Extremely low primary production after a decade long drought contributed to the local extinction of a group-living rodent

Running title: Drought caused local extinction of degus

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Abstract

Some species exhibit physiological and behavioral plasticity to survive adverse periods, such as changing climates or reduced food availability. Yet, during extreme climatic events the mechanisms to respond to these adverse periods may not be sufficient, potentially driving local population extinctions. We studied the population dynamics of a common degu (*Octodon degus*) population in central Chile using a 12-year long dataset (2009-2020) and investigated what environmental factors affected recruitment, survival and population growth. Our study period also coincided with a decade-long megadrought, allowing us to examine how this extreme climatic event contributed to the observed local extinction of this population in 2020. We used Pradel's capture–mark–recapture (CMR) modeling framework to assess what factors influence population parameters. We analyzed two seasons: the breeding season, which aligns with the austral winter and coincides with the mating, gestation and lactation period, and the nonbreeding season spanning austral spring, summer, and fall, which coincides with offspring care. We found that survival and recruitment varied by year, season, and sex. Female survival was higher during the breeding season than in the nonbreeding season whereas male survival was higher in the nonbreeding season. Recruitment primarily occurred during the breeding season and was higher for males. Population growth was positive from 2009 to 2019. When incorporating environmental covariates, season, and sex, we found that survival was primarily driven by gross primary production, and recruitment by seasonality and gross primary production. We suggest that a year with very low gross primary production, induced by a decade-long megadrought contributed to the local extinction of this population. Our results provide important insight into which populations may be vulnerable to population declines in face of a changing climate, or instead, will be resilient to forecasted climate change.

Keywords: Local extinction, population crash, mammal, population dynamics, human-induced climate change, extreme climatic event, semi-arid environment, drought

Introduction

Human-induced climate change and extreme climatic events are both driving adaptation and contributing to the extinction of current-day populations and species (Maclean and Wilson 2011; McLaughlin et al. 2002; Thomas et al. 2004; Urban 2015; Patrício et al. 2019). Sometimes, local extinctions are linked to the consequences of single, widespread factors such as marine heat waves (Montie and Thomsen 2023; Thomsen et al. 2019), El Niño Southern Oscillation (ENSO) events (Kelt, Wilson, and Konno 2005), or extended droughts (Ehrlich et al. 1980; Facka et al. 2010; Trape 2009). In some species, local extinctions are associated with a combination of perturbations, such as food reduction, anthropogenic factors, predation, climate change (Sergio et al. 2022), and climatic or environmental changes leading to habitat loss (Munday 2004; McLaughlin et al. 2002) or food depletion (Durance and Ormerod 2010; Epps et al. 2004). Overall, factors affecting vulnerability to climate change include exposure to or intrinsic sensitivity to changes in climatic conditions due to physiological or life-history constraints (Beever et al. 2011; 2010), such as reaching critical thermal maxima in ectothermic species (Sinervo et al. 2010), as well as habitat requirements and specialized feeding habits (Moritz and Agudo 2013). However, climate change remains a primary driver of most local extinctions by reducing food availability (Cahill et al. 2013).

Food availability is influenced by a myriad of environmental conditions that are projected to change. The anticipated worldwide temperature rise and increased variability in precipitation might negatively affect plant growth and productivity (Zhang et al. 2022; Gherardi and Sala 2015). Changes in precipitation and evaporative demand may result in increased drought severity (Vicente-Serrano et al. 2020). Drought effects include reduced annual plant production, stem growth, and leaf area index (Krishnan et al. 2006), or even vegetation die-off after extreme events (He et al. 2018). Droughts and heatwaves may be particularly severe in arid and semi-arid ecosystems (IPCC 2014) and climate change may affect species inhabiting those environments (Srivathsa et al. 2019; Polyakov et al. 2021).

We aimed to examine the impacts of a prolonged extreme climatic event (Grant et al. 2017), a decade-long megadrought termed the Central Chile Megadrought (Garreaud et al. 2020), on the population dynamics of a group-living and colonial rodent, the common degu (*Octodon degus*) (Ebensperger et al. 2014; 2021). Degus are small, diurnal, semi-fossorial social rodents that are endemic to Chile and inhabit semi-arid environments. Degus form social groups consisting of on average two other (range: 1-8) related and unrelated adult males and females (Ebensperger et al. 2004; Hayes et al. 2009; Davis et al. 2016; Hayes et al. 2019). Degus are considered annual, plural breeders. They mate in June, give birth in late August to early September after a relatively long gestation period, and communally rear their precocial offspring in October (Ebensperger, Veloso, and Wallem 2002; Ebensperger, Hurtado, and León 2007; Ebensperger and Hurtado 2005a). They occasionally produce second, smaller sized litters in early austral summer, but secondary litters are relatively uncommon (Meserve et al. 1995; Ebensperger et al. 2013). The degus exhibit a unique life history as they do not live long (the majority of adults do not survive to their second year (Ebensperger et al. 2009; 2011)) and wean six offspring on average (Long and Ebensperger 2010). Favorable ecological conditions for degus include abundant precipitation (Meserve et al. 2011; Ebensperger et al. 2014; Previtali et al. 2010) and high food abundance (Ebensperger et al. 2021; 2014), particularly a high abundance of green low fibre annual herbs (Bozinovic 1995). Deviations from these conditions pose significant challenges to degus. Degus have a low tolerance to heat stress (Kenagy et al. 2004) and may be constrained to forage in areas with shrub vegetation to avoid direct exposure to intense solar radiation (Lagos et al. 1995; Kenagy et al. 2004). Recently, we reported that per-female fecundity rate declines at relatively low degu densities (i.e., implying a population-level Allee effect), that this effect is more likely whenever low food conditions prevail, and that group size tracks population density (i.e., when population size is low, group size is also small) (Ebensperger et al. 2025). The implication is that group-living may not buffer low population density conditions, especially under the harshest of climatic conditions.

Our objectives were three-fold: we aimed to investigate 1) the demography and population dynamics of a degu population using a dataset that ran from 2009 to 2020, 2) what environmental factors affected population parameters and, 3) the factors that potentially caused or contributed to the local extinction of this population in 2020. Although the IUCN red list status classifies degus as ‘Least Concern’ (Roach 2016), it remains unclear why some populations are able to survive through adverse events while others experience local extinction. Examining what environmental factors affected the population dynamics of this population helps to identify which populations are most vulnerable to forecasted climate change and aids in developing strategies to mitigate future local extinctions from happening.

