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SPECIAL FEATURE: LONG-TERM RESEARCH

Long-term research in Bosque Fray Jorge National Park: Twenty years studying the role of biotic and abiotic factors in a Chilean semiarid scrubland

Investigación de largo plazo en el Parque Nacional Bosque Fray Jorge: Veinte años estudiando el rol de los factores bióticos y abióticos en un matorral chileno semiárido

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ABSTRACT

Since 1989, we have conducted a large-scale ecological experiment in semiarid thorn scrub of a national park in north-central Chile. Initially, we focused on the role of biotic interactions including predation, interspecific competition, and herbivory in small mammal and plant components of the community. We utilized a reductionist approach with replicated 0.56 ha fenced grids that selectively excluded vertebrate predators and/or larger small mammal herbivores such as the degu, *Octodon degus*. Although we detected small transitory effects of predator exclusions on degu survival and numbers, other species failed to show responses. Similarly, interspecific competition (i.e., degus with other small mammals) had no detectable numerical effects (although some behavioral responses occurred), and degu-exclusions had relatively small effects on various plant components. Modeling approaches indicate that abiotic factors play a determining role in the dynamics of principal small mammal species such as *O. degus* and the leaf-eared mouse (*Phyllotis darwini*). In turn, these are mainly related to aperiodic pulses of higher rainfall (usually during El Niño events) which trigger ephemeral plant growth; a food addition experiment in 1997-2000 verified the importance of precipitation as a determinant of food availability. Since 2004, we have expanded long-term monitoring efforts to other important community components including birds and insects in order to understand effects of abiotic factors on them; we report some of the first results of comprehensive surveys on the former in this region. Finally, we recently shifted focus to documenting effects of exotic lagomorphs in the park. We installed additional treatments selectively excluding small mammals, lagomorphs, or both, from replicated grids in order to evaluate putative herbivore impacts. In conjunction with increased annual rainfall since 2000, we predict that introduced lagomorphs will have increasing impacts in this region, and that more frequent El Niños in conjunction with global climatic change may lead to marked changes in community dynamics. The importance of long-term experimental studies is underscored by the fact that only now after 20 years of work are some patterns becoming evident.

Key words: birds, Chilean desert, ephemeral plants, LTER, small mammals.

RESUMEN

Desde 1989 hemos llevado a cabo un experimento ecológico a gran escala en un matorral espinoso semiárido de un parque nacional en el norte de Chile. Inicialmente, nos centramos en el rol de las interacciones bióticas incluyendo depredación, competencia interespecífica y herbivoría en micromamíferos y componentes vegetales de la comunidad. Usamos una aproximación reduccionista con parcelas replicadas cercadas de 0.56 ha que selectivamente excluían depredadores vertebrados y/o micromamíferos herbívoros más grandes como el degu, *Octodon degus*. Aunque detectamos efectos transitorios menores en la sobrevivencia y número de degus en las exclusiones de depredadores, otras especies no mostraron respuestas. Similarmente, la competencia interespecífica (i.e., degus con otros micromamíferos) no tenía efectos numéricos detectables (aunque ocurrieron algunas respuestas conductuales), y las exclusiones tuvieron efectos relativamente pequeños en varios componentes vegetales. Aproximaciones basadas en modelos indican que los factores abióticos juegan un papel determinante en la dinámica de las especies de micromamíferos principales como *O. degus* y la laucha orejuda (*Phyllotis darwini*). En cambio, estos están principalmente relacionados a pulsos no periódicos de lluvias más altas (usualmente durante los eventos El Niño) que gatilla el crecimiento de plantas efímeras; un experimento de adición de alimento en 1997-2000 verificó la importancia de la precipitación como un determinante de la disponibilidad de alimento. Desde el 2004 hemos expandido los esfuerzos de monitoreo de largo plazo a otros componentes comunitarios importantes incluyendo aves e insectos con el fin de entender los efectos de los factores abióticos sobre ellos; informamos algunos de los primeros resultados de censos comprehensivos de aves en esta región. Finalmente, hace poco cambiamos de foco para documentar el efecto de lagomorfos exóticos en el parque. Instalamos tratamientos adicionales excluyendo selectivamente micromamíferos, lagomorfos, o ambos, de parcelas replicadas con el fin de evaluar impactos de herbívoros. En conjunto con el aumento de la precipitación anual desde 2000, predecimos que los lagomorfos introducidos tendrán mayores impactos en esta región y que más frecuentes El Niño en combinación con el cambio climático global puede conducir a cambios marcados en la dinámica comunitaria. La importancia de experimentos de largo plazo es destacado por el hecho que solamente ahora después de 20 años de trabajo algunos patrones están siendo evidentes.

Palabras clave: aves, desierto chileno, LTER, micromamíferos, plantas efímeras.

INTRODUCTION

The historical debate on the relative importance of biotic interactions such as predation, competition, and herbivory vs. abiotic factors such as climate, has been contentious in population and community ecology (e.g., Nicholson 1933, Andrewartha & Birch 1954, Sinclair 1989, Turchin 1995, 2003). Although the present consensus is that both biotic and abiotic factors are important, it generally is accepted that biotic factors tend to operate in a density-dependent manner whereas abiotic ones do not. Thus, the former have the potential to regulate population density within a range of dynamic equilibria, whereas the latter may increase population variability outside that range (Sinclair 1989, Turchin 2003).

