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Effects of More Frequent and Prolonged El Niño Events on Life-History Parameters of the Degu, a Long-Lived and Slow-Reproducing Rodent

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Abstract: *Global climate change (GCC) can have profound effects on species whose ecology is governed primarily by climatic factors. The ecology of small mammals inhabiting semiarid Chile is strongly affected by the El Niño Southern Oscillation (ENSO). During La Niña events in this area, dry conditions prevail and species may disappear from the thorn-scrub habitat. Conversely, El Niño events bring high rainfall, and associated pulses of food trigger small-mammal population increases. We used capture–mark–recapture to study responses of the degu (*Octodon degus*), a dominant small mammal, to variation in rainfall over 18 years. In response to a recent trend toward wetter conditions, degus reached record-high densities and maintained more stable numbers in the area. Underlying mechanisms involved variation in adult survival, juvenile persistence, and fecundity linked to rainfall changes during consecutive years (i.e., rainfall phases). During prolonged droughts, degus had low survival and produced fewer offspring, with low persistence. Following high rainfall, these parameters reversed; consecutive wet years resulted in further increases. Weak declines in fecundity and adult survival and high persistence of juveniles explained delayed responses to deteriorating conditions in initial dry years. If GCC leads to increased frequency of El Niño events, we anticipate greater numerical dominance of degus in semiarid Chile and possible range expansion. Furthermore, degus have strong impacts on other small mammal and some plant species, are important prey species, and are agricultural pests and disease reservoirs. Hence, GCC has the potential to dramatically influence their ecology in northern Chile and to have cascading effects on other components of this system.*

Keywords: ENSO, global warming, life history, *Octodon degus*, rainfall variation, reproduction, semiarid, survival, vital rates

Efectos de Eventos El Niño más Frecuentes y Prolongados sobre Parámetros de Historia de Vida del Degu, un Roedor Longevo y de Reproducción Lenta

Resumen: *El cambio climático global (CCG) puede tener profundos efectos sobre las especies cuya ecología es controlada principalmente por factores climáticos. La ecología de mamíferos pequeños que habitan en Chile semiárido es afectada significativamente por la El Niño Oscilación del Sur (ENOS). Durante los eventos La Niña en este área, prevalecen las condiciones secas y las especies pueden desaparecer del hábitat de arbustos espinosos. Por el contrario, los eventos El Niño traen alta precipitación, y los asociados pulsos de alimento generan incrementos en las poblaciones de micromamíferos. Utilizamos captura-recaptura para estudiar respuestas del degu (*Octodon degus*), un micromamífero dominante, a la variación en la precipitación durante*

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18 años. En respuesta a una tendencia reciente hacia condiciones más húmedas, los degus alcanzaron densidades altas sin precedentes y mantuvieron números más estables en el área. Los mecanismos subyacentes involucraron variación en la supervivencia de adultos, persistencia de juveniles y fecundidad relacionada con los cambios de precipitación durante años consecutivos (esto es, fases de precipitación). Durante sequías prolongadas, los degus tuvieron una baja supervivencia y produjeron menos descendencia, con baja persistencia. Después de precipitación alta, estos parámetros se revirtieron; años húmedos consecutivos resultaron en mayores incrementos. Declinaciones mínimas en la fecundidad y la supervivencia de adultos y la alta persistencia de juveniles explicaron las respuestas tardías al deterioro de las condiciones en los años secos iniciales. Si el CCG lleva a un incremento de la frecuencia de los eventos El Niño, anticipamos una mayor dominancia numérica de los degus en Chile semiárido y una posible expansión de rango de distribución. Más aun, los degus tienen fuerte influencia sobre otras especies de micromamíferos y algunas especies de plantas, son una importante especie presa y son plaga agrícola y reservorio de enfermedades. Por lo tanto, el CCG tiene el potencial de influir dramáticamente en su ecología en el norte de Chile y provocar efectos en cascada sobre otros componentes de este sistema.

Palabras Clave: calentamiento global, ENOS, historia de vida, *Octodon degus*, semiárido, supervivencia, tasas vitales, variación en la precipitación

Introduction

Global climate change (GCC) is predicted to lead to increases in air and ocean temperatures, with consequences, for example, for snow and ice melt, sea levels, and precipitation patterns (IPCC 2007). Numerous studies document ecological impacts of GCC at every organizational level, over broad geographical ranges, and on many ecological characteristics, including organismal phenology, distribution, and dynamics (McCarty 2001; Walther et al. 2002). Effects of GCC will be greater among species whose ecology is influenced primarily by climatic factors. Nevertheless, long-term studies are needed to better understand ecological responses, underlying mechanisms, and the magnitude of such changes (Stenseth et al. 2002; Stenseth & Mysterud 2002; Walther et al. 2002).

Small mammal species in arid and semiarid ecosystems exhibit dramatic population fluctuations in response to variable environmental conditions, especially rainfall (e.g., Dickman et al. 1999; Lima et al. 1999; Ernest et al. 2000). In semiarid Chile, rainfall is strongly influenced by the El Niño Southern Oscillation (ENSO; Lima et al. 1999; Jaksic 2001). La Niña events (ENSO's cold phase) are marked by drought conditions, whereas El Niño events (ENSO's warm phase) trigger high rainfall, which generates pulses of food leading to large increases in small mammal populations (e.g., Lima et al. 1999; Jaksic 2001; Meserve et al. 2003). The demographic mechanisms underlying such responses, however, have been investigated in few species of small mammals. Rainfall and density affect survival, recruitment, maturation, and reproductive activity of *Phyllotis darwini*, a prolific, short-lived muroid rodent (Lima et al. 2001*a*). Similarly, rainfall positively influences reproduction and recruitment but negatively impacts survival of the marsupial, *Thylamys elegans* (Lima et al. 2001*b*).