We developed a priori hypotheses addressing population demographics, the influence of environmental factors on survival and recruitment rates, and what factors could have contributed to the local extinction of this population. We hypothesized that survival and recruitment fluctuate with year, season, and sex. Particularly, we predicted that survival and recruitment rates increase in years with favorable conditions, in the breeding season when preferred food is abundant, and that rates differed per sex. Furthermore, we hypothesized that survival and recruitment are positively associated with weather conditions that enhance plant growth and thus, food availability (Table 1). Specifically, we predicted that survival and recruitment would be 1) negatively influenced by conditions characterized by relatively high and more variable ambient temperatures due to their negative effects on food availability. Additionally, 2) we predicted degu survival and recruitment to increase with increasing mean rainfall and decreasing precipitation variability due to the positive effects of these conditions on food availability. We further predicted 3) positive effects of high mean and low variance in precipitation during the previous season because of the lag in plant growth after precipitation events, and 4) a positive influence of increased precipitation, especially during “El Niño” events, which can enhance resource availability through increased primary productivity. Often, “El Niño” events result in population growth among rodent populations that inhabit semi-arid and arid environments (Armas et al. 2016), including degus in northern Chile (Previtali et al. 2010). Finally, we hypothesized that the adverse effects of the Central Chile Megadrought, such as reduced precipitation, resulted in lower food availability and decreased survival and recruitment rates over time, ultimately resulting in the population's local extinction.

Table 1. Predicted effects of climatic variables on apparent survival and recruitment of a central Chile degu population. The last four variables were excluded due to multicollinearity.

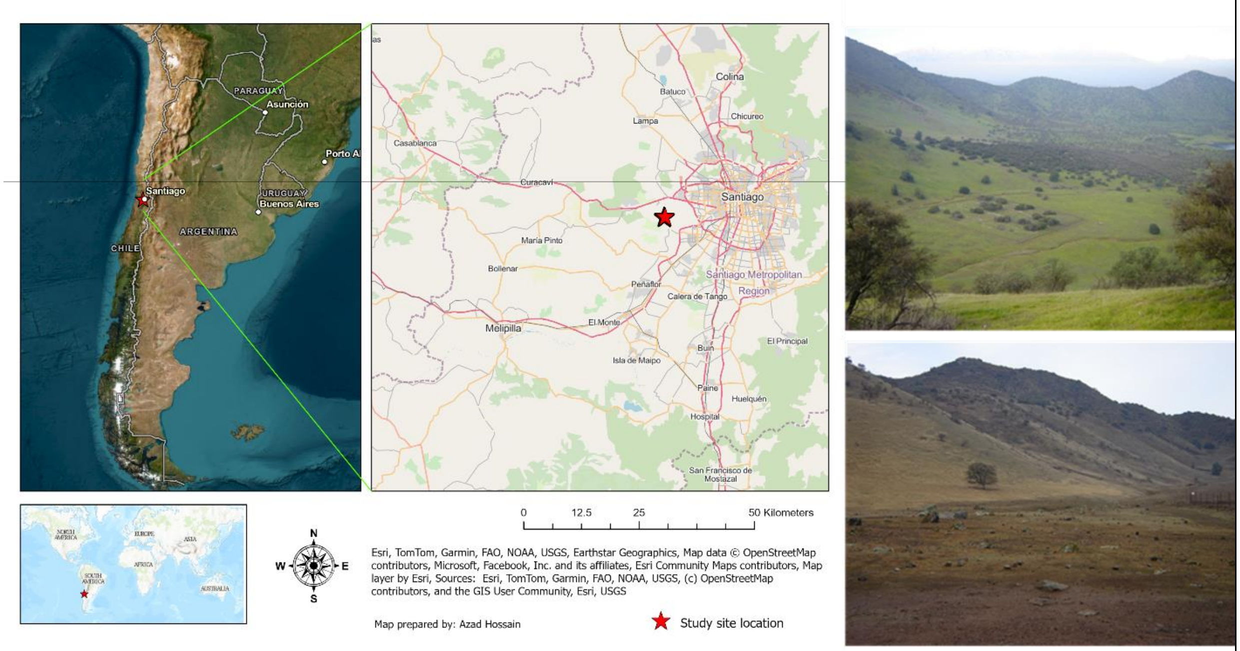
Variables and their abbreviations used in figures and tables	**effect on survival**	**effect on recruitment**
Coefficient of Variation (CV) in ambient temperature (T_CV)	-	-
Total seasonal precipitation (P)	+	+
Coefficient of variation in precipitation (P_CV)	-	-
Total seasonal precipitation from the previous season (P_lag)	+	+
Coefficient of variation in seasonal precipitation from the previous season (P_CV_lag)	-	-
Gross Primary Production (GPP) per season	+	+
El Niño Index (ONI) as the 3-month sea surface temperature average	+	+
Average Ambient Temperature (T)	-	0
Maximum Ambient Temperature (T_max)	0	-
Leaf Area Index (LAI) per season	+	+
Evapotranspiration (ET) per season	+	+

Methods

Data collection

This study was conducted at Estación Experimental Rinconada de Maipú (German Greve Silva Experimental Station), a field station of the Universidad de Chile (henceforth, Rinconada, 33º 23' S, 70º 31' W, altitude 495 m; Fig. 1). The total area examined was 2–3 ha and did not vary between years of the study. The predominant climate is Mediterranean with dry, warm summers and cold, wet winters. Vegetation consists mostly of grass and scattered shrubs that covered around 14% of the field site (Ebensperger and Hurtado 2005a). This field site is located closer to the southern most limit of degus' distribution, where range limits are defined by too wet conditions in the south and too dry in the north to support their main food sources (Contreras, Torres-Mura, and Yáñez 1987; Woods and Boraker 1975; Cadenillas and D'Elía 2021a; 2021b).

Figure 1. A map of the location of our field site at Estación Experimental Rinconada de Maipú (German Greve Silva Experimental Station), a field station of the Universidad de Chile (33º 23' S, 70º 31' W, altitude 495 m) with images of the field site during the breeding (top right panel) and nonbreeding (bottom right panel) season. The breeding season (mating/early gestation) corresponds to the austral winter, while the nonbreeding season (offspring care) corresponds to the austral spring, summer, and beginning of fall.



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Map prepared by: Azad Hossain

★ Study site location

From 2009 to 2020, we monitored a degu population at Rinconada using capture-mark-recapture (CMR) approaches. We trapped degus twice a year: in austral fall (May – early July) and spring (late August – early November) (SM1). We live-trapped degus at each burrow system (mean ± SD = 40.2 ± 2.6 burrow systems/season/year) by placing 10 Tomahawk traps (Tomahawk model 201, Tomahawk Live Trap Company, Hazelhurst, WI) around burrow openings. Burrow systems are groups of interconnected burrow openings from which individuals emerge during daytime and return to at nighttime (Fulk 1976).

Across years, which burrow systems monitored differed, but we used approximately the same number of traps (396.5 ± 20.3 traps/season/year). The area trapped across study years was 2.1 ± 1.7 ha (mean ± SD). Traps were opened and baited with rolled oats one hour prior to sunrise and closed one hour after sunrise to ensure that captures occurred at or near the home burrows of the individuals. Upon first capture, animals were fitted with ear tags (Monel 1005-1, National Band and Tag Co. Newport, KY) for individual identification. On the first and all subsequent captures, we recorded animal ID, burrow number, sex, reproductive and lactation status of adult females, and body mass (g). We noted 55 occurrences where we were certain that an individual had died, as we found the carcasses. We have no reliable information regarding dispersal.