The emphasis on biotic interactions as a central mechanism controlling populations culminated in the 1980's and 1990's with a call for multifactorial and reductionist approaches to studying field organisms (e.g., Lubchenco 1986, Roughgarden & Diamond 1986, Schoener 1986). At the same time, greater emphasis was put on ecological scale and the importance of studies over larger spatial and temporal scales (e.g., Wiens 1986, 1989, Wiens et al. 1986, Levin 1992). The issue is not whether any one scale in space or time is «correct,» but rather understanding exactly what is being measured at a particular scale in studying ecological phenomena (Levin 1992). Field manipulations need to be conducted at a scale which adequately distinguishes between changes in local membership and population levels, and those occurring at interhabitat or regional levels (Wiens 1989). Determining the appropriate scale requires an intimate knowledge of organismal biology, including dispersal and long-term population structure. The issue of scale becomes even more crucial when estimating the potential effects of very large-scale processes such as global climate change on smaller scale phenomena such as local and regional biodiversity, biotic interactions, and community structure and energetics (e.g., Risser et al. 1988, Woodmansee 1988, Field et al. 1992, Kareiva et al. 1992, Peters & Lovejoy 1992, Wessman 1992).

An increasing number of studies have investigated the effects of climatic forces on population dynamics (e.g, Leirs et al. 1997, Forchhammer et al. 1998, Grenfell et al. 1998, Lima et al. 1999a, 1999b, 2001a, 2001b, 2002a, 2002b, 2006, Coulson et al. 2001, Loeuille & Ghil 2004), and show the joint effects of endogenous and exogenous forces on dynamics of natural populations. Nonetheless, it is clear that in some instances exogenous factors (i.e., climate) are of major importance. For various organisms, feedback structure and climatic forces are key elements to understand numerical fluctuations (Royama 1992, Turchin 1995, Berryman 1999). Further, although linear feedback effects have traditionally been emphasized, nonlinear effects may be the rule rather than the exception (e.g., Stenseth et al.

1997, Grenfell et al. 1998, Bjørnstad et al. 1998, Berryman 1999, Kristoffersen et al. 2001, Coulson 2004), and they have increasingly been verified (e.g., Sæther et al. 2000, Mysterud et al. 2001, Stenseth et al. 2002, 2004, Ellis & Post 2004, Lima et al. 2006, Berryman & Lima 2007).

With evidence increasingly compelling for climatically-induced environmental change, global climatic change (GCC) has become a major focus in ecology. There is no longer doubt that major anthropogenically-induced alterations in organismal distributions, abundance, and dynamics are occurring (e.g., Walther et al. 2002, 2005, Parmesan 2006, Bodkin et al. 2007, IPCC 2007). Increased frequency, duration, and magnitude of El Niño events are one facet of ongoing GCC (Latif et al. 1998, Timmermann et al. 1999, Mann et al. 2000, Diaz et al. 2001, Herbert & Dixon 2002); although dispute about linkages persists (e.g., Rajagopalan et al. 1997, Kirtman & Schopf 1998, Kleeman & Power 2000, Stenseth et al. 2003), GCC may have already altered the El Niño Southern Oscillation (ENSO) phenomenon (Fedorov & Philander 2000, Kerr 2004, Wara et al. 2005) with current weather patterns reflecting the combination of natural variability and a changing baseline. Several stepwise shifts in climate appear to have occurred in the past 30 years. The eastern Pacific Ocean warmed around 1976 (CLIVAR 1992), and between 1976 and 1998, El Niño events were larger, more persistent and more frequent; the two largest El Niño of the 20th century occurred in this period. In western South America (especially NW Peru and semiarid north-central Chile) increasing rainfall tends to occur during El Niño Southern Oscillation (ENSO) warm phases; low rainfall occurs in other regions such as in Australia and southern Africa. The implications of ENSO-driven changes in precipitation for semiarid regions are multiple (reviews in Jaksic 2001, Holmgren et al. 2006a, 2006b). Elevated rainfall in semiarid Chile leads to dramatic increases in ephemeral plant cover (Dillon & Rundel 1990, Gutiérrez et al. 1997, Vidiella et al. 1999, Block & Richter 2000), although it often decreases during succeeding years of multiyear El Niño/high rainfall events, suggesting nutrient limitation (Gutiérrez et al. 1997, de la Maza et al. 2009). Other groups increase dramatically following El Niño including small mammals (e.g., Jiménez et al. 1992, Meserve et al. 1995, Lima & Jaksic 1998a, 1998b, 1998c, Lima et al. 2001a, 2001b, 2002a, 2002b, 2006), vertebrate predators (Jaksic et al. 1993, 1997, Arim & Jaksic 2005, Arim et al. 2006, Farias & Jaksic 2007), and birds (Jaksic & Lazo 1999). The responses appear due to upward-cascading effects of rainfall on productivity in regions which normally are arid (Holmgren et al. 2001, 2006a). Similar patterns hold for plant and animal groups where unusually high rainfall occurs during El Niño (e.g., North America, Brown & Ernest 2002, DeSante et al. 2003) or La Niña years (e.g., Australia, Letnic et al. 2004, 2005). Negative biological consequences of more frequent El Niño/high rainfall events may include the emergence or increased prevalence of certain pathogens as a result of more abundant vectors, reservoirs, and transmission agents (Kovats et al. 1999, Epstein 1999, 2000, Epstein & Mills 2005). Finally, another negative consequence of GCC and more frequent El Niño events may be a greater impact of introduced species (e.g., Arroyo et al. 2000, Hobbs & Mooney 2005, Parker et al. 2006, Gutiérrez et al. 2007).