Degus (*Octodon degus*) have a very different life history, including a longer life-span (>3 years; Meserve et al. 1995), and lower reproductive output (i.e., one litter annually of about five precocial and slow-maturing young after a 3-month gestation; Weir 1974; Woods & Boraker 1975). These life-history traits suggest that degus are likely to respond differently than muroid rodents to GCC. To better understand the influence of climate on the life-history traits of degus, we analyzed a unique, long-term data set on this species in northern Chile.

Degu population dynamics are driven by density-dependence and by current and previous year's rainfall (Previtali et al. 2009). At our study site, the last 8 years of our 18-year data set have been above-average in rainfall, leading to unusually high densities (Previtali et al. 2009) and sustained dominance (e.g., biomass) of degus in the community (Meserve et al. 2009). Changes in degu dynamics are likely to influence many other species in this system because of their ecological dominance (e.g., Kelt et al. 2004). They have a variety of effects on the plant community through their foraging, runway making, and digging behaviors (Gutiérrez et al. 1997; Gutiérrez & Meserve 2000), and they are agricultural pests (Fulk 1976; Lima et al. 2003) and disease reservoirs (e.g., *Trypanosoma cruzi*, the agent of Chagas disease; Rozas et al. 2005). They also are important prey of diverse predators (Jaksic et al. 1997). Thus, changes in the numbers or distribution of degus could have important impacts on numerous ecosystem processes.

Although predicting the influence of GCC on ENSO is fraught with uncertainty (Cane 2005; Collins et al. 2005), consensus is growing that it will promote increased frequency of El Niño events (Timmermann et al. 1999; Cai & Whetton 2000; Collins et al. 2005). We assumed such a scenario and considered the consequences of a recent increase in prolonged wet conditions on the population dynamics of the degu. By examining variation in degu life-history parameters, we sought to identify the mechanisms underlying recent increases in degu abundance (Meserve et al. 2009).

We used a process-oriented approach involving analysis of temporal changes in survival and reproductive parameters that contribute to population fluctuation (Coulson et al. 2000). We developed a series of a priori models to investigate the causes of temporal variation in degu life-history parameters, and related these to variation in density and rainfall. On the basis of the combined effect of density and rainfall on degu dynamics (Previtali et al. 2009), we predicted that density-dependence would interact with rainfall in shaping degu survival and reproduction. Because degu population growth is also affected by rainfall of the previous year (Previtali et al. 2009), we investigated lagged effects of rainfall on vital rates through the use of a variable that denoted 2-year rainfall phases. The effects of density and current and lagged rainfall should lead to strong annual variation in degu survival and reproduction. Nevertheless, we also were interested in assessing whether degu life-history parameters had changed due to wetter conditions since 1999. Evidence for this longer-term response would be the observation of a change in these parameters following the shift in climate.

These analyses shed light on processes underlying recent increases in degu abundance in the community; however, in broader terms, they should help forecast the regional response of this dominant species in the face of sustained climate change, including the potential for range expansion and changes in species composition of the community. Understanding the consequences of these effects on dominant species is crucial for anticipating the propagation of climatic effects on ecological communities via species interactions (Menge et al. 2008). Our study contributes to the understanding of demographic changes in a species that is likely to benefit from changing climatic conditions.

Methods

Study Site

We have studied the ecology of small mammals in Bosque Fray Jorge National Park (71° 40′ W, 30° 38′ S) in north-central Chile since March 1989. The climate is arid Mediterranean (López-Cortés & López 2004) with wet, cool winters (mean minimum temperature 4 °C) and dry, warm summers (mean maximum temperature 24 °C). Mean annual rainfall from 1989 to 2006 was 141.22 mm (SD 108.75) and ranged from 11 mm (1998, La Niña) to 356 mm (2002, El Niño). We documented five high-rainfall events that differed in duration (1–3 years) and magnitude (147–356 mm; Fig. 1). Since 1999 we observed an increase in the frequency of years with above-average rainfall and a corresponding lack of prolonged droughts (Fig. 1).

Our study plots were in Quebrada de las Vacas, a coastal valley dominated by thorn-scrub vegetation (Gutiérrez et al. 2004). Herbaceous growth is triggered by the first significant rains (>20 mm) in the rainy season (May through August or September; Armesto et al. 1993). Herbaceous cover peaks in the spring (September–November) and declines rapidly in the summer (December–February) (Gutiérrez et al. 2004).

Trapping Protocol

Small mammals were live-trapped for 4 nights per month from March 1989 to May 2007 on four 75 × 75 m plots (0.56 ha, enclosing a 5 × 5 m grid with 15-m spacing). Each station had two Sherman-type live traps (9 × 11 × 30 cm) baited with rolled oats and checked in the morning and in late afternoon. We marked individuals with ear tags and recorded sex, reproductive condition (females: perforate or imperforate; pregnant or lactating; males: noticeable or inconspicuous testes), and weight before releasing animals at the point of capture.