We chose two one-month trapping windows, one in June during the austral fall (Julian date 154 to 184 calculated from January first each year) that corresponds with the mating season and one in October during the austral spring (Julian date 279 to 309) that matches late lactation and offspring care. Most juveniles are born in austral spring in the months of September through October (Ebensperger et al. 2013), so our trapping window of October mainly represents juvenile emergence and the majority of juveniles are therefore captured in the breeding season interval from austral fall to spring. We chose a 30-day window to allow for a similar trapping effort over the years. We trapped degus on mean ± SD = 20.8 ± 5.2 days ranging from 5 (in fall 2020 due to COVID-19 restrictions) to 26 days (in spring 2014) during each 30-day period (SM1). In total, we had 24 trapping windows.

For the environmental covariates, we selected two periods. We selected the austral winter spanning from June to September. During this time, the region experiences most precipitation, the lowest temperatures, and an increase in food availability. This period also aligns with the mating season and the gestation period for females, hereafter termed the breeding season. We selected the 8-month period from October to May as the other period representing austral spring through summer and fall.

During this period, there is a decline in food availability, almost no rain, and the highest temperatures are recorded. This period includes the ending of offspring care, hereafter termed nonbreeding season.

We used temperature and precipitation records from 1975-2020 from the Pudahuel weather station (33°23'S, 70°47'W), the closest located weather station to the field site (see SM2 for the long-term trend of the weather variables). From these records, we obtained the following variables for the two seasons: average ambient temperature (T in °C) as the mean of monthly temperatures, coefficient of variation (CV) of ambient temperature (T_CV), the maximum ambient temperature during the season (T_max in °C), total cumulative amount of precipitation (P in mm) as the sum of monthly precipitation, the CV of precipitation (P_CV), a one-season lag in total precipitation (P_lag in mm) and CV (P_CV_lag) of precipitation due to the potential effect of precipitation in the previous season on plant growth (see Table SM3 for the descriptive statistics for all environmental covariates per season during our study period).

To examine different aspects of vegetation at our field site location (-33.475, -70.833), we used land surface data products retrieved from the Moderate Resolution Imaging Spectroradiometers (MODIS) (Salomonson et al. 1989) onboard Terra and Aqua satellites (https://modis.gsfc.nasa.gov/). The combined Terra and Aqua datasets, available at a temporal resolution of eight days and a spatial resolution of 500 m, for the pixel containing the study location, were retrieved using the Land Processes Distributed Active Archive Center (LP DAAC, https://lpdaac.usgs.gov/) AppEEARS tool (AppEEARS Team 2020). These include gross primary productivity (GPP in kgC/m²/8day, MOD17A2HGF Version 6.1) (Running and Zhao 2021), evapotranspiration (ET in kg/m²/8day, MOD16A2GF Version 6.1) (Running et al. 2021), and Leaf Area Index (LAI in m²/m², MCD15A2H Version 6.1) (Myneni, Knyazikhin, and Park 2021). Evapotranspiration includes both evaporation and transpiration and indicates the effect of soil moisture, which is important for the seed base. Leaf Area Index quantifies the amount of leaf material in a canopy and indicates food availability. Gross primary production quantifies the total influx of carbon into an ecosystem through the photosynthetic fixation of CO_2 and represents biomass production, and, indirectly, supports vegetation activity while partially contributing to evapotranspiration through transpiration.

We included the El Niño Index (ONI) value based on studies across multiple organisms reporting population declines (Cahill et al. 2013) or increases (Armas et al. 2016) linked to the El Niño-Southern Oscillation (ENSO). This index accounts for regional temperature and precipitation oscillations caused by El Niño conditions, characterized by average sea-surface temperatures in the Pacific Ocean that exceed 0.5°C for three consecutive months. In contrast, La Niña occurs when the average sea-surface temperature is 0.5°C below average for three consecutive months. The ONI values were obtained from the National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center (https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php).

Data analysis and modeling

We used a survival – recruitment parameterization of Pradel's temporal symmetry capture–mark–recapture (CMR) modeling framework (Pradel 1996; Nichols 2016; Williams, Nichols, and Conroy 2002) to estimate and model demographic parameters, and to test for the influence of climatic covariates on these parameters. This modeling framework estimates capture probabilities (p_t), apparent survival (ϕ_t) and recruitment rates (f_t). For completeness, p_t is the probability that a marked animal, alive and present in the sampled population is captured at sampling occasion t; ϕ_t is the apparent survival probability (probability that an animal alive at sampling occasion t survives to time $t + 1$ and remains in the population), and f_t is the number of new recruits between t and $t + 1$, per individuals in the population at sampling occasion t. The realized population growth rate λ_t is then calculated as a derived parameter, representing the sum of time-specific survival and recruitment rates (i.e., $\lambda_t = \phi_t + f_t$).

To discern seasonal, annual, and sex-specific variation in demographic rates, we first modeled ϕ, *f*, and *p* as constant parameters with season, year, and sex as singular, additive (‘+’), and interactive (‘:’, two-way only) effects. To assess the impact of climatic covariates on survival and recruitment rates, we allowed these rates to be affected by climate covariate(s) alone, as well as additively and interactively by season and year. Due to high variability in environmental covariates among years, we also ran the models with climate covariate(s), season, and sex (excluding year). We checked for collinearity among environmental covariates and discarded variables with Pearson correlation coefficients of $-0.5 \leq r \geq 0.5$ (SM4). We retained the following environmental covariates per season for the final analyses: the coefficient of variation of mean ambient temperature (T_CV), the cumulative amount of seasonal precipitation (P), the CV of precipitation (P_CV), the one-season lag in the cumulative amount of precipitation (P_lag), one-season lag in the CV of precipitation (P_CV_lag), gross primary production (GPP), and the El Niño index (ONI). We scaled all our quantitative variables by mean-centering and scaling by the standard deviation. Marked degus that were confirmed dead (i.e., 55 individuals whose carcasses were recovered) were censored.

We performed Pradel’s mark-recapture analyses in the program MARK (White and Burnham 1999) using the ‘RMark’ package (Laake 2013) for the R computing environment (R Core Team 2021). We used an information-theoretic approach with AIC_c (Akaike Information Criterion corrected for small samples) as a measure of model parsimony, considering the model with the lowest AIC_c as the best model, while models with $\Delta AIC_c \leq 2$ were assumed equally plausible and are discussed in the main text. In the supplementary material, we included the covariate effects on demographic parameters from models with $\Delta AIC_c > 2$, provided that the 95% confidence intervals for regression (or beta) coefficients did not overlap zero. We specified time intervals between austral fall and spring sampling occasions in months, implying that estimates of all demographic parameters were monthly rates. Unless otherwise stated, we report mean ± SE for observed metrics and point estimates with 95% confidence intervals for model parameters.

Results

From 2009 to 2019, we captured 2,547 individuals a total of 14,526 times (7,662 captures of 1,254 females and 6,864 captures of 1,293 males, including both adults and juveniles). During the entire study period, we trapped fewer degus (167 females and 232 males) in the austral fall (June) than in the austral spring (October) trapping window (1087 females and 1061 males). On average 141 (± 25.6 SE) degus were trapped each year with fewer degus trapped in the austral fall (61.0 ± 10.7) compared to the austral spring (221.5 ± 38.2). In 2020, we set traps, but no degus were captured, indicating the degu population had either gone locally extinct or was reduced to very low numbers. Observations made by one of us (LDH) and technicians in 2023 and 2024 confirmed that burrow systems within our original study area were inactive and that only a few active systems remained in the immediate areas outside the study area.

