Extreme drought impacts drove local extinction in a social rodent

Running title: Drought-driven local extinction in degus

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Open research statement: All data have been deposited at the GitHub repository https://github.com/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 and 02 March 2026). Climatic data from Pudahuel airport (station number 330021) are available at https://climatologia.meteochile.gob.cl/.

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Abstract

Wildlife populations worldwide are increasingly exposed to climatic extremes, yet demographic mechanisms linking environmental variability to local extinction remain poorly understood. We evaluated the population dynamics of a degu (*Octodon degus*) population in central Chile over a 12-year period (2009-2020) encompassing a decade-long megadrought. Using capture-mark-recapture models, we estimated apparent survival, recruitment, and population growth rates and assessed their relationships with climatic and ecosystem variables. Population growth remained positive throughout most of the study period despite prolonged drought conditions, indicating substantial resistance to long-term environmental stress. However, in 2019, an extreme drought year characterized by markedly reduced precipitation and resource availability, where gross primary productivity (GPP) crossed a critical threshold (tipping point) causing sharp declines in survival and recruitment, resulting in an abrupt state shift, rapid population collapse, and subsequent local extinction. Our analyses indicate that variation in GPP was the strongest predictor of both survival and recruitment, highlighting the importance of resource availability in mediating demographic responses to drought. These results show that the extreme environmental conditions in 2019 acted as the proximate driver of extinction, rather than a cumulative effect of the preceding megadrought. We discuss how species-specific traits, including short lifespan, seasonal reproduction, and social organization, may limit the ability of degus to buffer consecutive demographic failures under extreme conditions, contributing to threshold-like population collapse. Our findings suggest that populations may persist under prolonged adverse conditions yet remain vulnerable to rare but severe environmental events, emphasizing the importance of extreme climatic variability in driving local extinction risk.

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 & Wilson, 2011;

McLaughlin et al., 2002; Patrício et al., 2019; Thomas et al., 2004; Urban, 2015). Sometimes, local extinctions are linked to the consequences of single, widespread factors such as marine heat waves (Montie & Thomsen, 2023; Thomsen et al., 2019), El Niño Southern Oscillation (ENSO) events (Kelt et al., 2005), or extended droughts (Ehrlich et al., 1980; Facka et al., 2010; Trape, 2009). Alternatively, local extinctions are associated with a combination of perturbations (Sergio et al., 2022), and climatic or environmental changes leading to habitat loss (McLaughlin et al., 2002; Munday, 2004) or food depletion (Durance & Ormerod, 2010; Epps et al., 2004). 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., 2010, 2011), such as reaching critical thermal maxima in ectothermic species (Sinervo et al., 2010), alongside habitat requirements and specialized feeding habits (Moritz & Agudo, 2013). However, climate change remains a primary driver of most local extinctions in herbivores by reducing food availability (Cahill et al., 2013). Importantly, populations may achieve population persistence under prolonged environmental stress yet undergo abrupt state shifts when extreme climatic conditions exceed critical thresholds (Dai et al., 2013; Holling, 1973; Scheffer et al., 2001), highlighting the need to understand how environmental variability translates into demographic responses.

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 (Gherardi & Sala, 2015; Zhang et al., 2022). Changes in precipitation and in the atmosphere's evaporative demand may result in increased drought severity (Meseguer-Ruiz et al., 2024; Vicente-Serrano et al., 2020). Drought effects include reduced annual plant production, stem growth, and leaf area index (Krishnan et al., 2006). Droughts and heatwaves may be particularly severe in arid and semi-arid ecosystems (IPCC, 2014) where low and highly variable rainfall, high potential evapotranspiration, and limited soil water storage mean that climate change (e.g., reduced water availability or increases in temperature) can strongly affect primary productivity, species survival, and ecosystem services (Arroyo et al., 2020; Miranda et al., 2023; Mirzabaev, A et al., 2022; Polyakov et al., 2021; Srivathsa et al., 2019).

An extreme climatic event of prolonged rainfall deficit and elevated temperatures between 2010 and 2022 in central Chile (Garreaud, Boisier, Rondanelli, Montecinos, Sepúlveda, & Veloso-Aguila, 2020; Garreaud et al., 2025), called the Central Chile Megadrought (hereafter termed 'megadrought'), represents a multi-year drought period that departs strongly from the region's historical climate variability (Grant et al., 2017; Smith, 2011; van de Pol et al., 2017). This megadrought has caused socioeconomical and ecological impacts with negative effects on hydroclimate and primary productivity (Garreaud et al., 2017). Within this prolonged drought period, two extreme drought years stand out: 2019 and 2021 in which the standardized annual precipitation anomaly fell within the lowest 5 % of the historical distribution (Garreaud et al., 2025). We examined the impacts of these extreme climatic events (prolonged drought conditions of the *megadrought* and the *extreme drought year* of 2019) on the population dynamics of the common degu (*Octodon degus*) (Ebensperger et al., 2014, 2021).

We investigated 1) the demography and population dynamics of a degu population using a dataset spanning 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. Degus are small (range body mass 170 to 300g), diurnal, semi-fossorial social rodents that are endemic to Chile and inhabit semi-arid environments. Degus form social groups that typically include about two (range: 1-8) adult males and females, which may be either related or unrelated (Davis et al., 2016; Ebensperger et al., 2004; Hayes et al., 2009, 2019). Degus 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 et al., 2002, 2007; Ebensperger & Hurtado, 2005a). They occasionally produce second, smaller sized litters in early austral summer, but secondary litters are relatively uncommon

(Ebensperger et al., 2013; Meserve et al., 1995). Degus similarly 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, 2011a) and wean six offspring on average (Long & Ebensperger, 2010). Recently, we further reported that both per capita population growth rate and per-female fecundity rate increase with degu density, implying demographic and component population-level Allee effects, that these effects are 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 and, under the harshest of climatic conditions, may even magnify their negative effects, potentially increasing vulnerability to rapid population collapse under extreme environmental conditions. Although the IUCN red list status classifies degus as 'Least Concern' (Roach, 2016), it remains unclear why some degu populations are able to survive through adverse events while others experience local extinction (Previtali, Meserve, Kelt, Bryan Milstead, et al., 2010). Understanding how environmental variability influences population dynamics in this system can help identify which populations are most vulnerable to projected climate change and inform strategies to prevent local extinctions.

We developed a priori hypotheses addressing population demographics and the influence of environmental factors on survival and recruitment rates. Given that populations may persist under prolonged drought yet collapse under extreme conditions, we also evaluated whether demographic responses were consistent with a threshold-like response to environmental variability. First, we hypothesized that survival and recruitment fluctuate with year, season, and sex. Survival and recruitment rates would increase (1) in years with favorable conditions, which include abundant precipitation (Ebensperger et al., 2014; Meserve et al., 2011; Previtali, Meserve, Kelt, Milstead, et al., 2010) and high food abundance (Ebensperger et al., 2014, 2021), particularly a high abundance of green low-fibre annual herbs (Bozinovic, 1995); and (2) during the breeding season, when food is more abundant than in the nonbreeding season and when females communally rear their offspring. Furthermore, we predicted that (3) survival rates would be higher for females than males, whereas (4) recruitment rates would not differ between males and females. Female survival may be relatively high because females gain fitness per weaned offspring and thus benefit from increased longevity, and maintain more stable preferred associations than males (Wey et al., 2013). In contrast, males experience greater costs in the austral fall due to the mating season, during which they compete with other males for access to females to achieve breeding benefits (Ebensperger et al., 2019; Ebensperger & Hurtado, 2005b; Soto-Gamboa et al., 2005), which may increase male mortality, as observed in many mammals, although direct measurements are scarce. We did not expect recruitment rates to differ because immigration and dispersal for both sexes are more important drivers of group dynamics than adult fidelity and offspring philopatry in this study population (Ebensperger et al., 2009; Quirici et al., 2010).