Modeling Degu Population Dynamics

EXPLANATORY VARIABLES

Because winter (June through September) coincides with the peak of the rainy season, the beginning of plant growth, and degu reproduction, we defined years ecologically as extending from July through June. We estimated the minimum number known alive (Krebs 1966)

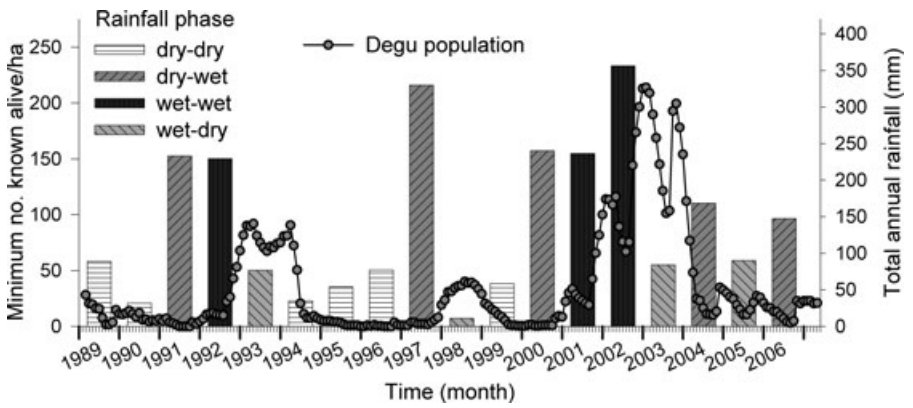

Figure 1. Variation in mean monthly population density of Octodon degus *(line and circles) and its relationship with total annual rainfall (bar) and rainfall phases (shade and pattern of bar). Data for 1988 were obtained from other sources that document that this was a dry year (approximately 40 mm of rainfall).*

for each monthly census and used the peak density in a year as an explanatory variable in models to determine density-dependent effects on life-history parameters. Given marked fluctuations in annual rainfall and population density, we developed a priori models to assess the relative influence of these and other temporal variables on degu life-history parameters.

We hypothesized that degu life-history parameters would be differentially affected by different combinations of rainfall (high or low) and density (high or low), which could be asynchronous due to delayed responses of degu population growth to changes in resources. We classified each year as wet or dry (above- vs below-mean annual rainfall, respectively) and identified four, 2-year phases (dry–dry, $n = 6$; dry–wet, $n = 5$; wet–wet, $n = 3$; and wet–dry, $n = 4$), which were used as categorical explanatory variables in our models.

From 1989 through 1998, our site was characterized by high-rainfall events isolated by prolonged droughts; however, from 1999 through 2006, it was dominated by above-average rainfall years. We tested the prediction that degu life-history parameters would respond to these changes in rainfall regime. Finally, we addressed the possibility of observing a more gradual change with time by evaluating the presence of a linear trend in the data across the 18 years of study.

REPRODUCTION

We investigated reproductive parameters only for females because male degus lack a scrotum, which renders assessment of their reproductive status problematic (Weir 1974). We defined the length of the breeding season separately for the four grids as the number of months from first to the last capture of females exhibiting reproductive activity. We investigated the influence of density, rainfall, and the temporal factors described above by fitting generalized linear mixed models (GLMMs; Breslow & Clayton 1993) with a Poisson distribution and a log link function. Treating the total number of adult females (a categorical variable, nested within grid) as a random factor accounted for lack of independence among observations from the same grid while controlling for the effect of female abundance.

We investigated variation in reproductive activity by modeling the proportion of reproductively active adult females in each grid each year. Individuals were considered adults if they showed signs of reproduction or if they weighed $\geq$90 g and were not born during the current year. Degus <90 g almost never appeared reproductively active (Meserve et al. 1995). We used GLMMs with a binomial error structure, a logit link function, and grid as a random factor to test the effects of the independent factors on reproductive activity.

We used the number of juveniles captured during the year in each grid as an indirect measure of annual fecundity. This provided a conservative estimate of weaned young because it excluded animals that died before being trapped. We used GLMMs with a Poisson error distribution and a log link function to investigate temporal variation in fecundity rates. We treated numbers of adult females (nested within grid) as random effects.

We constructed a set of candidate models to describe each of these variables (length of breeding season, reproductive activity, and fecundity rate). Independent variables were either peak annual density (maximum number of degus per hectare in the previous year), rainfall (current year), rainfall phases (dry–dry, and so on), gradual change (linear trend over time), or sudden shift in parameters (1989–1998 vs. 1999–2006). We also tested the interaction between density and rainfall.

All analyses were conducted with Proc GLIMMIX in SAS (version 9.1.3, SAS Institute, Cary, North Carolina). We treated "intercept" and grid or total females nested within grid as random effects. We based inferences on the pseudo-Akaike's information criterion adjusted for small sample size (pAICc). Because pAICc estimates can be affected by the linearization process in GLIMMIX, we treated these conservatively, accepting only large differences in pAICc (i.e., ΔpAICc $\approx$ 10) as indicative of a better model. For categorical explanatory variables, we estimated least-square means and investigated differences across levels through pairwise comparisons. Rainfall phases included multiple comparisons, so we used Tukey-adjusted significance values. Finally, we checked for evidence of overdispersion in models fitted with the Poisson distribution (i.e., length of breeding season, fecundity rates) by verifying that the ratio of generalized χ^2/df approximated unity.