Population demographics

The overall monthly apparent survival was 0.88 ± 0.01 (Fig. 2a). However, virtually all well-supported models without climatic covariates included year, season, and sex effects on apparent survival and recruitment rate suggesting that both survival and recruitment covaried with these factors (Table 2A, Fig. 2). Degus survived better during the breeding than during the nonbreeding season, and females experienced better survival than males (Fig. 2a). Compared with 2009, survival was higher in 2010, in 2012 through 2015, and in 2017 (Fig. 2b). The monthly recruitment rate varied by year, season, and sex (Fig. 2c). As expected, monthly recruitment rate was higher during the breeding than during the nonbreeding season and was lower for females compared with males, particularly in the nonbreeding season (Fig. 2d). Recruitment was higher in 2011 but lower in 2019 compared with 2009 (Fig. 2d). A competing model ($\Delta AIC_c < 2$) differed primarily in model structure for capture probability. Capture probability varied among years, with lower capture probabilities in 2012 compared to 2009; capture probabilities through all other years were similar to that recorded in 2009 (Table 2A, Fig. 3a). The monthly realized population growth rate (λ) ranged from 0.79 ± 0.02 in the nonbreeding season of 2009 to 1.62 ± 0.06 in the breeding season of 2011 and varied on average from 1.40 ± 0.03 during the breeding season to 0.84 ± 0.01 during the nonbreeding season. The overall annual growth rate was 1.13 ± 0.07 (Fig. 3b).

Table 2. Model comparison statistics testing for (A) the effect of year, season, time (as discrete variable), and sex on apparent survival (ϕ), capture probability (*p*), and recruitment rate (*f*) of a degu population in central Chile between 2009 and 2020. Model comparison statistics testing for (B) the effect of season, sex, and the selected environmental covariates on apparent survival (ϕ) and recruitment rate (*f*). Only the top five models are presented for each part. K represent the total number of parameters in a model, Akaike Information Criterion corrected for small sample size (AICc), the difference in AICc value from the best-supported model (ΔAICc), and the relative model probability (weight) for the five best-supported models are presented. Additive effects are indicated by a "+," and additive and interactive effects are indicated by ":". Models were ranked based on the AICc values, and the most parsimonious model is indicated by bold type face, while equally plausible models with ΔAICc ≤ 2 are indicated in italic type face. The climatic covariates GPP is the mean of seasonal gross primary production and P_lag is the cumulative amount of precipitation from the previous season.

Φ	***p***	***f***	***K***	**AICc**	**ΔAICc**	**weight**
A. Models without climatic covariates						
year + season:sex	**year**	**year + season:sex**	**39**	**17439.70**	**0.00**	**0.27**
year + season + sex	*time + sex*	*year + season:sex*	*50*	*17439.75*	*0.05*	*0.26*
year + season:sex	*year + sex*	*year + season:sex*	*40*	*17440.96*	*1.26*	*0.14*
year + season + sex	time	year + season:sex	49	17441.84	2.14	0.09
year + season + sex	time + sex	year:season + sex	58	17442.56	2.86	0.07
B. Models with climatic covariates excluding year						
GPP:season + sex	**time + sex**	**GPP + season**	**31**	**17529.09**	**0.00**	**0.83**
GPP:season	time + sex	GPP + season + sex	31	17532.35	3.26	0.16
GPP:season + sex	time + sex	P_lag + season + sex	32	17539.91	10.82	0.00
GPP:season + sex	time	GPP + season	30	17545.35	16.26	0.00
GPP:season + sex	time	P_lag:season + sex	32	17548.94	19.85	0.00

Figure 2. Estimates of monthly survival and recruitment rates for a degu population at Estación Experimental Rinconada de Maipú, Chile, from 2009-2020 based on the most parsimonious model in Table 2A. The left-hand panels show a) apparent survival (ϕ) and c) recruitment rate (ƒ) for females in purple and males in green for the breeding (B) and nonbreeding (NB) season. Error bars represent 95% confidence intervals. The right-hand panels show the regression parameter (beta estimates) with the 95% CI for b) survival, and d) recruitment. The reference values are females and the nonbreeding season, and 'NB:Males' corresponds to the interaction between season and sex. The breeding season (mating/early gestation) corresponds to the austral winter, while the nonbreeding season (offspring care) corresponds to the austral spring, summer, and beginning of fall.

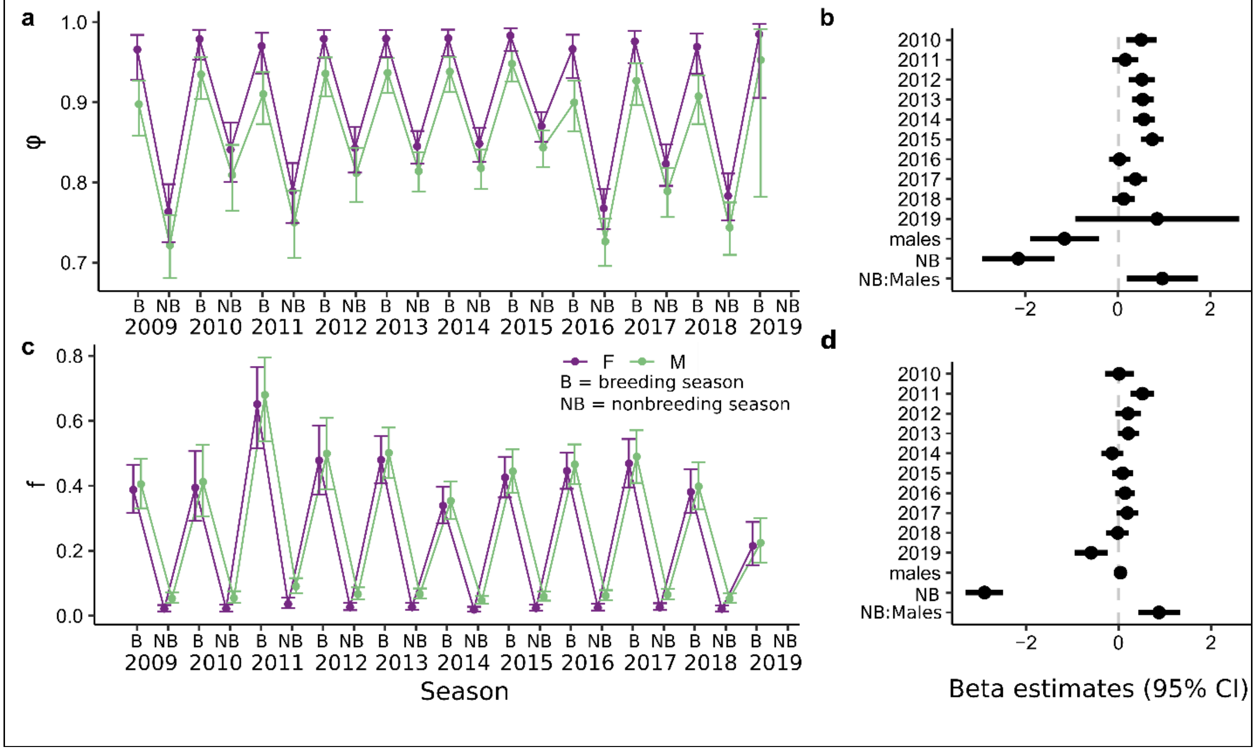
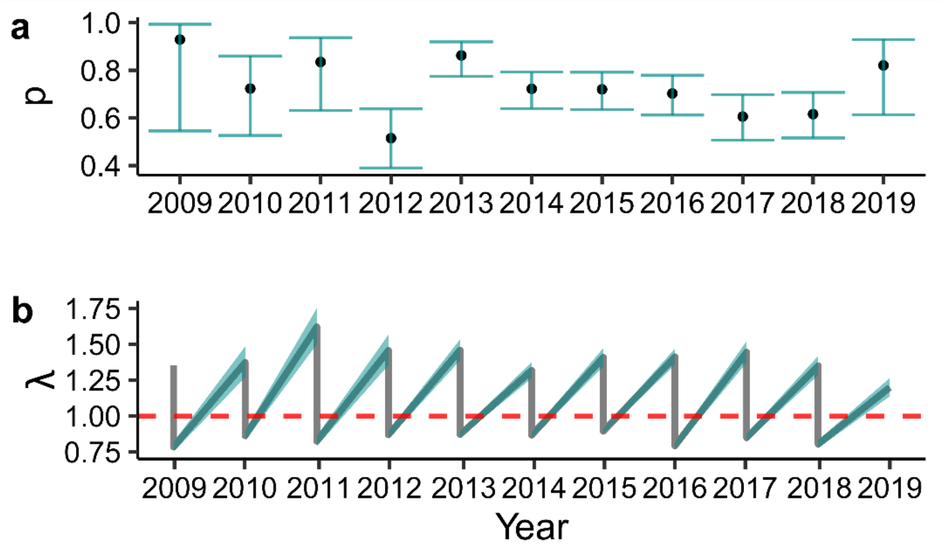