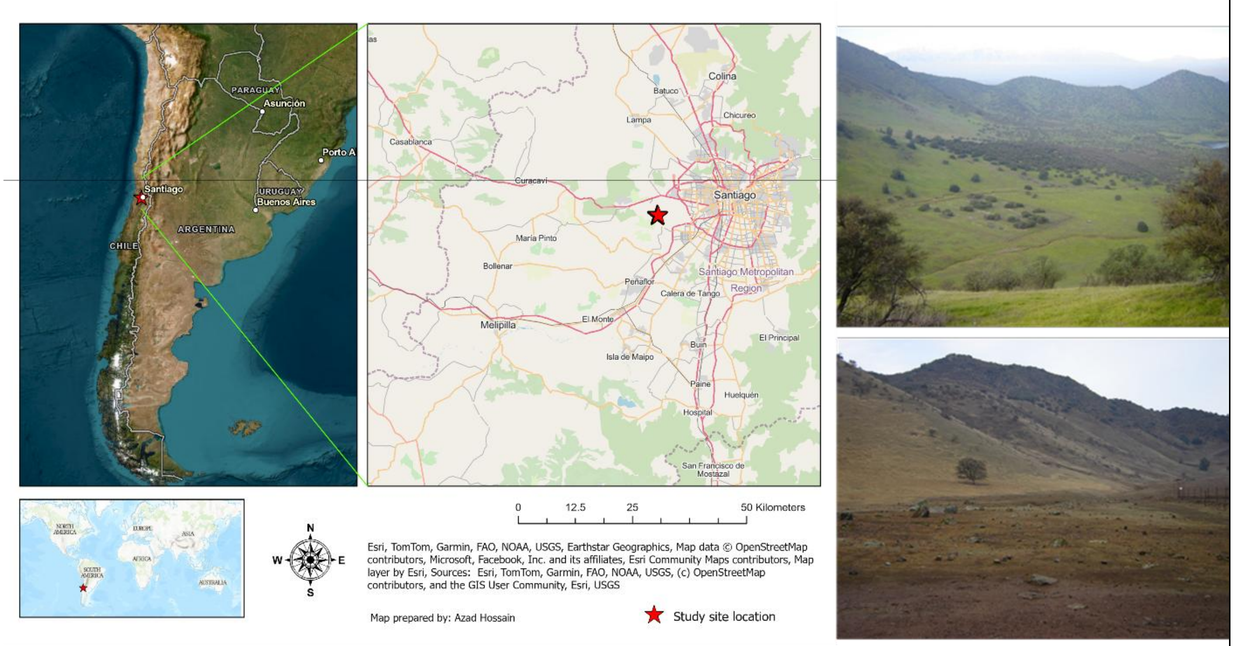
Second, we hypothesized that survival and recruitment would be positively associated with weather variables that enhance plant growth and resource availability (Table SM1), as favorable conditions for degus include abundant rainfall and high food abundance (Ebensperger et al., 2014, 2021). Furthermore, the studied population is situated near the southern limit of the species' distribution, with a predominant Mediterranean climate of dry, warm summers and cold, wet winters, where range limits are defined by conditions that are too wet conditions in the south and too dry in the north to support their main food sources (Cadenillas & D'Elía, 2021a, 2021b; Contreras et al., 1987; Woods & Boraker, 1975). Therefore, we predicted that survival and recruitment would be (1) negatively influenced by conditions characterized by relatively high and more variable air temperatures due to their negative effects on food availability and due to the degus' low tolerance to heat (Kenagy et al., 2004). Degus may be constrained to forage in areas with shrub vegetation to avoid direct exposure to intense solar radiation (Kenagy et al., 2004; Lagos et al., 1995). Additionally, we predicted that degu survival and recruitment would be positively influenced by rainfall patterns that have positive effects on food availability, such as (2) increasing mean rainfall and decreasing precipitation variability; (3) high mean and low variance in precipitation during the previous season reflecting lagged effects of plant growth following precipitation events; 4) increased biomass production (gross primary productivity); and (5) increased resource availability during “El Niño” events, which can enhance primary productivity and promote population growth. Consistent with this prediction, “El Niño” events often lead to population growth among rodents inhabiting semi-arid and arid environments (Armas et al., 2016), including degus in northern Chile (Previtali, Meserve, Kelt, Milstead, et al., 2010).

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 study site was established as a long-term study of degu social organization. Two grids were chosen based on degu presence. Vegetation consists mostly of grass and scattered shrubs that covered around 14% of the field site (Ebensperger & Hurtado, 2005a).

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, whereas the nonbreeding season (offspring care) corresponds to the austral spring, summer, and beginning of fall. The maps (three left panels) were prepared by Dr. Azad Hossein and the photos (right panels) were taken by Dr. Loren D Hayes.



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Map prepared by: Azad Hossain

From 2009 to 2020, we monitored a degu population at Rinconada using capture-mark-recapture (CMR) methods. We trapped degus twice a year: in austral fall (May – early July) and spring (late August – early November) (SM2). We live-trapped degus at 40 burrow systems each season and year (mean ± SD = 40.2 ± 2.6 burrow systems/season/year) by placing 10 Tomahawk traps (model 201, Tomahawk Live Trap Company, Hazelhurst, WI) around burrow openings in an area of 2.1 ± 1.7 ha (mean ± SD), depending on the abundance and spacing of degu social groups. Burrow systems are groups of interconnected burrow openings from which individuals emerge during daytime and return to at nighttime (Fulk, 1976). The home ranges of degus vary seasonally according to food conditions (Quirici et al., 2010), resulting in different burrow system usage. Across years and sometimes within seasons, the set of monitored burrow systems varied, but we used approximately the same number of traps (396.5 ± 20.3 traps/season/year). The decision to change at which burrow systems we trapped was based on several reasons: (1) Some burrow systems became inactive, as degus could switch the burrows they used—even on a nightly basis (Ebensperger et al., 2011b); (2) more social groups were targeted (so that not all traps were around burrow systems belonging to the same social group); (3) radio collars had to be retrieved; and (4) juveniles had to be trapped to collect genetic samples.

Trapped individuals consisted of degus that remained within the two grids but also degus that passed through or emigrated to the field site. Newly captured adult degus (i.e., degus from the surrounding area) in the fall season accounted for 9.9 ± 0.4 % (mean ± SE) and in the spring season for 2.9 ± 0.1 % of all the degus in the field site. 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 did not have reliable information on 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, resulting in 24 trapping windows. 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 (SM2). The year 2020 was excluded from the capture–mark–recapture (CMR) model because no degus were trapped despite similar trapping effort to other years (except fall 2020). Even with additional trapping periods in the austral summer of 2020 and 2021, no degus were trapped (Table 1).

For the environmental covariates, we selected two periods. We selected the austral winter spanning June to September, when 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, termed breeding season. We selected the 8-month period from October to May as the other period representing austral spring through summer and fall, when food availability declines and almost no precipitation occurs, and the highest temperatures are recorded. This period includes the ending of offspring care, termed nonbreeding season.

We used temperature and precipitation records from 1975-2025 from the Pudahuel Santiago weather station - (33∘22′42″S, 70∘47′16″W, elevation 474m, https://climatologia.meteochile.gob.cl/application/informacion/fichaDeEstacion/330021), the closest located weather station to the field site. From these records, we obtained the following variables for the two seasons (SM3): average air temperature (mean T in °C) as the mean of monthly temperatures, coefficient of variation (CV) of air temperature (T_CV), the maximum air temperature during the season (max T 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.