JUVENILE PERSISTENCE

We estimated juvenile persistence as the number of months from first to last capture. Juveniles captured only once were assigned a persistence of 1 month. We excluded individuals that died in traps, were injured, or were caught in other grids at any point during the study period. Because we did not always have sufficient power to develop a priori models of all relevant factors (density, rainfall, their interaction, or temporal trends in rainfall), we analyzed juvenile persistence as a function of the rainfall phase in which they were born and on the major differences before versus after 1999. We used the nonparametric LIFETEST procedure in SAS to analyze the survivorship curves and the log-rank test for determining differences between groups (phases or before vs. after 1999).

ADULT SURVIVAL

To assess adult survival, we excluded individuals that were injured or caught in other grids at any point during

the study period. Animals that died in traps were coded as being removed from the population. We condensed capture–recapture data from monthly to bimonthly encounter occasions corresponding to trapping sessions in odd months (e.g., January, March, and so on) to minimize dependency between consecutive trapping sessions and reduce the data to a size manageable by Program MARK (White & Burnham 1999). We analyzed sources of variation in bimonthly survival and capture probabilities with capture–mark–recapture statistical modeling by fitting variations of the Cormack–Jolly–Seber model.

We constrained temporal variation in survival and capture rates to be functions of the categorical variables year and season. The former extended from March to January, and the latter distinguished winter–spring (July–November) from summer–fall months (January–May). The former are characterized by small population sizes but abundant food and active reproduction, whereas the latter have larger populations, reduced food availability, and fewer nursing females. We also considered differences in survival or recapture between males and females. The logit link function was used to model the relationship between the explanatory variables and survival or capture probabilities. Models were built on the basis of our understanding of the ecology of degus and the probability that specific factors influenced survival and capture probabilities.

We initiated analyses with the most complex (highly parameterized) model possible for survival (Φ) and capture probabilities (p). This included an interaction between sex and season plus an additive effect of year in both parameters (i.e., Φ[sex $\times$ season + year] p[sex $\times$ season + year]). More complex models yielded several inestimable parameters due to sparse data at certain times. We tested for overdispersion with the median-$\hat{c}$ approach in MARK (White & Burnham 1999) and applied a quasi-likelihood adjustment as needed with the estimated median-$\hat{c}$.

The analysis consisted of three different steps. First, we built a set of simpler models for capture probabilities as a function of sex, season, and year while retaining the most complex model structure for survival (i.e., Φ[sex $\times$ season + year]). The most parsimonious model for capture probabilities was selected using the quasi-likelihood AICc (QAICc; Burnham & Anderson 2002). Second, we used this model for capture probabilities and fit a set of simpler models for survival as a function of sex, season, and year. We anticipated strong interannual variation in degu survival because populations fluctuated markedly; thus, we included annual variation in all models. We were unable to test either year $\times$ sex or year $\times$ season because these models yielded a number of inestimable parameters. Third, we used the most parsimonious model of survival with the intention of explaining interannual variation on the basis of the more mechanistic temporal variables rather than simple year effects. This involved fitting survival models in which yearly differences were substituted by peak density, annual rainfall, rainfall phases, change in rainfall regime since 1999, or a linear trend with time.

Results

Between March 1989 and May 2007, we captured 3444 individual degus; 91.4% were captured in only one grid, and 31.8% were first captured as juveniles. Degu populations exhibited large fluctuations in response to changes in rainfall (Fig. 1), with numbers increasing in late spring of the first high-rainfall year (i.e., dry–wet years 1991, 1997, 2000, 2004, and 2006). Increases were more pronounced and rapid in early spring of the following year when wet conditions continued (i.e., wet–wet years 1992, 2001, and 2002). Consequently, peak population size in wet–wet years reached over twice that after a single year of high rainfall (e.g., 92 individuals/ha after 1991–1992 vs. 39.3 individuals/ha after 1997). In the 3-year wet period of 2000–2002, degu populations reached the highest density recorded (213.8 individuals/ha). Densities remained high in the first year of dry conditions (i.e., wet–dry years 1993, 1998, 2003, and 2005), but a second year of dry conditions led to marked declines to extremely low numbers (i.e., dry–dry years 1989, 1994–96, and 1999; Fig. 1). On some occasions (e.g., July–October 1991 and August–October 1996), we captured no individuals for several months.

The pattern of degu population fluctuations changed after the 2000–2002 wet period. Degu populations did not decline to local extinction as before. Instead, they fluctuated at low to moderate levels in response to alternating years of moderately wet and dry conditions.

Reproduction

Initiation of the reproductive season varied from June to November, and its end occurred between July and May. From 1989 to 1999, we recorded several years with no degu breeding or only a short breeding season, mainly during dry years (Table 1). Breeding seasons lengthened in the latter third of our study, with the longest season lasting approximately 7 months (Table 1). The most parsimonious model for explaining variation in length of breeding season included change in rainfall regimes before versus after 1999 (Table 2). Prior to 1999 the breeding season averaged only 1.4 (SE 0.24) months, whereas subsequently it increased to an estimated 4.4 (0.62) months. Nevertheless, the trend toward increasing rainfall also influenced the duration of breeding activity (ΔpAICc = 6.0), as did rainfall phases (ΔpAICc = 8.7; Table 2). Specifically, breeding seasons during prolonged droughts (i.e., dry–dry phase) were brief (least-square mean estimate: 0.9 months [SE 0.24]), but increased to

Table 1. Variation in mean (SD) annual reproductive parameters of *Octodon degus* as a function of climatic conditions.