Although many authors have emphasized the need for long-term and manipulative field experiments in ecology (e.g., Likens 1989, Risser 1991, Cody & Smallwood 1996), to date there are relatively few such studies. We have maintained a field manipulation in a semiarid scrubland in north-central Chile for more than 20 years, making this the longest such study in temperate South America. The emphasis of the study has been modified as incoming data suggested important new directions for research. It began as a study on the relative importance of two forms of biotic interactions (competition vs. predation), but with the onset of the 1991-92 El Niño event, the overwhelming importance of abiotic factors on this semiarid system became clear. We have now tracked small mammals and plants through multiple El Niño/high rainfall periods, with similar (albeit not identical) biotic responses. Recent studies on seed consumption, however, have underscored the importance of birds (Kelt et al. 2004a, 2004b, 2004c), and observations have indicated that they also are strongly influenced by both abiotic and biotic influences, and possibly by our field manipulations as well.

The history of population and community ecology has shown that single factor or simplistic explanations for major phenomena often fail to endure. In community ecology, studies that emphasize multiple biotic interactions and both indirect and direct effects have become increasingly important (e.g., Strauss 1991, Menge 1995, Abrams et al. 1996). Notable examples are studies of herbivore and/or granivore interactions with plants and/or seeds (e.g., McNaughton 1976, Brown et al. 1986, Brown & Heske 1990, Brown 1998), inter-guild interactions and plants and/or seeds (e.g., Davidson et al. 1984, 1985, Brown et al. 1986, Guo et al. 1995, Ostfeld et al. 1996, Brown 1998), and effects of predators on prey and the role of food (e.g., Taitt & Krebs 1983, Desy & Batzli 1989, Krebs et al. 1995).

We have argued that ecological dynamics at our site shift between "top-down" and "bottom-up" control with important roles for both biotic and abiotic factors (Meserve et al. 2003). This may be possible in part because this region is a highly variable semiarid environment. Whereas the role of biotic interactions may receive more attention because of tractability for manipulation, our work shows that abiotic factors also are very important in this system, and deserve more attention in ecological studies generally (Dunson & Travis 1991, Karr 1992). Our study is helping to clarify the important role of such abiotic factors when superimposed on a suite of biotic interactions; it is largely the long-term baseline that our study affords that provides us with insights into the relative roles of these influences.

Work at our site provides important baseline data for interpreting long-term changes in semiarid Chile but has important implications for other arid and semiarid systems. Over the last 1,000 years, rainfall in northern Chile has declined within a more gradual aridity trend (Bahre 1979, Villalba 1994). Rainfall in the park averaged 209 mm year^{-1} in 1940-49, 185 mm in 1960-69, 127 mm in 1970-79, 85 mm in 1980-89, and 113 mm in 1990-99 (Kummerow 1966, Fulk 1975, Gutiérrez 2001). Although there has been little change in small mammal assemblage and shrub cover at Fray Jorge over 50 years, El Niño-related outbreaks of small mammals and effects on agriculture have become more dramatic elsewhere (e.g., Pearson 1975, Péfaur et al. 1979, Fuentes & Campusano 1985, Jiménez et al. 1992, Jaksic & Lima 2003). The surrounding north-central semiarid region ("Norte Chico") has become highly desertified (Bahre 1979, Schofield & Bucher 1986), with 44 % of ca. 3.5 million ha of the IV Region (within the Norte Chico) characterized as "sterile" by the mid-1970s due to overgrazing, overcutting, and neglect (Ovalle et al. 1993). Desertification has occurred at a rate of about 0.4-1.4 % year^{-1} (Bahre 1979); by the early 1990's, less than 0.1 % of the Norte Chico was cultivated, and unrestricted grazing and fuelwood collection continued in the predominantly rural areas (Ovalle et al. 1993). Interestingly, El Niño events may offer opportunities for restoration of such systems (Holmgren & Scheffer 2001). However, until recently, little was known about the dynamics of plant-animal interactions here (but see Armesto et al. 1993, Gutiérrez 1993, 2001, Ovalle et al. 1993, Whitford 1993). Consequently, northern Chile and this study in particular, provide important sources of baseline data for ecologists as well as conservation and restoration biologists.

STUDY AREA AND METHODOLOGY

In 1989, we began a large-scale manipulation in Bosque Fray Jorge National Park (71°40' W, 30°38' S; Fray Jorge hereafter), a 10,000 ha Biosphere Reserve in the north-central Chilean semiarid zone. The park contains semiarid thorn scrub vegetation and remnant fog forests that have been protected from grazing and disturbance since 1941 (Squeo et al. 2004). The thorn scrub includes spiny drought-deciduous and evergreen shrubs and understory herbs on a primarily sandy substrate (Muñoz & Pisano 1947, Muñoz 1985, Hoffmann 1989, Gutiérrez et al. 1993a). The climate is semiarid Mediterranean with 90 % of the mean annual 133 mm (average between 1989 and 2008) precipitation falling in winter months (May-Sept.), and warm, dry summers. Since 1989, there have been five El Niño/high rainfall events in this region: 1991-92 (233-229 mm), 1997 (330 mm), 2000-2002 (236-339 mm), 2004 (168 mm), and 2006 (147 mm); intervening years have been dry (11 to 89 mm).