Figure 3. Estimates of capture probability and realized population growth parameters for a degu population at Estación Experimental Rinconada de Maipú, Chile, from 2009-2020 based on the most parsimonious model in Table 2A. The panels show a) capture probability (p), and b) monthly estimate of realized population growth (λ) for each year of the study. The data point in spring 2019 is missing, because degus did not enter our traps in the fall of 2020, and so there is no interval from spring season 2019 until the next season. Error bars in blue represent 95% confidence intervals.



Effects of environmental covariates on population demographics

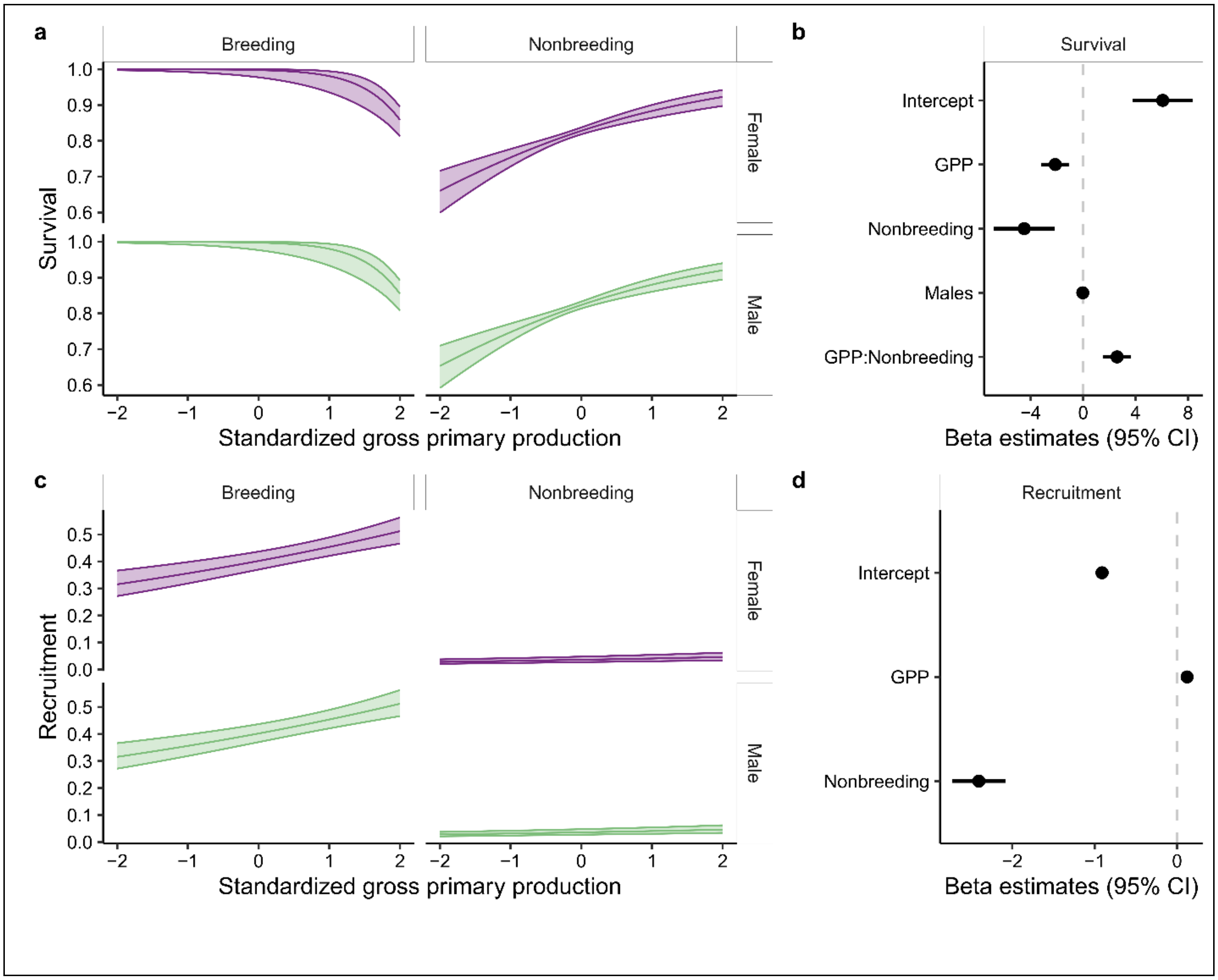
When examining the models with environmental covariates, year, season and sex, we found that the cumulative amount of precipitation had a significant effect on survival; all top models incorporated precipitation either as an additive effect or as an interaction with season (SM5). Year and sex also affected survival probability. Recruitment was affected by variability in precipitation during the previous season, which was supported by two other models with a $\Delta AIC_c < 2$ from the most parsimonious model, indicating that these models are equally supported (Table SM5.1). We observed high interannual variation in survival/recruitment and environmental covariates (SM5); therefore, we excluded year as fixed factor to better examine how seasonal differences in environmental covariates affected survival and recruitment.