Year	*Phase*[a]	*Number of months of breeding*	*Total number of females*	*Number of reproductively active females*	*Number of juveniles*[b]
1989	dry–dry	1.8 (2.87)	8.5 (3.79)	2.0 (3.37)	6.5 (7.68)
1990	dry–dry	0.0 (0.00)	5.8 (2.36)	0.0 (0.00)	0.3 (0.50)
1991	dry–wet	0.0 (0.00)	4.8 (4.35)	0.0 (0.00)	3.5 (3.70)
1992	wet–wet	4.3 (3.10)	26.3 (10.40)	1.8 (1.71)	23.3 (10.78)
1993	wet–dry	3.0 (0.82)	54.0 (11.80)	8.0 (4.08)	10.5 (7.85)
1994	dry–dry	2.5 (1.91)	19.3 (3.10)	3.0 (2.16)	2.0 (0.82)
1995	dry–dry	0.3 (0.50)	2.8 (1.89)	0.3 (0.50)	0.3 (0.50)
1996	dry–dry	0.0 (0.00)	1.3 (1.26)	0.0 (0.00)	2.5 (1.73)
1997	dry–wet	2.3 (3.20)	9.8 (4.72)	0.8 (0.50)	10.0 (5.83)
1998	wet–dry	0.5 (0.58)	30.5 (9.88)	0.8 (0.96)	0.3 (0.50)
1999	dry–dry	1.8 (2.22)	3.3 (1.89)	0.8 (0.50)	0.5 (0.58)
2000	dry–wet	2.3 (2.22)	10.5 (2.52)	2.0 (1.83)	7.0 (5.94)
2001	wet–wet	6.3 (1.50)	37.3 (7.68)	4.5 (1.29)	36.8 (8.58)
2002	wet–wet	7.3 (0.50)	68.8 (14.66)	15.5 (5.20)	66.0 (30.66)
2003	wet–dry	5.3 (0.50)	82.8 (9.95)	21.3 (6.85)	83.0 (58.59)
2004	dry–wet	4.5 (2.38)	13.0 (4.16)	3.3 (1.71)	9.3 (7.41)
2005	wet–dry	7.0 (2.16)	11.5 (1.73)	3.8 (0.96)	8.8 (8.92)
2006	dry–wet	6.8 (3.95)	14.0 (4.24)	2.5 (1.00)	3.8 (2.22)

[a] *Wet and dry indicate above or below average rainfall, respectively, during the previous and current year.*
[b] *Indicator of fecundity.*

2.1 months (0.46) in dry–wet years, 3.6 months (0.81) in wet–dry years, and 5.6 months (1.41) in wet–wet years. The variance components of the total number of adult females and grid as random factors ranged from 0.44 to 0.80 (SE range 0.16–0.24). Neither density, rainfall, nor their interaction were important predictors (Table 2).

The proportion of reproductively active females varied temporally but was very low in all years (Table 1). This variation was best explained by a change since 1999 (Table 2), after which the estimated mean probability of reproductive activity doubled (0.1 [SE 0.013] to 0.2 [0.019]). In this model, the variance component estimated with grid as a random factor was 0.025 (0.034). No other environmental factors were good predictors of variation in reproductive activity (Table 2).

Fecundity fluctuated noticeably over time (Table 1). Some years, especially wet–dry years, yielded very few juveniles relative to adult females. Fecundity was best modeled as a function of rainfall phases (Table 2). Although similar in dry–wet and wet–dry phases (4.8 juveniles/grid [SE 0.42] vs 4.3 [0.50]), this doubled in the wet–wet phase (8.2 [0.42]) and decreased by more than half during the dry–dry phase (1.6 [0.23]). Treating the number of adult females and grid as random factors, the variance component was 1.13 (0.26). All other models had considerably higher pAICc values (Table 2), suggesting a lesser effect on fecundity rates.

Juvenile Persistence

We excluded 38 of 1058 juveniles due to trap death, injury, or emigration. The resulting sample size precluded

Table 2. Models evaluating the influence of different factors on the temporal variation of degu reproductive parameters.[a]

	Length of the breeding season			*Reproductive activity*			*Fecundity*		
Parameter	*estimate (SE)*	*pAICc*	*ΔpAICc*	*estimate (SE)*	*pAICc*	*ΔpAICc*	*estimate (SE)*	*pAICc*	*ΔpAICc*
Density	0.00 (0.001)	249.2	28.7	0.01 (0.001)	243.1	28.2	0.00 (0.001)	299.7	49.7
Rainfall	0.00 (0.001)	247.9	27.4	0.00 (0.001)	242.7	27.8	0.01 (0.001)	278.7	28.7
Density* rainfall	0.00 (0.000)	280.2	57.7	0.00 (0.000)	285.3	70.4	0.00 (0.000)	312.7	62.7
Phases[b]									
dry–dry	−1.38 (0.345)	229.2	8.7	−0.31 (0.24)	240.8	25.9	−1.55 (0.358)	250.0	0
dry–wet	−0.55 (0.300)			−0.18 (0.21)			−0.69 (0.339)		
wet–wet	0.44 (0.337)			−0.17 (0.15)			1.47 (0.413)		
Sudden change[c]									
before 1999	−1.15 (0.212)	220.5	0	−0.94 (0.152)	214.9	0	0.70 (0.229)	281.6	31.6
trend	0.11 (0.021)	226.5	6.0	0.09 (0.016)	230.2	15.3	0.03 (0.019)	292.8	42.8