Based on earlier work (e.g., Meserve 1981a, 1981b, Meserve et al. 1983, 1984, 1987, Meserve & Le Boulengé 1987), we initially focused our attention on the role of biotic interactions in the community, specifically, vertebrate predation, small mammal herbivory, and interspecific competition among small mammals. Much of our earlier interest has been on the biology of an important herbivore, *Octodon degus* (Molina, 1782) (degu), a medium-sized (ca. 120-150 g) caviomorph rodent characteristic of Mediterranean Chile; Fray Jorge is near the northern limits of the degu's range. Other small mammals include the uncommon *Abrocoma bennetti* Waterhouse, 1837 (150-250 g) and several smaller (20-80 g) omnivorous to granivorous/insectivorous species such as *Abrothrix olivaceus* (Waterhouse, 1837), *A. longipilis* (Waterhouse, 1837), *Phyllotis darwini* (Waterhouse, 1837), *Oligoryzomys longicaudatus* (Bennett, 1832), and *Thylamys elegans* (Waterhouse, 1839) (Meserve 1981a, 1981b). Principal small mammal predators include owls (*Tyto alba* [Scopoli, 1769], *Athene cunicularia* [Molina, 1782], *Bubo magellanicus* [Lesson, 1828], *Glaucidium nanum* [King, 1828]) and the culpeo fox (*Lycalopex culpaeus* [Molina, 1782]; Fulk 1976a, Jaksic et al. 1981, 1992, 1993, 1997, Meserve et al. 1987, Salvatori et al. 1999). Other predators are snakes (*Philodryas chamissonis* [Wiegmann, 1835]) and a large teiid lizard (*Callopistes maculatus* Gravenhorst, 1838; Minn 2002, Jaksic et al. 2004). Numbers of predators are unusually high because the park contains the largest remaining intact scrub habitat in north-central Chile (Bahre 1979).

The initial experimental complex consisted of 16 small mammal live-trapping grids (75 x 75 m = 0.56 ha) in thorn scrub habitat in an interior valley of the park ("Quebrada de las Vacas," 240 m elev.; "central grid complex" in Fig. 1) previously studied by Fulk (1975, 1976a, 1976b), Meserve (1981a, 1981b), and Meserve & Le Boulengé (1987). The original design included four treatments each with four randomly assigned grids: 1) controls, with low (1.0 m h) 2.5 cm mesh fencing buried ca. 40 cm with 5 cm d holes at ground level to provide access by all small mammals and predators (+D +P); 2) predator exclusions, with tall (1.8 m h) 5 cm mesh fencing buried 40 cm, 1 m overhangs, and polyethylene mesh (15 cm) netting overhead, excluding predators but allowing small mammal access (including degus; +D -P); 3) degu exclusions, with low (1.0 m h) 2.5 cm mesh fencing without holes to exclude degus but not other small mammals or predators (-D +P); or 4) degu & predator exclusions, with tall (1.8 m h) 5 cm mesh fencing, with high overhangs, and netting to exclude predators, supplemented with 2.5 cm fencing to exclude degus (-D -P). Our manipulations have utilized a long-term "press" approach (sensu Bender et al. 1984) to examine these biotic interactions. Sampling methods are as follows (see also Meserve et al. 1993a, 1993b, 1995, 1996, Gutiérrez et al. 1993a, 1993b, 1997, Jaksic et al. 1993, 1997): 1) Small mammals are trapped for four days/month/grid (5 x 5 stations, 15 m interval, two traps/station). We estimate population size with minimum number known alive (MNKA; Hilborn et al. 1976). 2) Perennial shrub cover is measured every three month with four permanent 75 m parallel transects/grid and point intercept method (0.5 m intervals). 3) Ephemeral (annuals + geophytes) cover is measured monthly in the growing season (April-Aug. to Oct.-Dec.) on 10 random 1.5 m segments subdivided into 30 points (5 cm intervals) on the transects. 4) Soil samples (n = 20 random samples [3 cm d x 5 cm depth = 35.35 cm^3] $grid^{-1}$) are collected every four month. 5) Fox scats and owl pellets are collected monthly from the site and nearby roosts; predators are monitored monthly with sightings and olfactory lines.

We have employed various approaches to data analysis. Initially, we used repeated measures analysis of variance (rmANOVA, PROC GLM; SAS 1990a, 1990b, Potvin et al. 1990, von Ende 2001), and mixed model rmANOVA (PROC MIXED; Wolfinger & Chang 1995, SAS 1996). Small mammal survivorship was analyzed with PROC LIFETEST (SAS 1990b) and nonparametric log-rank tests (Lee 1980, Fox 2001). Results of analyses on small mammals and predators were reported in Jaksic et al. (1993, 1997), Meserve et al. (1993a, 1993b, 1995, 1996, 1999, 2001, 2003), and Milstead (2000).

Recently (Previtali 2006) we investigated the effects of predator/competitor exclusions using Log Response Ratios (LRRs), calculated as the log of the ratio of the density of the target species in the competitor or predator exclusion treatment over its density in the control (LRR = Ln (N_t exclusion / N_t control); Schmitz et al. 2000, Berlow et al. 2004). We assumed that biotic interactions (competition, predation) would vary depending on the duration of wet or dry phases since this relates directly to resource availability. Consequently, we categorized each year based on whether wet vs. dry conditions (i.e., above- or below-average rainfall, respectively) prevailed in that year and the preceding year. Thus, we defined each year as part of a Dry-Dry, Dry-Wet, Wet-Wet, or Wet-Dry phase. Given the lag in demographic responses to resource availability, we posited that Dry-Wet years would have high resource availability (the wet year) but low population densities (due to the preceding dry year). Similarly, Wet-Dry years should have low resources (current, dry year) but high population densities (in response to the preceding wet year), and so on.