To examine different aspects of vegetation at our field site location (UTM coordinates -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 gC/m²/8day, MOD17A2HGF Version 6.1) (Running & 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 et al., 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://psl.noaa.gov/data/timeseries/month/DS/ONI/).

Data analysis and modeling

We used a survival – recruitment parameterization of Pradel’s temporal symmetry capture–mark–recapture (CMR) modeling framework (Nichols, 2016; Pradel, 1996; Williams et al., 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). Specifically, 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 individual in the population at sampling occasion t. The realized population growth rate λ_t is 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. We checked for collinearity among environmental covariates and discarded variables with Pearson correlation coefficients of $|r| \geq 0.5$ (SM4). We retained the following environmental covariates per season: the coefficient of variation of mean air temperature (T_CV), the cumulative seasonal precipitation (P), the CV of precipitation (P_CV), the one-season lag in the cumulative precipitation (P_lag), one-season lag in the CV of precipitation (P_CV_lag), gross primary productivity (GPP), and the El Niño index (ONI). We scaled our quantitative variables by mean-centering and scaling by the standard deviation. Because environmental covariates varied substantially among years (SM5), we also fitted models including climate covariate(s), season, and sex, while excluding year effects (presented in the result section). Marked degus that were confirmed dead (i.e., 55 individuals whose carcasses were recovered) were censored.

We performed CMR analysis in program MARK (White & Burnham, 1999) using the 'RMark' package v3.0.0 (Laake, 2013) for the R computing environment v4.3.2 (R Core Team, 2025). Tables with full model results are included in the Supplemental Material 6. We used an information-theoretic approach with

AIC_c (Akaike Information Criterion corrected for small sample size) 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 considered equally plausible and are discussed in the main text. For completeness, we reported covariate effects from models with ΔAICc > 2 but when 95% confidence intervals for regression coefficients did not overlap zero in Supplementary Material 7, and univariate effects of environmental covariates in Supplementary Material 8. We specified time intervals between austral fall and spring sampling occasions in months, such that estimates of all demographic parameters represent monthly rates. Unless otherwise stated, we report mean ± SE for observed metrics and point estimates with 95% confidence intervals for model parameters.

In addition to the information-theoretic approach, we conducted likelihood ratio tests (LRTs) to evaluate specific hypotheses regarding the effects of demographic and environmental covariates on survival and recruitment. LRTs were used to compare nested models fitted to the same dataset, in which a single effect differed between models while other parameters (e.g., p and f) were held constant, thereby allowing formal assessment of the contribution of individual covariates. We applied LRTs to models evaluating the effects of season, year, and sex, as well as to models including climate covariates (with and without seasonal effects). We excluded year from LRT-based comparisons of climate covariates due to high interannual variability. We retained the information-theoretic framework for primary inference because it permits comparison of both nested and non-nested models, whereas LRTs are restricted to nested model structures. Results of LRTs are presented in Supplementary Material 9.

Results

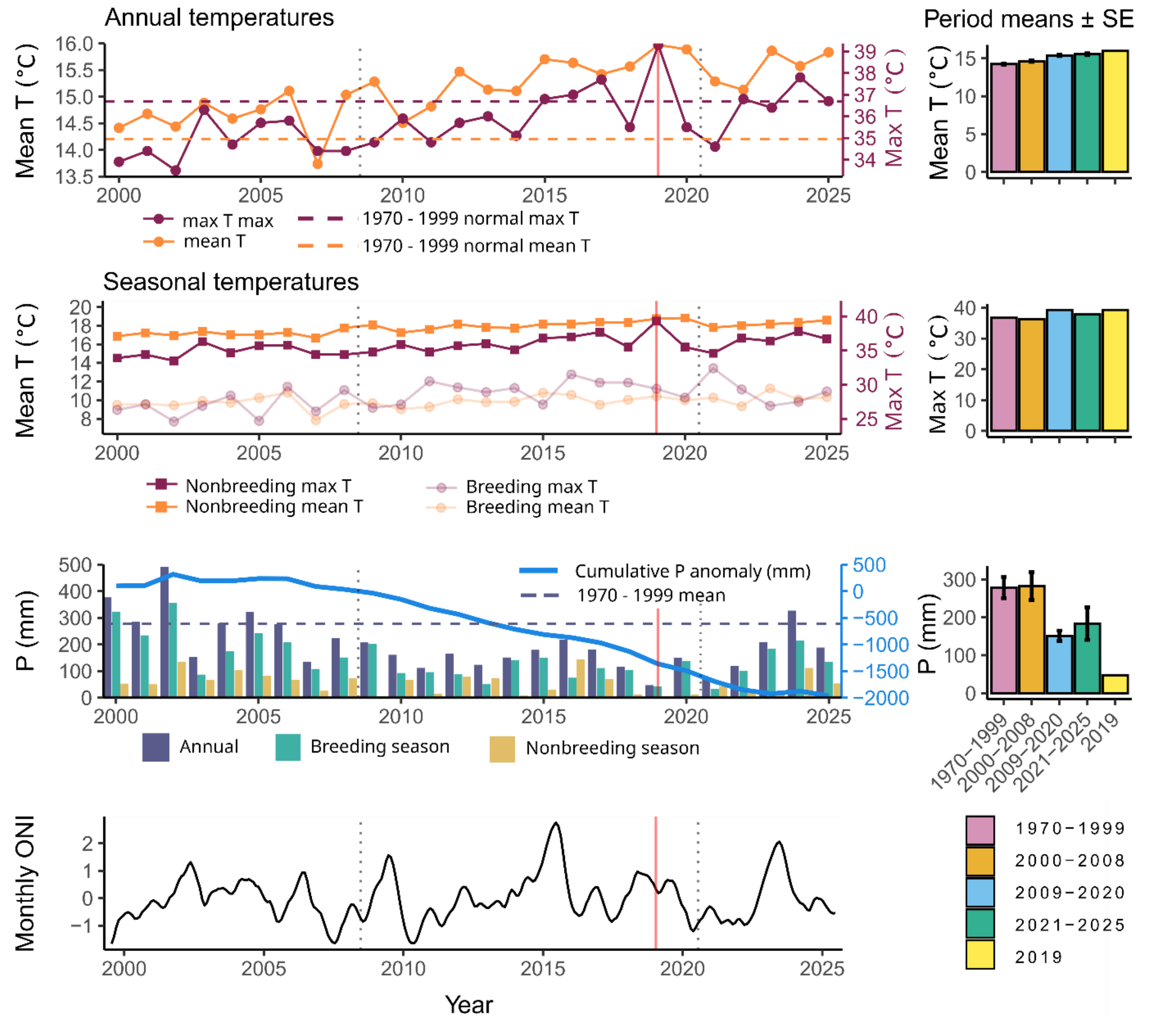
From 2009 to 2019, we captured 2,547 unique individuals, including both adults and juveniles, a total of 14,526 times, comprising 7,662 captures of 1,254 females and 6,864 captures of 1,293 males. On average 141 (± 25.6 SE) degus were trapped each year with fewer degus captured in the austral fall (61.0

± 10.7) compared to the austral spring (221.5 ± 38.2). In 2020 and the summer of 2021, we set traps, but no degus were captured despite comparable sampling effort (Table 1), 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 adjacent areas outside the study area.