[a] *The pAICc is the pseudo Akaike information criterion corrected for small sample size estimated after the linearization process in GLIMMIX.*
[b] *Estimates for 2-year rainfall phases relative to those in the wet–dry phase.*
[c] *Estimates under dryer conditions (before 1999) with respect to wetter conditions (since 1999).*

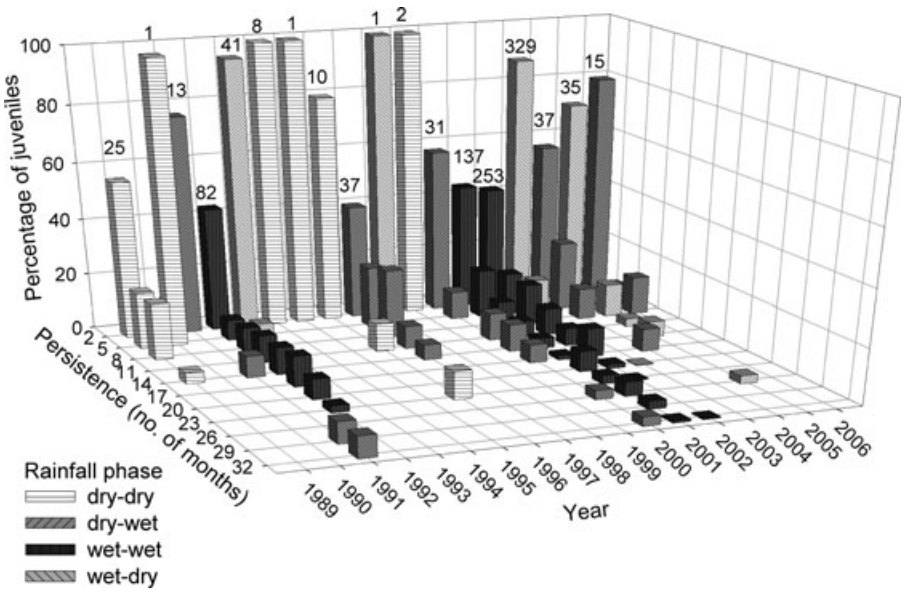

Figure 2. Proportion of juvenile Octodon degus *persisting in the population at 3-month intervals as a function of the year they were born. Numbers on top of bars are the initial number of individuals in each cohort. Shade and pattern of the bar represents rainfall phase.*

analysis of this parameter with GLMMs, so we used a reduced set of nonparametric models instead. Sexes displayed similar persistence (log-rank test for equality over strata, $\chi^2 = 0.02$ df=1, $p = 0.8$) and were combined in subsequent analysis. The maximum persistence recorded was >33 months (Fig. 2). Juvenile persistence differed across rainfall phases ($\chi^2 = 238.10$ df=3, $p < 0.001$) from 2.05 months (SE 0.104) in wet–dry years to 3.28 months (0.610) in dry–dry years, 5.67 months (0.588) in dry–wet years, and 7.24 months (0.326) in wet–wet years. Juvenile persistence did not differ before versus after 1999 ($\chi^2 = 0.93$ df=1, $p = 0.3$).

Adult Survival

We based models of adult survival on 4675 records of 1789 adult degus captured in the six selected months of each year (e.g., March, May, and so on). Estimated median-ĉ was 1.33 (SE 0.010) and was used to account for overdispersion by means of a quasi-likelihood variance inflation adjustment.

The most parsimonious model for capture probability highlighted the importance of seasonal and annual variation (Table 3). Removal of either of these factors from more complex models always increased model deviance, whereas addition of sex markedly reduced model fit (ΔQAICc > 3; Table 3). Estimated mean recapture probabilities were moderately lower in winter–spring than summer–fall months (MLE: 0.63 [SE 0.052] vs. 0.78 [0.012]); year had an even greater effect, with recaptures ranging from near zero in 1996 to approximately one in 1998–1999.

Given the best model for capture probability, survival was most parsimoniously explained as a function of year and an interaction between sex and season (Table 3). When we substituted year with potential mechanistic variables to investigate the drivers underlying interannual variation in survival, rainfall phase was the most parsimonious alternative explanatory variable tested (all ΔQAICc > 33, Table 3). Thus, survival probabilities were greater for females than males only in the winter–spring months (Fig. 3) and were highest during the wet–wet phase, least during dry–dry phases, and intermediate during transition phases (i.e., dry–wet and wet–dry; Fig. 3).

Discussion

Degus responded to changes in rainfall variability by adjusting life-history parameters, and we documented two different processes driving these changes. First, changes in rainfall between consecutive years (i.e., rainfall phases) were the main driver of temporal variation in adult survival, juvenile persistence, and fecundity rates. Second, the prevailing wetter conditions since 1999 led to longer breeding seasons and a greater proportion of reproductively active females. The association among these parameters was expected because the parameters in each group should be linked to each other. For instance, differences in fecundity rates should be associated with changes in juvenile persistence because fecundity estimates were dependent on the probability of juveniles surviving long enough to be trappable. Similarly, variation in duration of the breeding season could explain differences in proportion of reproductively active females (or vice versa).