The model selection routine used with environmental covariates, season, and sex (excluding year) revealed that the most supported covariate CMR model was driven by the effect of gross primary production on survival and recruitment (Table 2B; Fig. 4; model #146 Table SM6.3). Similar to our model results where we excluded environmental covariates, survival covaried with season. Survival was higher in the breeding season and although sex is included in the top model, survival did not vary with sex (Fig. 4a). Survival increased with higher gross primary production in the nonbreeding season (Fig. 4b). Although survival decreased with higher gross primary production in the breeding season (Fig. 4a), it has little effect on survival. Overall, gross primary production has a positive effect on survival independent of season (slope of 0.45). Likewise, recruitment increased with higher gross primary production and varied with season (Fig. 4c, Table 2B), with higher recruitment occurring during the breeding season (Fig. 4d).

Other environmental variables also influenced survival and recruitment, but these results were based on multivariate models that demonstrated the lowest ΔAIC_c from the top model but no weight and a $\Delta AIC_c >$ 2 (Table 2B and Table SM6.3). We found that all environmental variables influenced survival (Table SM7.1, Fig. SM7.1). Most covariates, except CV in temperature, lag in precipitation, and gross primary production, positively influenced survival. The covariates, CV in the cumulative amount of precipitation, lag in CV in precipitation and gross primary productivity showed an effect in the opposite direction than what we predicted. We also found that the cumulative amount of precipitation (without and with a one-season lag), variability in precipitation and gross primary production increased recruitment, while higher variability in precipitation during the previous season negatively affected recruitment, and the CV in temperature and the El Niño index did not influence recruitment (Table SM7.1, Fig. SM7.2). The CV in precipitation was the only covariate that showed an opposite effect on recruitment from what we predicted.

The analysis of the effect of individual climatic covariates (univariate models) indicated that all covariates affected survival (Table SM6, Fig. SM8.1). Most covariates positively influenced survival, except for the CV in temperature and the El Niño index. The covariates, CV in the cumulative amount of precipitation, lag in CV in precipitation and the El Niño index showed an effect in the opposite direction than what we predicted. The univariate models similarly indicated that most environmental covariates affected recruitment. The CV in temperature, cumulative amount of precipitation, CV of precipitation during the previous season, and gross primary production positively influenced recruitment (Fig. SM8.1), whereas El Niño index and CV in precipitation negatively affected recruitment (Fig. SM8.1). The lag in precipitation did not affect recruitment. The covariates, CV in temperature, lag in CV in temperature, and the El Niño index showed an effect in the opposite direction than what we predicted, although the effect is small.

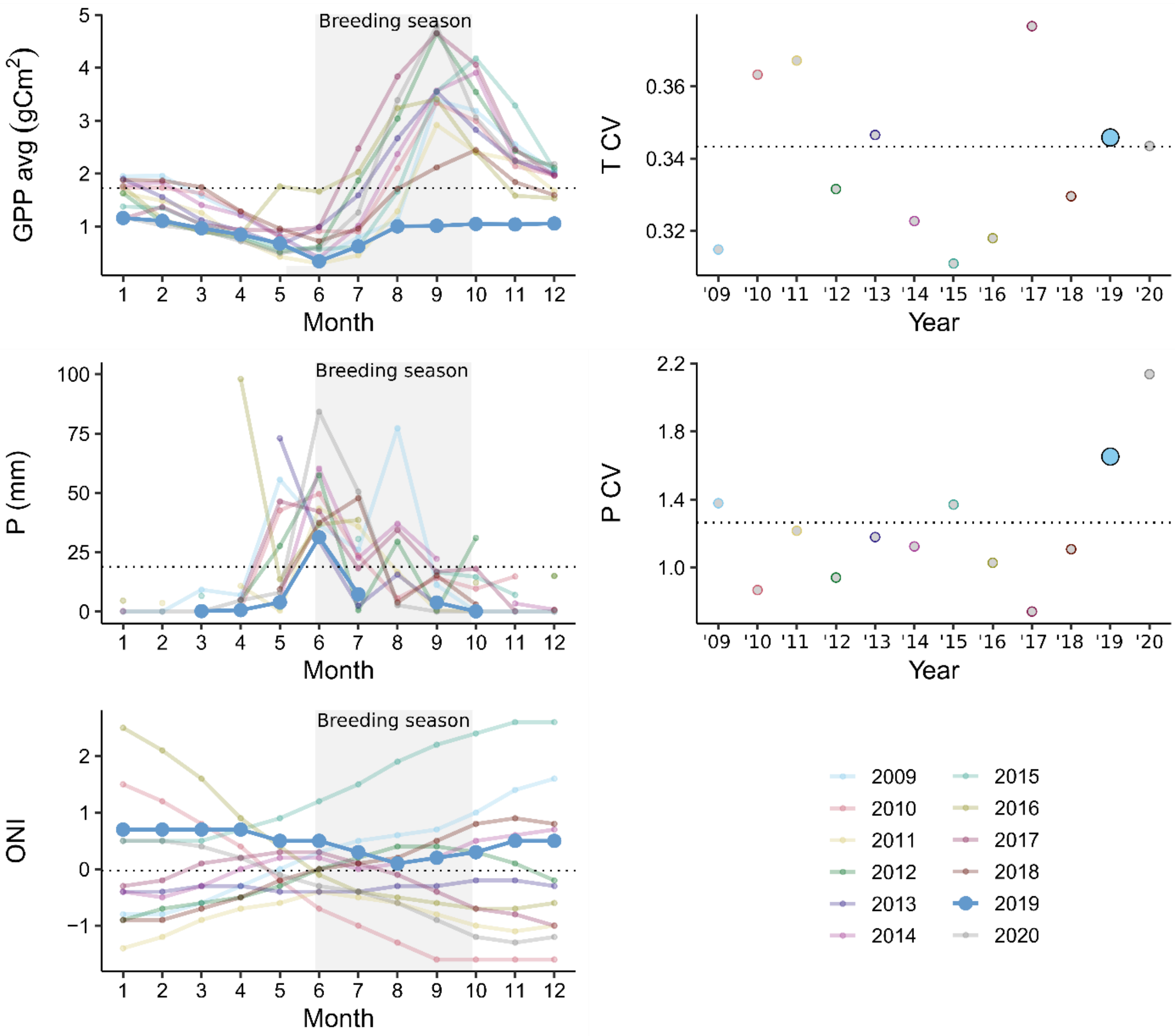
Figure 4. Survival and recruitment results in a degu population at Estación Experimental Rinconada de Maipú, Chile, based on the most parsimonious model including climatic covariates, season, and sex, in Table 2B. A) Survival is mainly driven by gross primary production (GPP) and is higher in the nonbreeding season with more GPP. B) Survival is significantly affected by GPP, season, and the interaction between GPP and season (GPP:Nonbreeding) but does not vary by sex. C) Recruitment is higher with more GPP and in the breeding season. D) Recruitment is significantly affected by GPP and season. The reference values in panels c and d are females and the breeding season. The breeding season (mating/early gestation) corresponds to the austral winter, while the nonbreeding season (offspring care) corresponds to the austral spring, summer, and beginning of fall. Females are shown in purple and males in green.