The meteorological and ecosystem variables at Rinconada followed the patterns observed across central Chile during the Central Chile Megadrought (Garreaud, Boisier, Rondanelli, Montecinos, Sepúlveda, & Veloso-Aguila, 2020; Garreaud et al., 2025), showing elevated temperatures, and reduced rainfall and primary productivity (Fig. 2 and 3). Over the study period (2009–2020), precipitation was 45% lower than the 30-year historical baseline period (1970–1999) (Fig. 2), gross primary productivity (GPP) was 13%, evapotranspiration (ET) was 14%, and leaf area index (LAI) was 14% lower than the 2000–2008 mean (Fig. 3). The mean LAI value (~0.5) indicates consistently sparse vegetation. Together with reduced GPP and ET, these patterns indicate sustained reductions in water and food availability during the study period.

Figure 2. Annual and seasonal variation in climate variables at the Pudahuel Santiago weather station (33∘22’42”S, 70∘47’16”W, elevation 474m), from 2000 to 2025 relative to historical conditions. Left panels show mean annual and mean seasonal variation in mean temperature (mean T), the maximum daily temperature recorded by year and season (max T) to highlight extreme conditions, the annual and seasonal variation in total precipitation (P), and the monthly Oceanic Niño Index (ONI). The breeding season (mating/early gestation) corresponds to the austral winter, whereas the nonbreeding season (offspring care) corresponds to the austral spring, summer, and beginning of fall. Horizontal dashed lines indicate the mean annual values for the 30-year historical baseline period (1970–1999). In the precipitation panel, the blue curve represents the cumulative precipitation deficit for 2000-2025, calculated as the running sum of annual anomalies relative to the multi-year mean. The vertical red line marks the extreme drought year of 2019, and the vertical black dotted lines indicate the focal study period (2009–2020). Right panels show mean ± SE of mean T, max T, and P for four periods (1975–1999, 2000–2008, 2009–2020, and 2021–2025), with the value for 2019 shown separately to highlight the extreme drought conditions during that year.

Figure 2

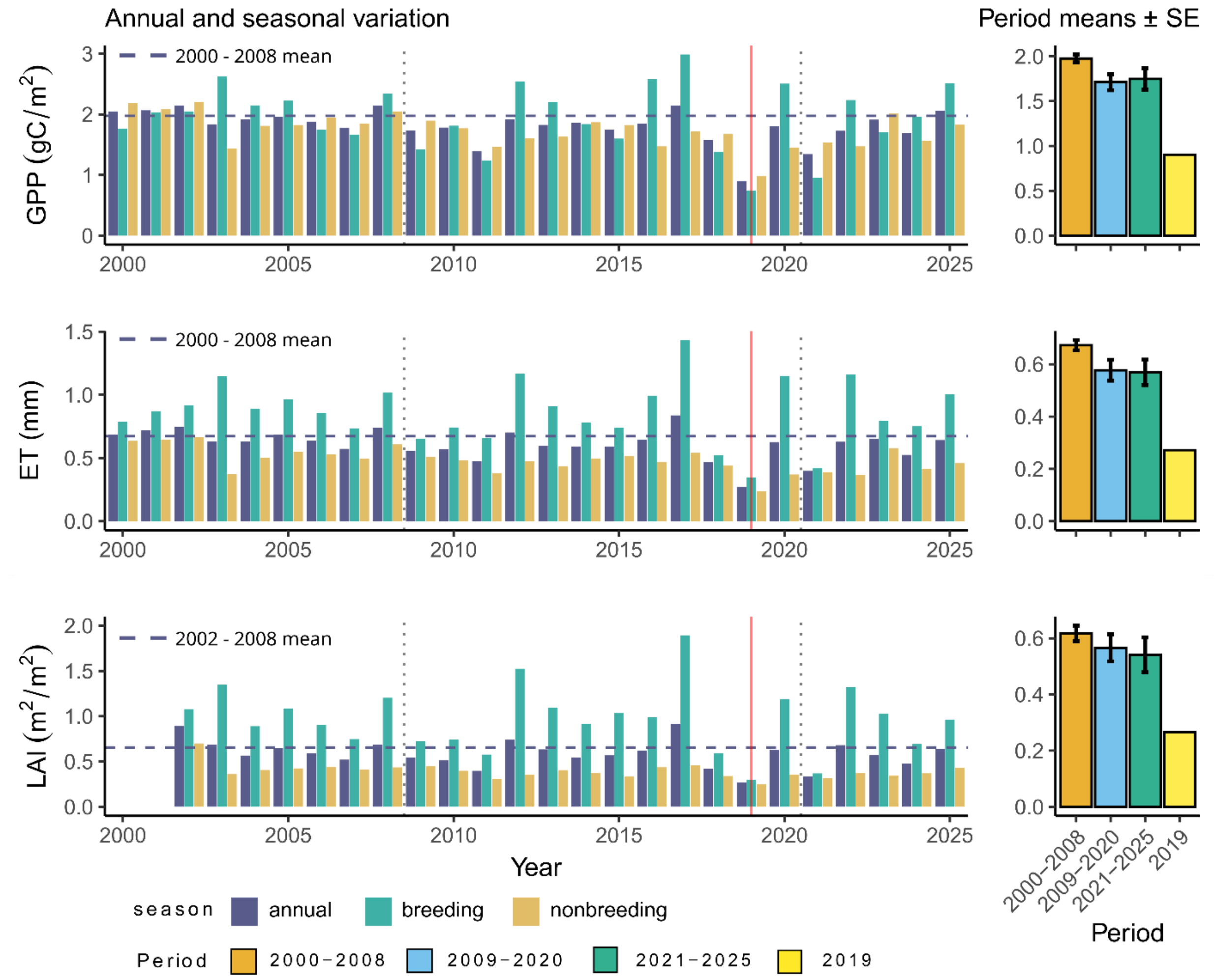


Conditions in 2019 were markedly more extreme than in the preceding years (Fig. 2 and 3), consistent with the observed patterns across central Chile (Garreaud, Boisier, Rondanelli, Montecinos, Sepúlveda, & Veloso-Aguila, 2020; Garreaud et al., 2025). Precipitation was 83% lower than the historical baseline, and the maximum temperature reached 39.3 °C (Fig. 2), imposing extreme heat and water stress. GPP, LAI, and ET declined by 54%, 55%, and 59%, respectively, relative to the 2000–2008 mean (Fig. 3), reflecting severely reduced food availability, very sparse vegetation, and limited shade, indicating exceptionally poor environmental conditions during that year. Based on the austral winter mean ONI, El

Niño conditions occurred in 2009 and 2015, and La Niña conditions in 2010, whereas ocean temperatures in other years remained intermediate and did not correspond to strong ENSO events (Garreaud, Boisier, Rondanelli, Montecinos, Sepúlveda, & Daniel Veloso-Aguila, 2020). These results indicate that the observed long-term trends in temperature, precipitation, and ecosystem variables primarily reflect chronic climatic and drought stress, rather than short-term variability associated with ENSO events.

Figure 3. Variation in ecosystem variables at Estación Experimental Rinconada de Maipú, Chile, from 2000 to 2025. Left panels show annual and seasonal variation in ecosystem variables, gross primary productivity (GPP), evapotranspiration (ET), and leaf area index (LAI), relative to the 2000-2008 mean (dashed blue horizontal line). The breeding season (mating/early gestation) corresponds to the austral winter, whereas the nonbreeding season (offspring care) corresponds to the austral spring, summer, and beginning of fall. The vertical red line marks the extreme drought year of 2019, and the vertical black dotted lines indicate the focal study period (2009–2020). Right panels show mean ± SE of GPP, ET, and LAI, respectively, for the periods, 2000–2008, 2009–2020, and 2021–2025, with the value for 2019 shown separately to highlight the extreme drought conditions during that year.