Perhaps not surprisingly for a species with K-selected life-history traits, the factors that appear to drive their dynamics in Fray Jorge were associated more with longer-term patterns (e.g., phases or change since 1999) than with annual fluctuations in rainfall or density. During prolonged droughts, adult individuals had low survival and produced fewer offspring, which also had lower persistence. Together, these mechanisms kept population

Table 3. Models for capture and survival probability of degus (*Octodon degus*) in northern Chile.

Model[a]	*QAICc*	*ΔQAICc*	*QAICc weights*	*Number of parameters*
Capture probability[b]				
p (season + year)	6798.0	0	0.72	41
p (season × sex + year)	6801.3	3.3	0.14	43
p (season + sex + year)	6801.3	3.3	0.14	42
p (year)	6875.0	77.0	0	36
p (sex + year)	6884.7	86.7	0	41
p (season)	6885.4	87.5	0	24
p (season + sex)	6887.4	89.5	0	25
p (season × sex)	6889.4	91.4	0	26
p (.)	6930.7	132.7	0	23
p (sex)	6932.7	134.7	0	24
Survival probability[c]				
Φ (season × sex + year)	6798.0	0	0.9	41
Φ (season + sex + year)	6803.6	5.7	0.1	40
Φ (sex + year)	6806.7	8.8	0.0	39
Φ (season + year)	6814.1	16.1	0.0	39
Φ (year)	6817.0	19.0	0.0	38
Interannual temporal variation survival probabilities[c]				
Φ (season × sex + phase)	6843.4	0.0	1	27
Φ (season × sex + density × rain)	6877.1	33.7	0	27
Φ (season × sex + density + rain)	6879.6	36.2	0	26
Φ (season × sex + rain)	6888.9	45.5	0	25
Φ (season × sex + density)	6981.7	138.3	0	25
Φ (season × sex + change)	6995.8	152.4	0	25
Φ (season × sex + trend)	6997.3	153.9	0	25

[a]*Models are ordered on the basis of their fit to the data (i.e., ascending QAIC$_c$ [quasi-likelihood Akaike information criterion corrected for small sample size]) (*p*, capture probability; Φ, survival probability).*
[b]*The survival model used was the most parameterized model possible, Φ(sex × season + year).*
[c]*The recapture model used was* p *(season + year).*

size low and prevented growth; degus even disappeared locally during prolonged droughts. Subsequent recolonization may have occurred from refuges in more mesic peripheral habitats, where degus maintained breeding populations even during dry years (Milstead et al. 2007). Following high rainfall, increased adult survival and fecundity led to population increases. Juveniles born during dry–wet years had higher persistence, such that more individuals reached sexual maturity in subsequent years. The contribution of these juveniles, plus higher fecundity and adult survival during consecutive wet years, appears to explain the cumulative and rapid increases in population size experienced during wet–wet phases (Fig. 1). The delayed decline of population size during wet–dry phases can be explained by the relatively weak decline in fecundity and adult survival (Fig. 3), and the high persistence of juveniles born during the previous wet year.

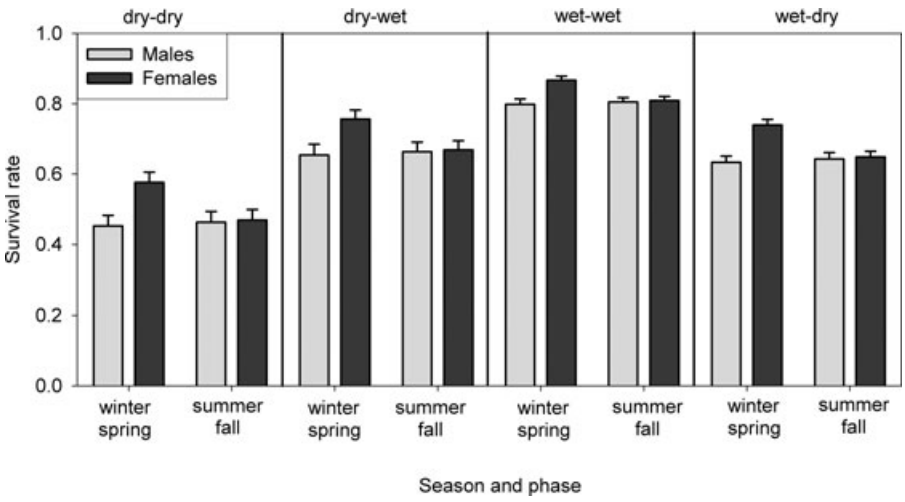

Figure 3. Survival estimates (SE) of male and female degus as a function of season and rainfall phases.

The greater persistence of young born during high rainfall years reflected better maternal contributions because vegetation is starting to senesce by the time young are weaned. Female degus with access to better or more food produce larger offspring (Veloso & Bozinovic 2000), which likely increases offspring survival. The additional increase in survival during the second consecutive wet year suggests that body condition improved for individuals that experienced a subsequent year of high food availability. In a food-addition experiment that mimicked the consequences of El Niño events, degus increased both mean body weights and reproductive activity (Meserve et al. 2001). Further evidence for improved body condition during wet–wet years was the observation of a few late pregnancies in the summer, which suggests there was a postpartum estrus during these years (Weir 1974; Fulk 1976; Meserve et al. 1984).