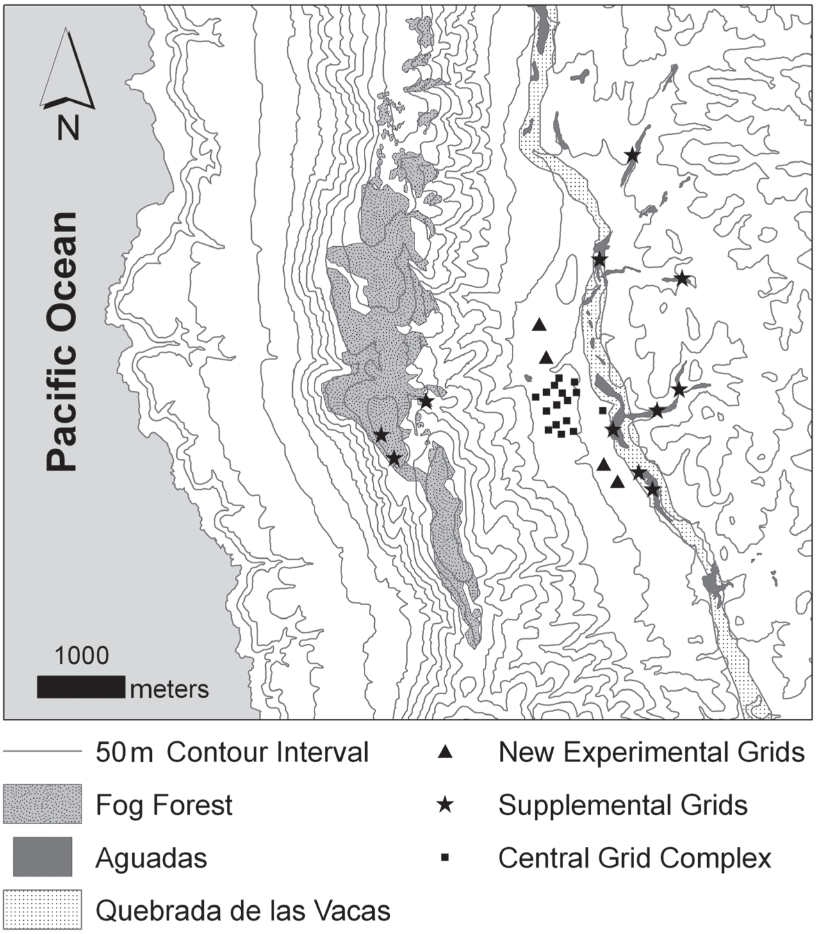

Fig. 1: Location of study area, grids and major habitats in Fray Jorge. Light shaded areas are predominantly thorn scrub habitat. Sixteen grids in the "central grid complex" have been used since 1989; "supplemental grids" located in other habitats (i.e., fog forest, aguadas + quebradas) were sampled during 1996-2003. "New experimental grids" were added in 2007-2008 and target lagomorphs with and without small mammal exclusions.

Ubicación del área de estudio, parcelas y hábitats principales en Fray Jorge. Áreas con sombreado claro son predominantemente hábitat de arbustos espinosos. Desde 1989 se han usado dieciséis parcelas en el "complejo de parcelas centrales"; "parcelas adicionales" ubicadas en otros hábitats (i.e., bosque de neblinas, aguadas + quebradas) se muestrearon durante 1996-2003. "Parcelas experimentales nuevas" se agregaron en 2007-2008 con exclusiones de lagomorfos y micromamíferos.

We assessed behavioral (foraging) responses to predator removal with "giving up densities" from foraging trays (Yunger et al. 2002, Kelt et al. 2004a, 2004b, 2004c). This allowed us to evaluate whether experimental treatments have had functional effects of small mammal foraging independent of their numerical responses to manipulation of predator and/or interspecific competition.

For plant responses, we estimated cover (angular transformed) and seed densities (log-transformed) and used annual peak values (due to varying length of the annual growing season) to allow balanced between-year analyses with rmANOVA (Gutiérrez et al. 1997). Elsewhere we compared plant densities and biomass across our experimental treatments (log-transformed; Gutiérrez & Meserve 2000).

Prior to manipulations we documented no significant between-treatment differences (small mammals: pre-test period = March-May 1989; plants: 1989). Plant nomenclature follows Marticorena & Quezada (1985).

RESULTS AND DISCUSSION

Effects of predation on small mammals

O. degus responded positively to predator exclusions (Previtali 2006), with greater LRRs during prolonged droughts (i.e., Dry-Dry years, 1994-1996, and 1999; Fig. 2). Other