Figure 3



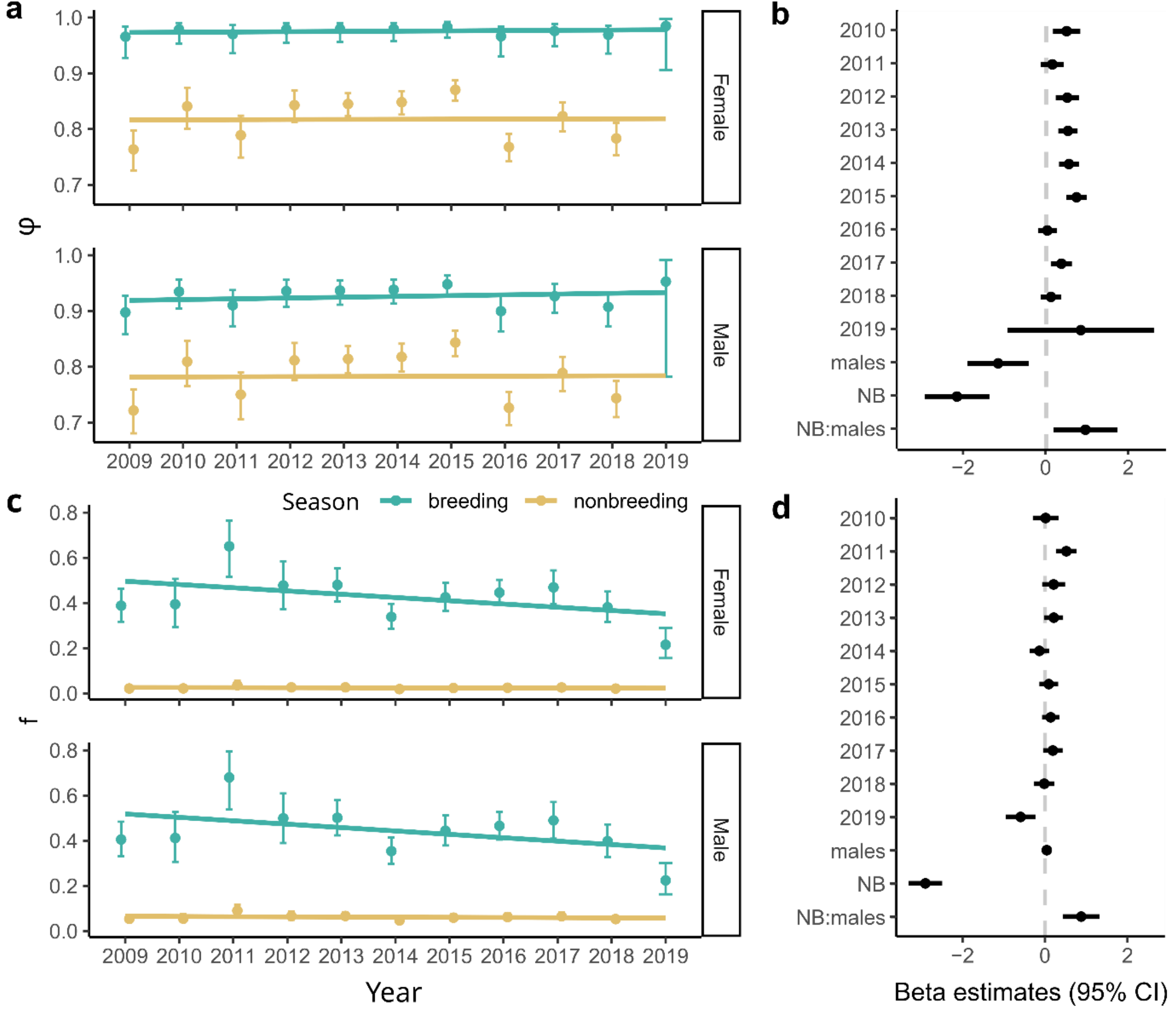
Population demographics

The overall monthly apparent survival was 0.88 ± 0.01 and was relatively stable across the study period (Fig. 4a). However, 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. 4). Degus had higher survival during the breeding than during the nonbreeding season, and females experienced higher survival than males (Fig. 4a). Compared with 2009, survival was higher in 2010, in 2012 through 2015, and in 2017 (Fig. 4b). The monthly recruitment rate varied by year, season, and sex, but showed an overall decline throughout the study period (Fig. 4c).

Recruitment was higher in 2011 but lower in 2019 compared with 2009 (Fig. 4d). Recruitment rate was higher during the breeding than during the nonbreeding season (Fig. 4d). In contrast to our prediction, recruitment rate was lower for females compared with males, particularly in the nonbreeding season (Fig. 4d).

Figure 4. 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 1A. The left-hand panels show a) apparent survival (ϕ) and c) recruitment rate (ƒ) for females in the top panel and males in the bottom panel for the breeding (B; green) and nonbreeding (NB; yellow) season. Error bars represent 95% confidence intervals. We included fitted lines by sex. The right-hand panels show the regression parameter (beta estimates) with the 95% CI for b) survival, and d) recruitment. The reference values are 2009, 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.