Factors contributing to the population's local extinction

To determine which environmental covariates contributed to the local extinction of our study population, we visualized the yearly and monthly trend of the included environmental variables (Fig. 5). Gross primary productivity showed a decline in 2019, the year before the population crash (Fig. 5). We observed that gross primary productivity was much lower during most of 2019 (cumulative amount of GPP of 159.85 gCm^2 and average GPP of 0.84gCm^{2}versus a total of 329.71 and average 1.86 gCm^2 across all study years, excluding 2019) but particularly during the breeding season (91.2 gCm^2 and average 0.75 gCm^{2}in 2019 versus 245.04 and average 2.01 gCm^{2}across all study years, excluding 2019) compared to other years of our study (Fig. 5). Furthermore, the variation in precipitation was relatively higher in 2019 compared to the other study years and the long-term average together with a lower-than-average amount of precipitation, suggests that there were very few months with precipitation in 2019 (Fig. 5). The CV in temperature followed average trends and changes in average ocean temperature in 2019 were intermediate (Fig. 5).

Figure 5. The included environmental variables per year and month. The year 2019 is highlighted in blue to demonstrate which environmental variables contributed to a population crash in the degu population at Rinconada, Chile in 2020. Horizontal dotted lines are the long-term average, except for the cumulative amount of precipitation (P) as the long-term average of 245 mm fell outside of the precipitation range from 2009-2019, so we use the average for the study period. The grey rectangle corresponds to the period from June to October, which includes the mating season, gestation, and early lactation (breeding season). The coefficient of variation (CV) in temperature and precipitation is provided by year as we did not have daily measures. ONI = El Niño Index.



Discussion

We used a 12-year long dataset of mark-recapture data to investigate the population demographics and environmental factors influencing demographic parameters and population dynamics of a degu population in central Chile that went locally extinct in 2020. We found that survival varied by year, season, and sex, similar to what was observed in a northern-central Chile degu population (Previtali et al. 2010). Recruitment varied seasonally and annually. Capture probability varied by year, and population growth was on average positive. When we included environmental covariates (excluding year), we found that survival was affected by gross primary production, while seasonality and gross primary production influenced recruitment. Therefore, food availability affected the population dynamics of degus, supporting the conclusion that an extreme and prolonged drought was a main driver of the local extinction of this population.

We found an interaction between season and sex in survival and recruitment. These interactions may reflect sex-specific differences in reproduction costs. Males experience greater reproductive costs in the austral fall due to the mating season, during which they compete with other males for access to females (Ebensperger and Hurtado 2005b; Soto-Gamboa, Villalón, and Bozinovic 2005; Ebensperger et al. 2019). For females, the austral winter and spring are energetically more demanding because they produce large, precocial young, with their gestation period lasting around three months (Woods and Boraker 1975). In years of high food availability, females can have a postpartum estrus, leading to a second litter emerging in early austral summer (Ebensperger et al. 2013; Meserve et al. 1995). The presence of second litters could also explain the seasonal difference in recruitment; degus breed primarily during austral winter, with first litters born in late August/September, so primary recruitment occurs in the breeding season. The limited recruitment that occurs in the nonbreeding season (austral spring, summer, and fall) can be explained by those second litters born in early summer, by juveniles born during the breeding season but not marked by the observers until the following year, and by immigration. Immigration and dispersal are more important drivers of group dynamics than adult fidelity and offspring philopatry in our study population (Ebensperger et al. 2009; Quirici et al. 2010). In summary, the interplay between seasonal demands and sex-specific reproductive costs significantly influences survival and recruitment patterns, highlighting the complex ecological dynamics that shape population dynamics in degus.

Density-independent factors influencing population dynamics

Gross primary production was the main driver of survival, particularly in the nonbreeding season, and of recruitment, particularly in the breeding season. Thus, food availability has a great impact on degu' population dynamics and contributed to the population crash in this population. We hypothesize that lower than average amount of precipitation resulted in reduced primary productivity, and that plant cover was reduced due to water deficits, soil nutrient depletion (Gutierrez and Whitford 1987), or a change in the plant community or plant quality (Gutiérrez and Meserve 2003). For example, koalas (*Phascolarctos cinereus*) experienced a population decline after a drought that caused water stress and the disappearance of edible leaves (Gordon, Brown, and Pulsford 1988). The preferred food of degus, green low fibre annual herbs (Bozinovic 1995), are most abundant during the austral winter and spring (i.e., the breeding season). However, the fact that primary productivity was almost absent in the 2019 breeding season (Fig. 5) emphasizes that food was unavailable for the degus. In summer, when these herbs are absent, degus shift their range to include shrubs (Quirici et al. 2010) and individuals consume lower-quality food sources, such as the foliage, seeds, and conductive tissue of shrubs (Quirici et al. 2010; Ebensperger and Hurtado 2005a). Our study site was also characterized by only 14% shrub coverage (Ebensperger and Hurtado 2005a). Such conditions likely limit opportunities to forage under shade, exposing foraging degus to a greater risk of heat-stress, while degus show low tolerance to heat stress (Kenagy et al. 2004), if they attempt to compensate for reduced energy intake by spending more time foraging under particularly harsh environmental conditions (Caraco 1980). During the summer months, degus show a bimodal activity pattern, foraging and remaining active right after dawn and right before dusk (Kenagy et al. 2002; Bacigalupe et al. 2003), thereby retreating into their burrows during the hottest times of the day. Degus remain active aboveground whenever they can forage under shrub covered microhabitats (Bacigalupe et al. 2003), implying that the scarce availability of shrub cover in our study population further increased the risk of local extinction. Degus demonstrate physiological plasticity by minimizing total energy expenditure (Bozinovic et al. 2004), recycling micronutrients via coprophagy (Kenagy, Veloso, and Bozinovic 1999), and conserving water in the dry and hot summer months (Ardiles et al. 2013; Bozinovic et al. 2003). Our result that gross primary production affects survival and recruitment indicates that physiological and behavioral plasticity does not buffer degus from low food availability throughout the year. Therefore, primary productivity provides essential food and shade for the degus. Subsequent research could use biophysical ecology to forecast the species' response to climate change (Briscoe et al. 2023).

In contrast to our prediction that the CV in temperature and El Niño index would negatively and positively, respectively, affect survival and recruitment, these covariates showed a small effect on survival and did not influence recruitment. Furthermore, our results indicate that recruitment is strongly driven by seasonality and the biology of the species than by environmental covariates. Variability in temperature most likely does not influence degus as they are a semifossorial species, where they can retreat into their burrows during harsher conditions. We noted that El Niño conditions occurred in 2009 and 2015 and La Niña conditions occurred in 2010. Changes in average ocean temperature during the other years were intermediate and did not result in strong ENSO events, suggesting a relatively small impact of the precipitation deficit during the megadrought (discussed below) (Garreaud et al. 2020). Although a degu population in northcentral Chile showed a delayed response in population growth after a strong ENSO event in 1990-1992 (Meserve et al. 1995), we did not observe a similar effect in our study population.