The strong interaction between season and sex on estimates of adult survival may reflect the costs of reproduction for males early in the breeding season due to aggressive interactions with conspecifics and greater vigilance (Ebensperger & Hurtado 2005). Later in the breeding season, females confront increased energetic costs due to gestation and lactation because of their large, precocial young, with extended dependency times (Weir 1974; Woods & Boraker 1975; Naya et al. 2008). We observed a low proportion of reproductively active females, even during favorable years. Although degu social structure could inhibit reproduction by some females, Ebensperger et al. (2004) found signs of reproductive activity in all females within a social group in more mesic central Chile. Alternatively, the observed low reproductive activity may be an artifact of low trappability of females during the breeding season.

In species with delayed maturity and low reproductive rates (such as degus, and typically, larger mammals) survival should be most influential on population growth, whereas, reproductive parameters should have greater influence in species with early maturation and high reproductive rates (e.g., most small mammals; Oli & Dobson 2003). Our results suggest that variation in the parameters associated with survival probabilities (juvenile persistence and adult survival) can be linked to changes in population size observed in different rainfall phases. The magnitude of change in these variables was large and, therefore, they may have greatly influenced dynamics of degu populations. Additionally, changes in fecundity also appeared to be associated with observed population fluctuations. The weak relationship between interannual variation in population size and reproductive activity or duration of breeding season suggests a lesser role for reproduction versus survival as the main mechanism underlying degu population dynamics.

Responses by degus to increased rainfall in the last 8 years of our study may represent phenotypic plasticity, which enables short-term adjustment to prevailing weather conditions. Alternatively, their responses could reflect selection on these traits due to the recent trend toward a wetter climate. Both of these processes were responsible for advancing the breeding times of red squirrels (*Tamiasciurus hudsonicus*) over 10 years (Réale et al. 2003). The data necessary for disentangling these two processes, however, are rarely available (Réale et al. 2003), and such is the case for degus. In our system, dominated by large oscillations in rainfall with a recent trend toward wetter conditions, one can expect dry years to exert temporary "setbacks" amidst an overall increased reproductive activity (Walther et al. 2002).

Our study site is close to the northern limits of the geographic range of degus (Woods & Boraker 1975), near the transition to the hyperarid Atacama Desert, and thus may be marginal habitat for degus. Nevertheless, if increased precipitation leads to more mesic conditions in this region, we anticipate a northward expansion of the species' range. Furthermore, at our site, we expect degus to become increasingly dominant members of the assemblage of small mammals, as has been confirmed by recent trends (Meserve et al. 2009). Normally, with El Niño and high-rainfall events occurring every 2–5 years, irruptive muroid species with rapid demographic responses including frequent, short-interval litters, and rapidly maturing young (e.g., *P. darwini*) should dominate numerically in many if not most years. Under such conditions, caviomorph rodents, such as degus, with single litters each year and delayed maturation, should remain a numeric minority. Nevertheless, with increased frequency and duration of high-rainfall events, degus can respond with cumulative increases such as in 2000–2002. Thus, in these circumstances, degus are favored over smaller, irruptive species in the community because they can survive occasional dry years and manifest responses to the long-term increase in precipitation. This illustrates the greater importance of lagged effects of rainfall on degu demography than on the more irruptive *P. darwini* (Previtali et al. 2009). Ultimately, a more stable presence and greater abundance of degus in the community may have negative impacts on associated plants and animals due to increased herbivory and intensified competition with subordinate species.

An alternative GCC scenario could occur in this region because there is much to learn about interactions between global warming and ENSO and between ENSO and local environments. For example, increased rainfall during El Niño events increases productivity at lower elevations in this region, but productivity decreases at higher elevations due to colder temperatures (Squeo et al. 2006). Furthermore, the influence of fog from the Pacific Ocean, an important contributor to local moisture in this semiarid region, is reduced during El Niño years (Garreaud et al. 2008).

We acknowledge uncertainty regarding the strength and even reality of a causal link between the observed

demographic patterns and GCC (McCarty 2001), especially due to a number of constraints that exist when attempting to anticipate the effects of GCC on the basis of current knowledge (Berteaux et al. 2006). Nevertheless, our results contribute to the growing body of studies in this field that is helping to develop a more comprehensive understanding of the potential effects of GCC (McCarty 2001). Our study is unique in that it implicates increased rains as the climate change driver, documents clear responses in life-history parameters, and provides insight to climatic influences on a small mammal species, all of which are seldom reported in the literature on the impacts of climate change.

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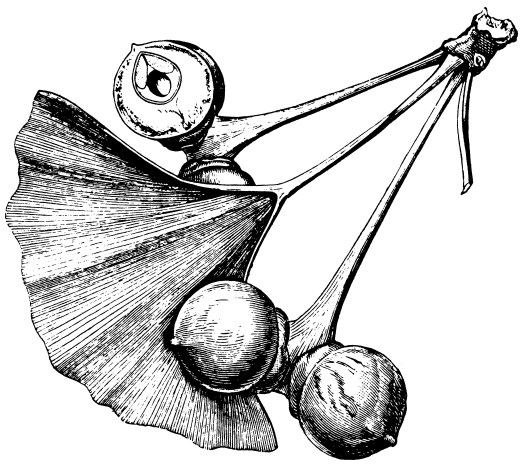
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