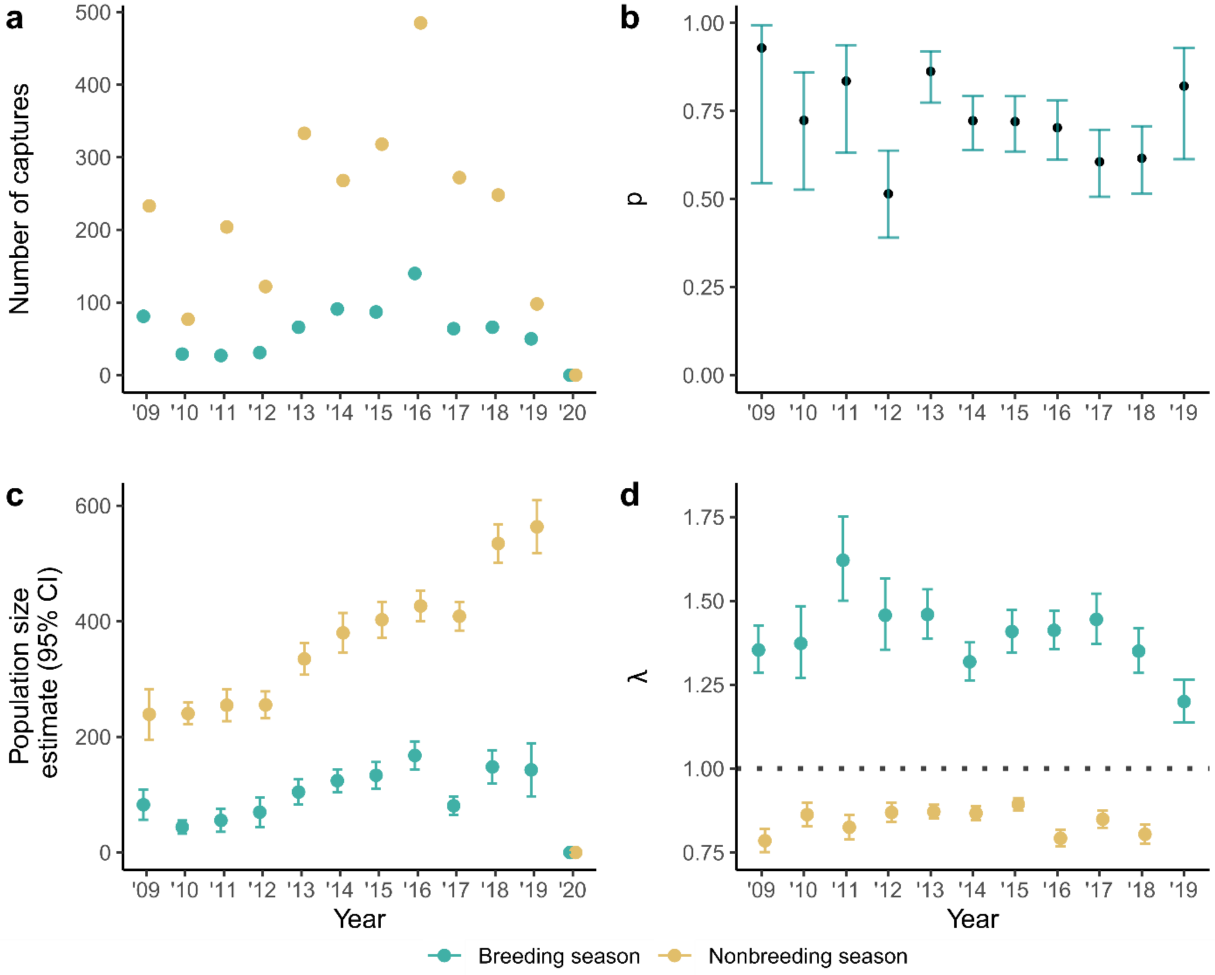
Figure 4



A competing model (ΔAIC$_c$ < 2) differed primarily in model structure for capture probability. Number of captures varied among years, with a peak in 2016. Each year more degus were captured in the nonbreeding season as this season consisted of both adults and juveniles (Fig. 5a). Capture probability varied among years, with lower capture probabilities in 2012 compared to 2009; capture probabilities in other years were similar to that recorded in 2009 (Table 2A, Fig. 5b). The estimated population size during our study period ranged from 142.2 degus in 2010 to 353.3 in 2019 and was higher in the nonbreeding season (336.7 ± 44.0) than the breeding season (96.1 ± 14.3). The estimated population size exhibited an increasing trend until the crash in 2020 (Fig. 5c). 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. 5d).

Figure 5. Capture estimates and population size parameters for a degu population at Estación Experimental Rinconada de Maipú, Chile, from 2009-2020 based on the most parsimonious model in Table 1A. The panels show a) the number of degus trapped, b) capture probability (p), c) population size estimate, and d) 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 represent 95% confidence intervals. The horizontal dotted line in d) shows a stable population (λ=1).

Figure 5

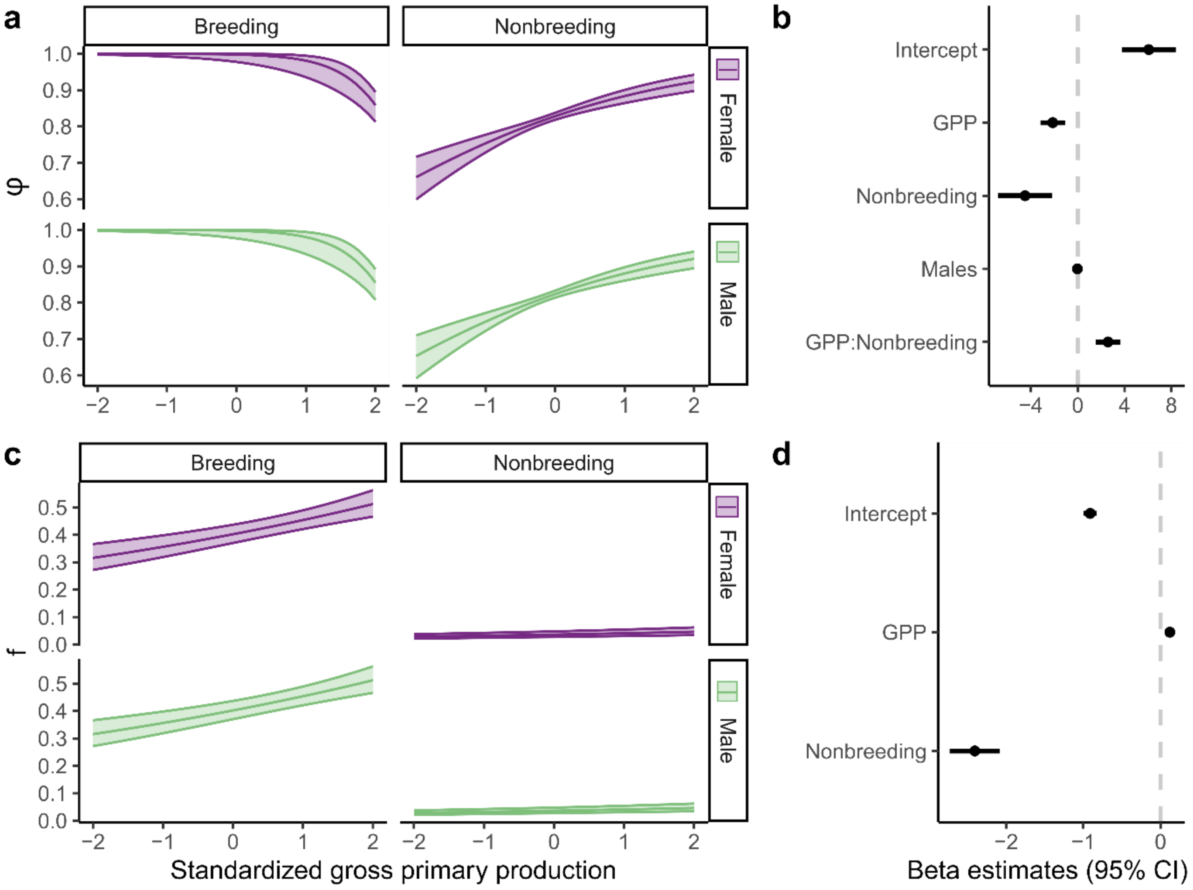


Effects of environmental covariates on population demographics

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. Model selection results revealed that gross primary production (GPP) was the strongest predictor of survival and recruitment (Table 2B; Fig. 6; model #146 Table SM6.3). Similar to models without environmental covariates, survival covaried with season with higher survival in the breeding season. Although sex was included in the top model, survival did not vary substantially with sex (Fig. 6a). Survival increased with GPP in the nonbreeding season (Fig. 6b). In contrast, the GPP influence on survival during the breeding season was weak (Fig. 6a). Overall, GPP has a positive effect on survival independent of season (slope of 0.45). Likewise, recruitment increased with GPP and varied with season (Fig. 6c, Table 2B), with higher recruitment occurring during the breeding season (Fig. 6d).

Figure 6. Survival and recruitment results in a degu population at Estación Experimental Rinconada de Maipú, Chile, based on the most parsimonious model including environmental covariates, season, and sex, in Table 1B. 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.

Figure 6



370

371 Other environmental variables also influenced survival and recruitment, but these effects were not supported in the top 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). These models suggested that several environmental

covariates influenced survival (Table SM7.1, Fig. SM7.1) and recruitment, although these effects were inconsistent across parameters (Table SM7.1, Fig. SM7.2). Univariate analysis indicated that all environmental covariates were associated with survival and recruitment (Table SM5, Fig. SM8.1). Likelihood ratio tests (LRTs) further supported gross primary productivity (GPP) as the strongest and most consistent environmental predictor of both survival and recruitment, whereas support for other covariates was weaker and model-dependent (Table SM9).