The Central Chile Megadrought

The decade-long megadrought that occurred during our study (Garreaud et al. 2020) represents an extreme climatic event (Smith 2011; van de Pol et al. 2017), with negative effects on the hydroclimate and severe ecological effects, such as vegetation loss (Garreaud et al. 2017). The average precipitation between 2009 and 2019 was 45% lower than that between 1976 and 2008 at our study site (SM2). We hypothesize that these conditions represented a tipping point for degus likely causing the population crash observed in 2020. The cumulative effect of similar droughts has been associated with population crashes in a number of other species, including black-tailed prairie dogs (*Cynomys ludovicianus*) (Facka et al. 2010), Glanville fritillary butterflies (*Melitaea cinxia*) (van Bergen et al. 2020), burrowing owls (*Athene cunicularia*) (Cruz-McDonnell and Wolf 2016), bumble bees (*Bombus* spp.) (Thomson 2016), and degus in northern central Chile (Previtali et al. 2010). Degus at our study site persisted for at least 10 years of drought, suggesting that this population was robust rather than resilient through periods of low food availability, but could not persist when food was unavailable throughout the entire year (Figure 5). Resiliency requires that species not only show resistance to disturbances but also demonstrate the ability to recover to a stable state after a perturbation (Hodgson, McDonald, and Hosken 2015; Holling 1973; Morecroft et al. 2012; Nelson 2011). If or when these extended droughts recur in the future, other degu populations may be at risk of local extinction. Thus, understanding the interplay between environmental stressors and the adaptive strategies of degus is crucial for predicting the resilience of degu populations in the face of climate change and for informing conservation efforts.

Potential density-dependent factors influencing population dynamics

Besides density-independent factors, density-dependent factors such as predation, changes in social relationships, and Allee effects, may have influenced population demographics. For example, degus may have faced increased mortality due to heightened predation (Meserve, Gutiérrez, and Jaksic 1993). Whenever population density is low, the impact of predation may be more pronounced (Meserve, Gutiérrez, and Jaksic 1993). The main predators of adult degus at our field site are culpeo foxes (*Pseudalopex culpaeus*) and black-chested buzzard eagles (*Geranoaetus melanoleucus*) (Ebensperger and Wallem 2002). Yet, population density and precipitation, but not predation by foxes, influence changes in population growth rate in a north-central degu population (Previtali et al. 2009), and the foxes change their preference for degus in this site and may select degus just because they are abundant (Kelt et al. 2025). Future research is needed to monitor whether predation increases during drought periods in central Chile.

Animals may respond to extreme environmental conditions by altering social relationships. For example, superb fairy-wrens (*Malurus cyaneus*) change group sizes to promote cooperative behaviors under harsh conditions (Camerlenghi et al. 2024). Rhesus macaques (*Macaca mulatta*) on Cayo Santiago island made new connections and became more tolerant of group members in response to heat stress after a hurricane destroyed most of the vegetation on the island resulting in shade becoming a limiting resource (Testard et al. 2021; 2024). In other species, extreme climatic conditions may negatively affect social and parent-offspring relationships. For example, in the cooperatively breeding pied babbler (*Turdoides bicolor*), adults reduce offspring provisioning (Wiley and Ridley 2016) and helpers stop helping (Bourne, Ridley, and Cunningham 2023) when it is hot. Thus, it is not surprising that living in groups does not confer survival benefits during periods of both extreme heat and drought in pied babblers (Bourne et al. 2020b). In degus, communal breeding may not work as a buffer against the harshest environmental conditions (Hayes et al. 2024). Although we did not quantify social restructuring, social network analyses conducted on three years of data at this study site indicate that females exhibit stronger relationships with other females during lactation than during mating and produce the most offspring per capita when social relationships with other females are homogeneous (Wey et al. 2013). Future analyses could investigate whether changes in social relationships during harsh environmental conditions affect fitness.

Positive density-dependence involves a positive relationship between population growth rate and population density (Courchamp, Clutton-Brock, and Grenfell 1999). Consequently, populations whose sizes fall below a critical threshold may face increased extinction risk, as the inability to maintain sufficient numbers exacerbates challenges in survival (Vercken et al. 2021). Critically, the risk of extinction faced by populations of group-living species characterized by positive-density dependence seems contingent on the extent to which group size is decoupled from population density. This condition results in populations with varying sized social groups (Angulo et al. 2018; Fryxell et al. 2007), implying that a few relatively medium to large sized groups may be present under low density conditions (Courchamp, Grenfell, and Clutton-Brock 1999; Keynan and Ridley 2016). Critically, fewer large-sized groups may buffer individuals from low density conditions, and ultimately, decrease population extinction risk (Angulo et al. 2013). A recent study with this degu population found that positive-density dependence occurred at the population level and that group size decreased with decreasing population density (Ebensperger et al. 2025). These findings suggest that positive-density dependence similarly contributed to the extinction of our study population.

Implications of this local extinction

Degus are important species within xeric ecosystems in north-central Chile (Meserve et al. 2016). Furthermore, degus are important prey for avian and mammal predators throughout their distribution (Meserve, Gutiérrez, and Jaksic 1993; Ebensperger and Wallem 2002). They are ecosystem engineers because other species use their burrow systems (Davidson, Detling, and Brown 2012) and are more successful foragers in areas with high density of degu runways (Root-Bernstein et al. 2013). Degus are also important seed dispersers of native plants (Loayza, Luna, and Calviño-Cancela 2020; Cordero, Gálvez, and Fontúrbel 2021). Therefore, the local extinction of degu populations could have cascading effects on ecosystem functioning, such as the opening of niche space for competitors (Prugh et al. 2018) or the collapse of native plants that rely on degus to disperse seeds (Loayza, Luna, and Calviño-Cancela 2020; Núñez-Hidalgo, Fleury, and Bustamante 2023).

Determining what factors contribute to local population extinctions helps us understand what populations are subject to population decline or, on the other hand will be resilient to climate change. Species with greater physiological and behavioral plasticity and the capacity for compensatory breeding following years with adverse climatic conditions may be the most resilient to environmental challenges (Bourne et al. 2020a; Testard et al. 2024; Camerlenghi et al. 2024; Boutin and Lane 2014; Hetem et al. 2014).

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Ethics

Procedures for handling and sampling from live animals were approved by the University of Tennessee at Chattanooga Animal Care and Use Committee and by the Faculty of Biological Sciences at Pontificia Universidad Católica de Chile (DFCB-021-2008 and CBB-229/2012), under Chilean permits issued by the Servicio Agrícola y Ganadero (1-109/2008 (3542), 1-31/2009 (1956), 2826/2013, and 1-49/2010 (2332). Protocols adhered to the guidelines outlined by the American Society of Mammalogists Animal Care and Use Committee (Sikes 2016).

Data availability statement: All data have been deposited at the GitHub repository annemarievdmarel/degu-pop-crash (van der Marel 2025). The used MODIS data are available at https://lpdaacsvc.cr.usgs.gov/appeears (accessed 17 December 2023).

Conflict of interest: The authors declare no competing interests.

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