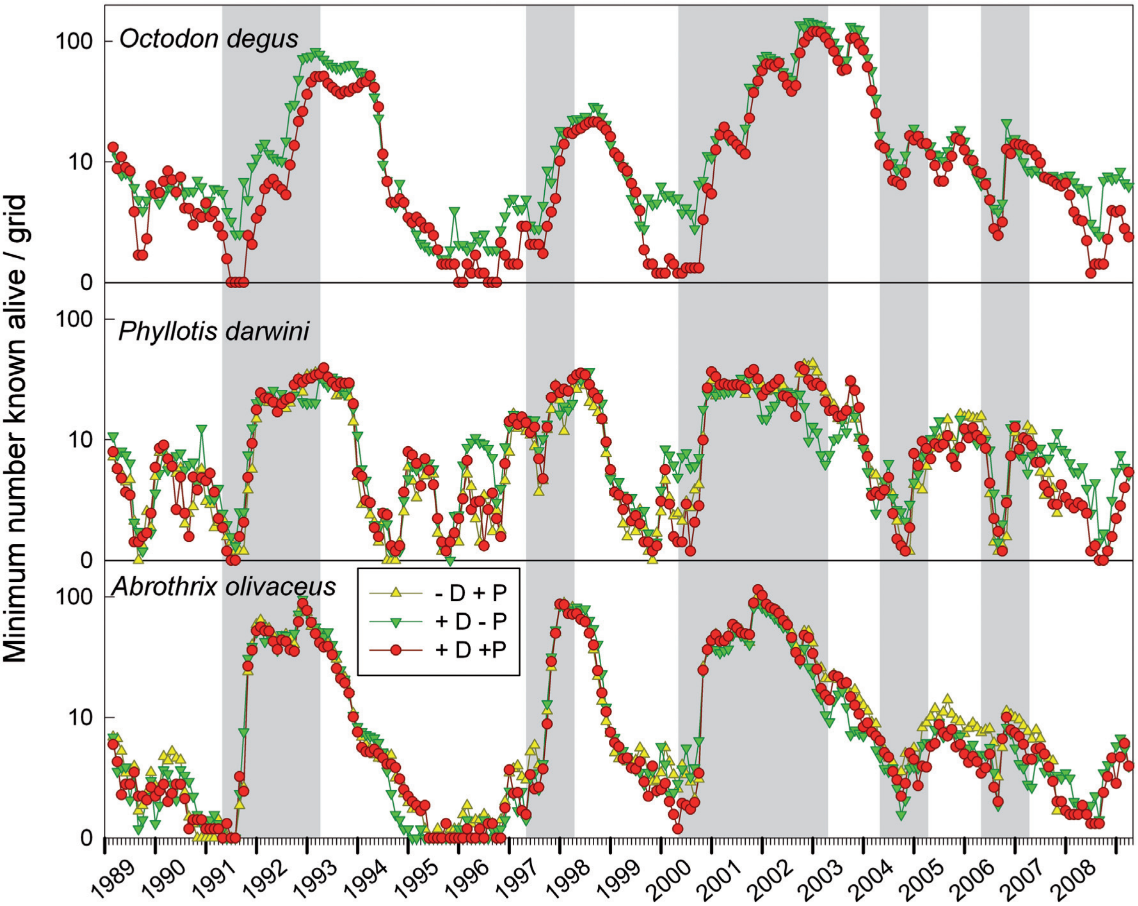

Fig. 2: Population trends for three small mammals in Fray Jorge during 1989-2007. Treatments indicated by symbols and letters (+/- D = presence or absence of degus; +/- P = presence or absence of predators).

Tendencias poblacionales de tres micromamíferos en Fray Jorge durante 1989-2007. Los tratamientos están indicados por símbolos y letras (+/-D= presencia o ausencia de degus; +/-P= presencia o ausencia de depredadores).

species (*Phyllotis* and *A. olivaceus*) showed only slight or even negative effects of predator exclusion. Degu survival probabilities were significantly greater on exclusions than control grids (Previtali 2006). Although we have documented behavioral changes in *Octodon* and other species under predator exclusion conditions (Lagos 1993, Lagos et al. 1995, Yunger et al. 2002, 2007, Kelt et al. 2004a), these often are not manifested in numerical responses to predation.

Predator numbers and diets

Both owl and fox diets are dominated by *O. degus*, *Phyllotis*, and *Abrocoma* (Jaksic et al. 1993, 1997, Silva et al. 1995). Predators showed numerical responses to changes in prey abundance, with increases after El Niño events and declines as prey decreased (Jaksic et al. 1997, Salvatori et al. 1999). Foxes and some owls were more omnivorous at low small mammal levels with increased importance of insects (*G. nanum*, *A. cunicularia*: Silva et al. 1995) and seeds + fruits (*L. culpaeus*: Castro et al. 1994).

Effects of competition by Octodon *on other small mammals*

Octodon negatively impact trophically-dissimilar species such as *A. olivaceus* (Meserve et al. 1996, Yunger et al. 2002, Kelt et al. 2004a, Previtali 2006), *Oligoryzomys* (Milstead 2000), and *Thylamys* (Meserve et al. 2001). Surprisingly, degus may have a facilitative influence on *Phyllotis*; this species exhibited higher densities in controls than degu exclusions.

Effects of herbivores and predators on plants

Vegetative responses to herbivore (i.e., degus) and/or predator exclusions have been heterogeneous (Gutiérrez et al. 1997, Gutiérrez & Meserve 2000). Perennial cover showed no significant treatment responses, but diversity increased on degu exclusions. Some species showed greater cover in plots excluding degus (i.e., *Baccharis paniculata* DC., *Chenopodium petiolare* H.B.K.) or predators (i.e., *Proustia cuneifolia* D. Don). *Chenopodium petiolare* is a suffructicose perennial and an important degu food (Meserve 1981b, 1983, 1984). Ephemerals (annuals + geophytes) showed no significant main treatment effects on cover or diversity, but total biomass was significantly higher in plots accessible to degus and predators (Gutiérrez & Meserve 2000). Overall, consumptive effects of degus were relatively small, whereas their indirect activities appeared to increase ephemeral biomass. Seed densities of annual species, including those of *Erodium* and *Moscharia pinnatifida* R. et P., were higher in degu-access grids (Gutiérrez et al. 1997). Widespread, adventitious herbs (e.g., *Erodium*) may be facilitated by disturbance due to runway development and activity as well as digging under bushes.