Discussion

Using a 12-year mark–recapture dataset, we show that a degu population in central Chile persisted demographically through nearly a decade of drought, with survival and recruitment varying by year, season, and sex, similar to patterns observed in a northern-central Chile degu population (Previtali, Meserve, Kelt, Milstead, et al., 2010). Capture probability varied by year, and population growth was on average positive throughout most of the study period. When environmental covariates were included (excluding year), survival was affected by gross primary production, whereas seasonality and gross primary production influenced recruitment, indicating that food availability affected degu population dynamics. Despite these positive demographic trends, degus at our study site showed resistance to prolonged periods of low food availability but experienced an abrupt state shift when food availability passed a critical threshold during the extreme 2019 drought. This contrast indicates high resistance to chronic stressors but no resilience to acute extremes, as the population failed to recover. Resiliency requires that species not only resist disturbances but also recover to a stable state following perturbation (Hodgson et al., 2015; Holling, 1973; Morecroft et al., 2012; Nelson, 2011). The extreme drought in 2019 may have represented a tipping point crossed via a critical threshold in primary production, leading to the population crash in 2020. Together, these results support persistence under chronic drought conditions but vulnerability to extreme climatic events. If such extreme drought conditions recur (Cook et al., 2022), and given projections of increasing drought severity in central Chile under high emissions scenarios (Meseguer-Ruiz et al., 2024), other degu populations exposed to similar environmental conditions may face local extinction. Understanding how environmental stressors interact with species' adaptive strategies is therefore critical for predicting population persistence under climate change.

Sex-specific seasonal effects on survival and recruitment

Consistent with our first hypothesis, we found a season by sex factor interaction in survival and recruitment, indicating that demographic rates are shaped by sex-specific reproductive strategies and seasonal energetic demands, consistent with observed patterns in survival and recruitment (Fig. 4). Males experience greater reproductive costs during the austral fall when they compete for access to females during the mating season (Ebensperger et al., 2019; Ebensperger & Hurtado, 2005b; Soto-Gamboa et al., 2005), a period that matches relatively low GPP (Fig. SM3.1), potentially increasing vulnerability under conditions of limited food availability. In contrast, females face higher energetic demands during austral winter and spring, when they produce large, precocial offspring following a gestation period of approximately three months (Woods & Boraker, 1975). Because female fitness depends on the number of weaned offspring, it is more strongly constrained by survival than male fitness, making persistence through these energetically demanding periods critical for reproductive success. This dependence is enhanced by the matching between lactation and peak GPP during the austral spring (Fig. SM3.1), when resource availability is the highest.

Seasonal patterns of recruitment reflect this reproductive timing. Degus breed primarily during the austral winter, with first litters born in late August/September, resulting in peak recruitment during the breeding season. Additional recruitment during the nonbreeding season may arise from second litters produced under favorable conditions (Ebensperger et al., 2013; Meserve et al., 1995), immigration (Ebensperger et al., 2009; Quirici et al., 2010), or delayed marking of juveniles. Contrary to our prediction, recruitment differed between sexes, particularly during the nonbreeding season, suggesting that sex-specific differences in reproductive timing or detection may influence apparent recruitment rates. Because recruitment is closely tied to seasonal peaks in primary productivity, extreme reductions in GPP (e.g., that observed in 2019) are likely to disproportionately reduce reproductive output and juvenile survival.

These sex-specific and seasonal dynamics imply that reductions in primary productivity can have asymmetric demographic consequences. In a short-lived species such as the degu, where population persistence depends on sustained recruitment, disruption to the timing or magnitude of reproductive output can lead to rapid declines even when prior population growth has been positive. Moreover, the social and communal breeding system of degus, which under some conditions enhances reproductive success, may fail to buffer populations under extreme environmental stress and low food availability (Hayes et al., 2024). Together, these results indicate that the interaction between seasonal resource dynamics and sex-specific reproductive strategies can amplify the demographic consequences of extreme reductions in primary productivity, thereby increasing the likelihood of rapid population collapse under severe drought conditions, particularly in populations exposed to extreme climatic variability.

Gross primary productivity drives demography across seasons

Consistent with our second hypothesis, survival and recruitment were positively associated with environmental conditions that enhance plant growth and resource availability, with gross primary productivity (GPP) emerging as the strongest and most consistent predictor of both demographic rates (Table 2B; Fig. 6; model #146, Table SM6.3). These results indicate that primary productivity regulates demographic processes through its effects on food availability.

The relationship between GPP and demographic rates provides a mechanistic explanation for the observed population dynamics. Despite persistently reduced precipitation and primary productivity during much of the study period, these conditions did not prevent population growth but likely increased vulnerability to extreme events. GPP was almost absent during both the breeding and nonbreeding seasons of 2019 (Fig. 3), indicating that food resources were severely limited. This extreme reduction in GPP coincided with sharp declines in recruitment and survival (the tipping point), indicating that demographic responses were not driven by gradual deterioration over the course of the megadrought (Garreaud et al., 2017, 2025), but by a critical threshold in resource availability. These results are consistent with a threshold-like response to environmental variability (Grant et al., 2017; Smith, 2011; van de Pol et al., 2017), in which populations can persist under prolonged resource limitation but collapse when critical limits are exceeded.

The ecological mechanisms linking GPP to demographic rates are consistent with known behavioral and physiological responses of degus to resource limitation. Degus are well adapted to arid conditions and exhibit considerable behavioral plasticity, including shifts in diet, space use, and activity patterns. Their preferred food, green low-fibre annual herbs (Bozinovic, 1995), is most abundant during austral winter and spring (i.e., the breeding season). During summer, when these resources are scarce, degus expand their range to include shrubs (Quirici et al., 2010) and shift to lower-quality food sources such as foliage, seeds, and conductive tissues (Ebensperger & Hurtado, 2005a; Quirici et al., 2010). They also adopt a bimodal activity pattern, foraging primarily at dawn and dusk to avoid thermal stress (Bacigalupe et al., 2003; Kenagy et al., 2002), and retreat into burrows during the hottest parts of the day. Although degus can remain active aboveground when shrub cover provides shade (Bacigalupe et al., 2003), our study site was characterized by only 14% shrub cover (Ebensperger & Hurtado, 2005a), which likely limited opportunities for thermally buffered foraging. Under such conditions, individuals may face trade-offs between energy acquisition and increased exposure to predation and heat stress (Caraco, 1980; Kenagy et al., 2004).

In addition to behavioral adjustments, degus exhibit physiological plasticity that may buffer moderate resource limitation, including reduced energy expenditure (Bozinovic et al., 2004), coprophagy to recycle nutrients (Kenagy et al., 1999), and water conservation mechanisms (Ardiles et al., 2013; Bozinovic et al., 2003). However, the extreme environmental conditions observed during 2019–2020, including documented heatwaves with maximum temperatures reaching 40 °C (Dirección Meteorológica de Chile, 2019; Silva et al., 2024); Fig. 2), likely exceeded the capacity of these mechanisms to buffer resource scarcity. Thus, while physiological and behavioral plasticity may allow persistence under moderate drought conditions, they do not appear sufficient to offset the demographic consequences of severe reductions in primary productivity.

Although other environmental variables influenced survival and recruitment, these effects were not supported in the top multivariate models (Table 2B; Table SM6.3) and were inconsistent across parameters (Table SM7.1; Fig. SM7.1; Fig. SM7.2). Univariate analyses indicated associations between environmental covariates and demographic rates (Table SM5; Fig. SM8.1), but likelihood ratio tests further supported GPP as the strongest and most consistent predictor of both survival and recruitment (Table SM9). This convergence of evidence across modeling approaches reinforces the conclusion that food availability was the primary environmental driver of population dynamics in this system.

