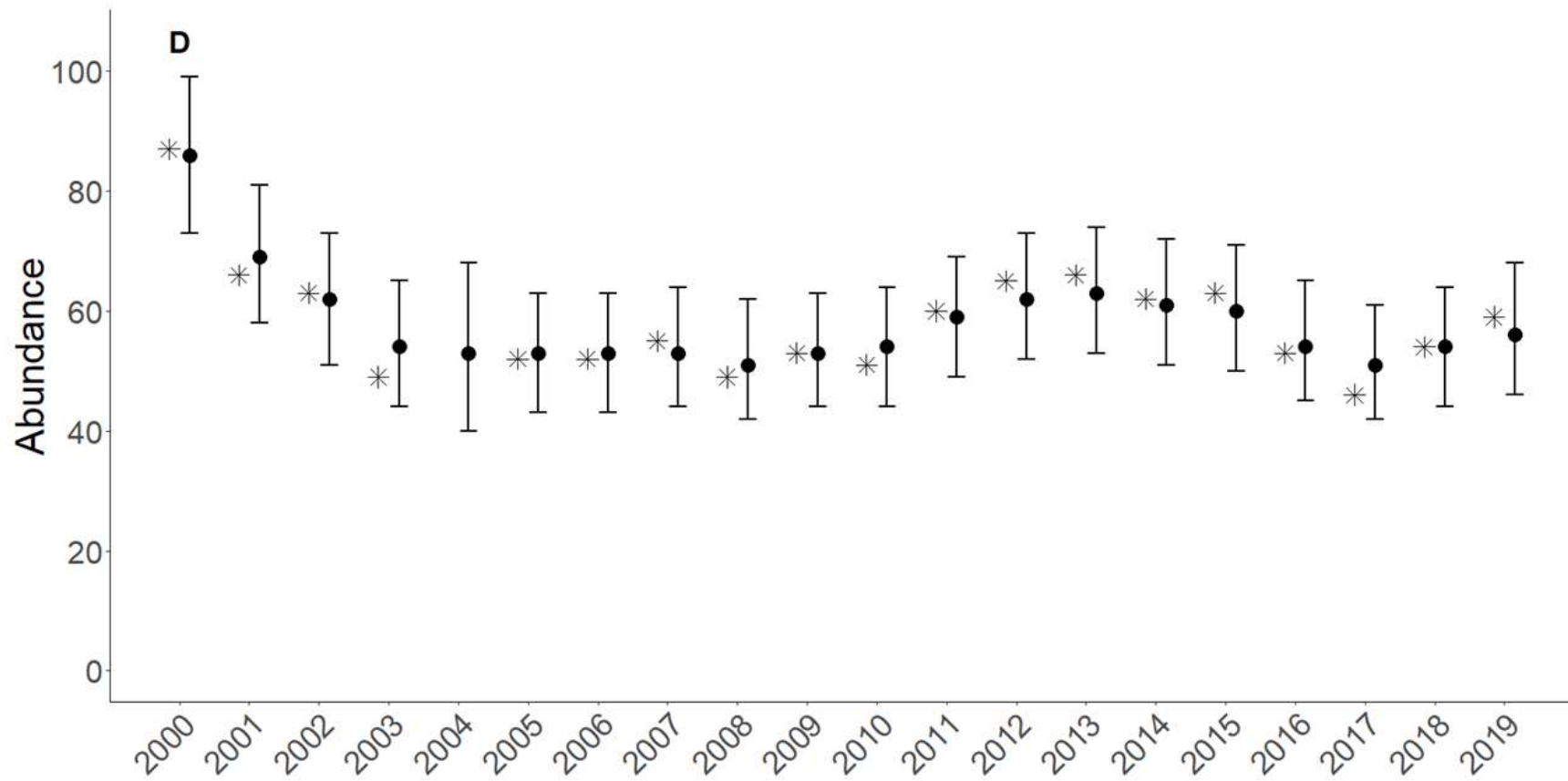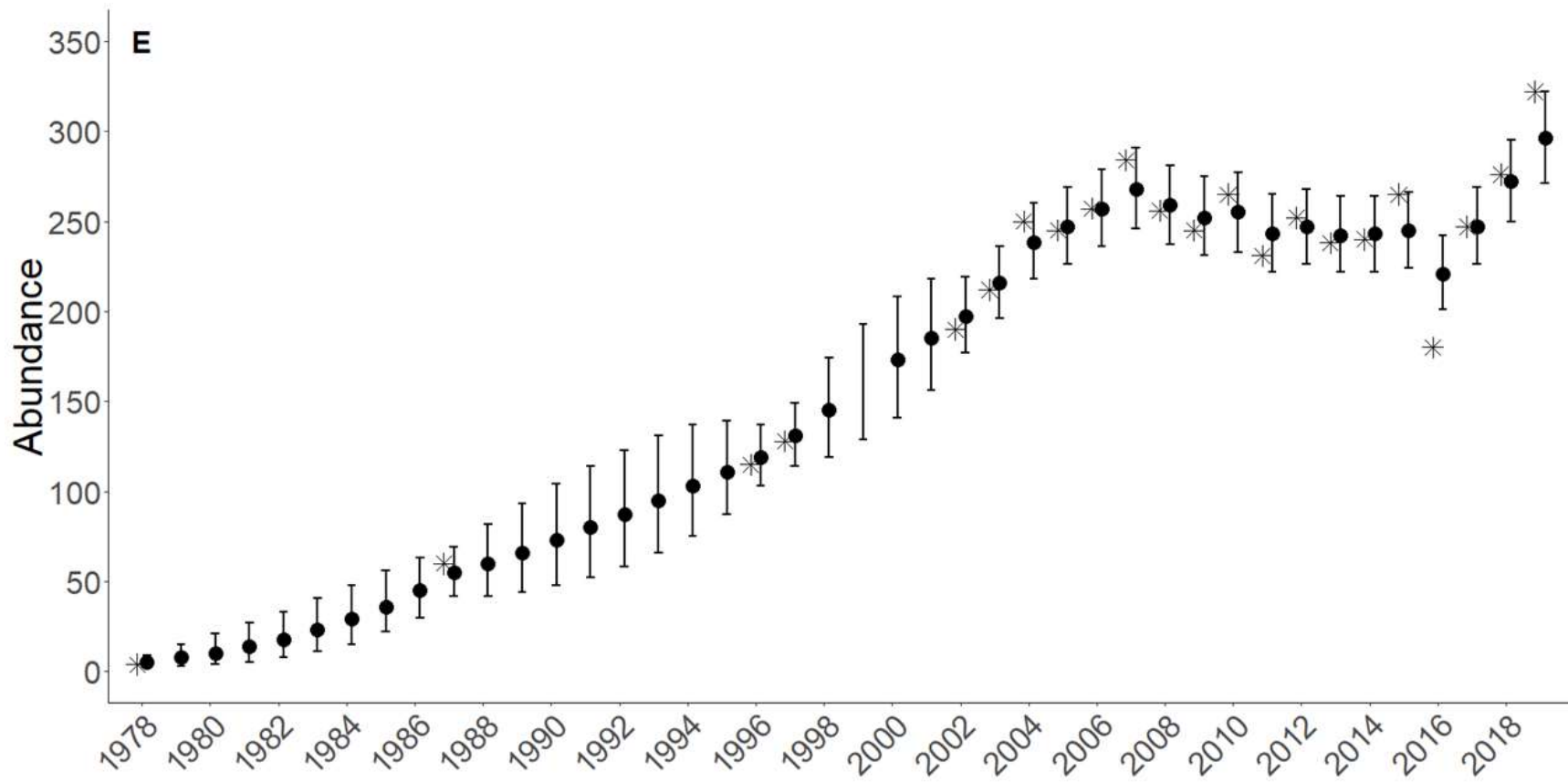
Figure A2. Predicted demographic variation (var_{dem}) (solid), variation due to changes in strength of density dependence (var_β) (dashed), and variation due to changes in r_{max} ($dem_{r_{max}}$) (dotted) for six elk herds. Letter designations are the same as in Figure 1. The vertical line represents the estimated carrying capacity (K) of each herd.

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