Thus, degus appear to exert complex effects including both depression and facilitation of plants and seeds. However, the effects of other rodents (most notably *Phyllotis* and *A. olivaceus*, which comprised 74.8 % of individuals captured of the three most common species) could not be separated from those of degus, suggesting density or energetic compensation (re Ernest & Brown 2001a, 2001b). Given this limitation, in 2001 we converted four former degu & predator exclosures (-D -P) to all-small mammal exclosures (-SM) by removing the original netting and fencing, and installing 1.5 m h 0.25 inch hardware cloth fencing topped with ca. 20 cm metal flashing. These plots were selected because they had shown the least vegetative changes in over 12 yrs. Trapping procedures remained identical, but captured animals were marked and then released ~1 km away. Although not completely effective, all-small mammal exclusions have reduced most species to 23.4 ± 9.8 % (±SE) of control populations since 2002. Some plants responded immediately and dramatically. In the first year of these treatments, cover by *Plantago hispidula* R. et P. increased to ca. four times that in control grids. Although this species is an important food of herbivorous rodents in the study area (Meserve 1981b), seed densities were similar in –SM and control treatments. Consequently, the best explanation for the increase of *P. hispidula* here and not in degu exclusion grids was absence of herbivory by non-degu species, most likely the herbivorous *Phyllotis*. However, this difference in cover was not maintained in subsequent years, so the general importance of this effect is not clear to us. Another immediate response was that *Adesmia bedwellii* Skottsb., a perennial shrub comprising ~8 % of shrub cover at our study site, produced significantly more new leaves and buds in –SM plots. Other shrubs (e.g., *Porlieria*, *Proustia*) have not shown these responses, indicating that small mammal impacts on perennial shrub species were selective. Overall, effects of excluding native small mammals have been relatively small. We currently are investigating other aspects such as plant community responses to rainfall events (Gaxiola et al. unpublished data). Using a 20-year datastream on annual plants and climatic factors at Fray Jorge, Gaxiola et al. (unpublished data) documented that annual plant cover (a proxy of productivity) was strongly enhanced by community evenness but not by species richness. Years with > 100 mm rainfall led to linear increases in community evenness, whereas species richness saturated by 100 mm. Annual rainfall and species richness exerted strong indirect effects on annual plant cover via community evenness. These authors concluded that community evenness is relevant for explaining climate-driven changes in productivity of semiarid areas, where increased variability in rainfall is predicted by global climate models.

Effects of ENSO on small mammals and plants

Our initial field design assumed a central ecological role of biotic interaction. However, it is apparent that understanding the impact of abiotic factors is fundamental to interpreting long-term trends. The five El Niño/high rainfall events recorded since 1989 (shaded in Fig. 2) are natural "pulse" experiments that trigger large increases in plant and small mammal populations and thus, alter the role of biotic vs. abiotic factors in the community. Data from control grids provide insights to organismal responses to these events (Meserve et al. 1995, 1999, 2003, Gutiérrez et al. 1997, 2000a, 2000b, Gutiérrez & Meserve 2000, Previtali 2006). For example, of 401,861 captures of 69,029 individuals of 10 small mammal species on all grids through April 2009, 23.5 % and 24.1 %, respectively, have been on controls. Of these, 56.4 % and 65.7 % (captures and individuals, respectively) have occurred during high rainfall periods comprising only 39.7 % of the 242 month of study. Although responses of small mammal species to rainfall events differ in timing, they are similar in being 2-3 orders of magnitude in both numbers and biomass (Meserve et al. 2003), which contrasts strongly with patterns for North American arid/semiarid systems where relative stability in numbers and biomass of small mammals over time suggests homeostasis (Ernest & Brown 2001a).

Spatial dynamics are pivotal to understanding patterns in our system (Meserve et al. 1999, Milstead 2000, Milstead et al. 2007). In thorn scrub, *O. degus*, *Phyllotis*, and *Thylamys* are resident "core" species that occur in all surveys. *A. olivaceus* is a "quasi-core" species, almost always present but with explosive increases after high rainfall years. "Opportunistic species" (e.g., *Oligoryzomys*, *A. longipilis*) disappear from thorn scrub during drought periods but persist in peripheral habitats such as "aguadas" and quebradas (areas with mesic vegetation and/or standing/subsurface water) and fog forest on coastal ridges ("supplemental grids" Fig. 1). Milstead (2000) verified haplotypic variation among some taxa such as *Phyllotis* and *Oligoryzomys* in different habitats within the park, suggesting spatial isolation at a rather small scale, at least during dry periods.

Plants also have shown heterogeneous, and in some cases dramatic, responses to ENSO/high rainfall events (Gutiérrez et al. 1997, 2000a, 2000b, Gutiérrez & Meserve 2003; Fig. 3). Perennial cover only varied from 48.5 % to 64.4 % in 20 years, similar to values of 50 and 35 years ago (Muñoz & Pisano 1947, Meserve 1981a, Gutiérrez et al. 1993a). In contrast, ephemeral cover varied from 0 % during a La Niña event (1998, 11 mm ppt.) to 80-86 % during El Niño/high rainfall years (1991, 1997, 2002). Decreases during ensuing years of multiyear high rainfall events (i.e., 1992, 2001-02) suggest nutrient depletion (Gutiérrez et al. 1993b, 1997). Maximum seed densities reached 41,832 m^{-2}, similar to North American deserts (Inouye 1991), but they do not track rainfall as closely as does ephemeral cover (Gutiérrez & Meserve 2003). Similar responses have been documented elsewhere in semiarid Chile (Dillon & Rundel 1990, Gutiérrez et al. 2000a).