Together, these results indicate that while this population persisted through prolonged periods of reduced productivity, it remained vulnerable to extreme resource reductions. Because recruitment is closely tied to seasonal peaks in primary productivity, severe declines in GPP—such as those in 2019—likely suppressed reproductive output and juvenile survival, thereby increasing the likelihood of rapid population collapse in short-lived species such as the degu. More broadly, these findings highlight how climatic variability, rather than mean conditions alone, can govern population persistence by driving nonlinear demographic responses to environmental extremes.

Climate extremes and the collapse of the study population

Our study highlights the consequences of extreme climatic events, such as the megadrought and the extreme drought year, on population dynamics. The warm and dry megadrought conditions prior to 2019 likely created legacy effects in vegetation (Krishnan et al., 2006), reflected in reduced leaf area index (LAI), gross primary productivity (GPP), and evapotranspiration (ET) during the study period (Fig. 3). These changes likely increased ecosystem vulnerability and reduced resource availability for degus by limiting both food and shelter. Legacy effects on vegetation are species dependent, with herbs and shrubs showing delayed responses on the order of approximately 1–2 years, respectively, largely determined by rooting depth and water access (Wu et al., 2018).

Superimposed on these conditions, the extreme 2019 drought (Garreaud et al., 2025), with severe water deficits and associated heatwave activity (Fig. 2), likely amplified existing environmental stress, as plant communities were already operating under reduced productivity and resilience. Additional ecological impacts of this extreme drought year included reduced plant seed set and disrupted plant–pollinator interactions (Arroyo et al., 2020), as well as declines in forest productivity (Miranda et al., 2023), indicating system-wide responses to extreme climatic conditions. In our study system, the near absence of primary productivity in 2019 (Fig. 3), together with extreme temperatures reaching 39.3 °C (Fig. 2), likely resulted in a critical reduction in food availability (representing a tipping point) and foraging opportunities for degus, thereby contributing to the population collapse observed in 2020.

Importantly, our results suggest that the degu population did not decline gradually over the course of the megadrought but instead persisted under prolonged environmental stress and collapsed following an extreme climatic event. This pattern is consistent with a threshold response in which chronic reductions in resource availability increase system vulnerability, but population collapse is triggered when environmental conditions exceed critical limits. Similar drought-associated population crashes have been documented in a range of taxa, 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 & Wolf, 2016), bumble bees (*Bombus* spp.) (Thomson, 2016), plains viscachas (*Lagostomus maximus*) (Branch et al., 1994), and degus in northern central Chile (Previtali, Meserve, Kelt, Milstead, et al., 2010). Together, these findings reinforce the role of extreme climatic events in driving rapid population declines, particularly when they occur in systems already exposed to prolonged environmental stress.

Conclusions and implications for population persistence under climatic extremes

Our results demonstrate that population persistence under climate change cannot be inferred from responses to mean environmental conditions exclusively. Despite nearly a decade of reduced precipitation and primary productivity, this degu population maintained positive population growth and did not exhibit a gradual demographic decline. Instead, population collapse during the extreme 2019 drought followed a severe reduction in primary productivity, indicating that demographic responses were driven by threshold-like dynamics rather than cumulative effects of prolonged drought. These results provide a rare empirical example of how resistance, resilience, and tipping points interact to determine population persistence. The population remained resistant to prolonged drought, maintaining demographic stability despite sustained environmental stress. However, this persistence likely masked a progressive loss of resilience, as reduced resource availability eroded the system's capacity to absorb additional perturbations. When primary productivity collapsed in 2019 (tipping point), the system crossed a critical threshold, triggering an abrupt state shift resulting in rapid demographic decline and ending in local extinction. Such dynamics are consistent with ecological theory describing abrupt state shifts when systems are pushed beyond resilience limits (Holling, 1973; Scheffer et al., 2001) and with evidence that populations become increasingly vulnerable as they approach tipping points (Dai et al., 2013).

The demographic mechanisms underlying this collapse were closely linked to resource-dependent processes, especially recruitment in this short-lived species. Because population persistence depends on sustained reproductive output, extreme reductions in food availability can disproportionately reduce recruitment and juvenile survival, leading to rapid declines even when prior population growth has been positive. These dynamics may be further amplified in social species such as degus, where reproductive success and group size and individual composition are closely tied to population density and resource availability (Ebensperger et al., 2014, 2025; Hayes et al., 2009), and where cooperative behaviors do not necessarily buffer populations under extreme environmental conditions (Hayes et al., 2024).

Our study design, while not originally aimed at assessing extinction risk or population differences, nonetheless provides critical insight into how a degu population at the edge of its range responds to extreme climatic events. Our study was based on a subset of burrow systems within a single population, reflecting the design of a long-term study focused on social organization rather than extinction risk. Nevertheless, the complete absence of degu activity following intensive trapping in 2020–2021 supports the conclusion that a local extinction event occurred. Although our study site is located near the southern limit of the species' geographic range, our findings are consistent with those reported for a population at the northern limit, where populations declined dramatically in periods of consecutive dry years (Meserve et al., 2011; Previtali, Meserve, Kelt, Bryan Milstead, et al., 2010). Together, these studies suggest that degus are vulnerable to climate change across their distribution, even at different range limits. These results also highlight how populations respond matters: while our study population went locally extinct, others may show resilience, for example, pied babblers (*Turdoides bicolor*) compensatory breed when conditions improved (Bourne et al., 2020; Ridley et al., 2021). Differences in habitat structure may further modulate these responses. Shrub cover, as observed at nearby occupied sites (~10 km away; AM, LAE, LDH, personal observations) or in the semiarid thorn scrub community in north-central Chile, may buffer degus against environmental stressors, such as thermal stress (Bacigalupe et al., 2003; Kenagy et al., 2002, 2004). Although the study design was not developed specifically to assess extinction risk or to compare populations across its geographic distribution, it underscores the value of long-term studies for detecting demographic changes and adds to the literature on single-event studies as few opportunities exist to investigate these events (Altwegg et al., 2017).

Local extinction of degus may have cascading ecological consequences due to their roles as prey (Ebensperger & Wallem, 2002; Meserve et al., 1993), ecosystem engineers (Davidson et al., 2012; Root-Bernstein et al., 2013), and seed dispersers (Cordero et al., 2021; Loayza et al., 2020), with potential effects on community structure and plant–animal interactions (Núñez-Hidalgo et al., 2023; Prugh et al., 2018). In addition to environmental drivers, density-dependent processes such as Allee effects (Ebensperger et al., 2025) and changes in social structure may further influence population dynamics under extreme conditions. Integrating these processes with environmental variability in future models will improve predictions of population responses to climate change (Briscoe et al., 2023).

Overall, this study provides a rare empirical example of how extreme climatic events can drive rapid population collapse in a small mammal, even after extended periods of demographic stability under chronic environmental stress. As climate change is projected to increase the frequency and intensity of extreme events, understanding how environmental variability interacts with ecological thresholds to produce nonlinear demographic responses will be critical for predicting extinction risk and informing conservation strategies.

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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).

Tables

Table 1. Trapping effort and total number of individual degus captured at Rinconada de Maipú from austral spring 2019 through austral summer 2021.

Year	Season	Months	Burrow systems trapped	Traps/day deployed	Total days trapped	Individual degus captured
2019	Spring	August-November	40	400	61	108
2020	Summer	January	40	400	8	21
2020	Fall	June	40	400	5	0
2020	Spring	August-October	40	400	60	0
2020-2021	Summer	December-January	40	400	17	0

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 and for (B) the effect of season, sex, and the selected environmental covariates on apparent survival (ϕ) and recruitment rate (*f*).

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

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.

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