In summary, we have documented some biotic responses to predation, competition, and herbivory, but interactions vary among species and over time. Predation appears to affect numbers and survival of some core species, but has weak or no effects on opportunistic ones. Interspecific competition generally appears weak among small mammals although there is evidence for behavioral interactions. Herbivore effects are heterogeneous, with both negative and positive responses to degu exclusions as well as some indirect (positive) effects of predators. In contrast, responses of both plants and animals to abiotic factors related to El Niño/high rainfall events are dramatic, implicating the importance of pulsed resources (e.g., Ostfeld & Keesing 2000, Stapp & Polis 2003); similar responses have been documented in North American deserts (Valone & Brown 1996), but these studies contrast markedly with ours in documenting strong effects of small mammal granivores in North America (e.g., Brown et al. 1986, Brown & Heske 1990a, 1990b; Curtin et al. 2000) or a relatively minor role for precipitation vs. biotic interactions there (Ernest et al. 2000, Brown & Ernest 2002).

ON-GOING STUDIES

Ongoing studies at our site have developed as data allowed us to refine or refocus our attention. As noted above, we initially argued for a “shifting control” view of the relative importance of various biotic and abiotic factors in this system (Meserve et al. 1999, 2001, 2003, Gutiérrez et al. 2000b). However, Previtali (2006) showed that the top-down influence of predators had strongest effects primarily when prey numbers were low near the end of prolonged droughts; data from Aucó, roughly 115 km SSE of Fray Jorge, also implicated predation in density-dependent dynamics of *Phyllotis* (Lima et al. 2001a, 2002a, 2002b). However, at least at Fray Jorge neither predators nor herbivores appear to “control” their respective resources. Although transitory and variable effects of predators and herbivores can be demonstrated on some

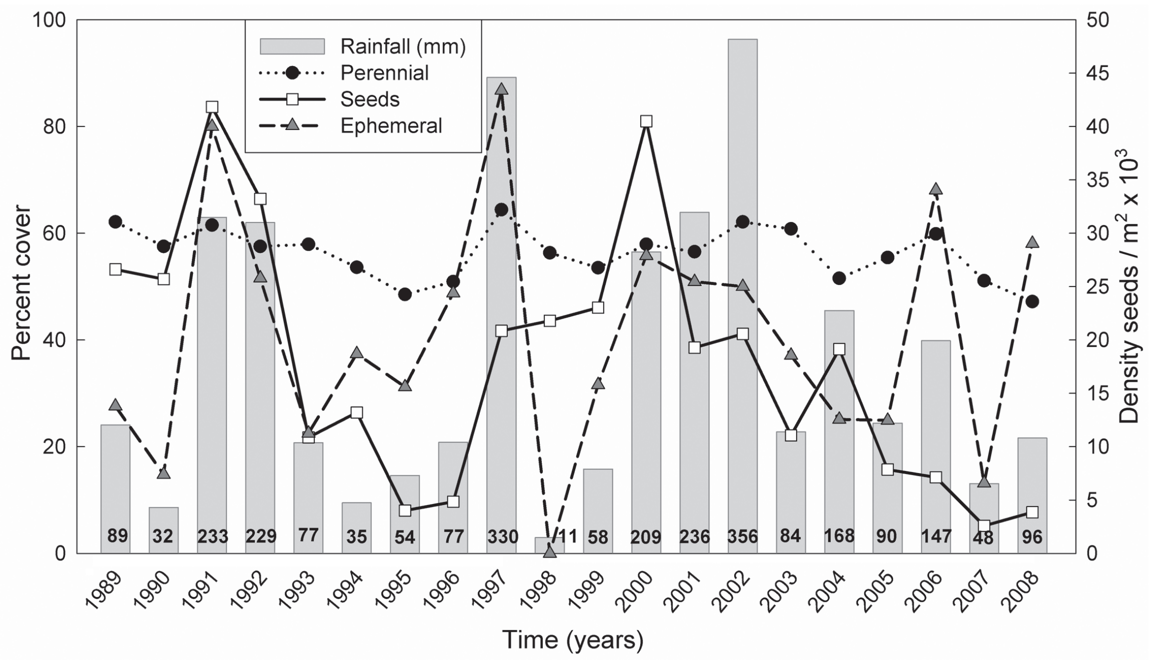

Fig. 3: Annual peak plant cover, seed densities, and total rainfall for control grids (+D + P) for 19 years during 1989-2008.

Cobertura máxima anual de plantas, densidad de semillas y lluvia total en las parcelas control (+D+P) para 19 años durante 1989-2008.

components of the community, it is increasingly clear that "bottom-up" factors –rainfall and nutrients for plants, food for small mammals and their predators– are the dominant drivers at our study site (see also Karr 1992, Polis et al. 1997, Polis 1999, Holmgren et al. 2001). The transition between El Niño and non-El Niño years is abrupt; "bottom-up" control appears to prevail generally, interrupted by brief periods of "top-down" effects; even the regulatory nature of such top-down influences, however, remains unclear in the light of recent demographic modeling (Previtali 2006, Previtali et al. 2009, see below). Thus, there may be a productivity threshold above which we see a covarying relationship between consumer and resource abundances (Oksanen et al. 1981, McQueen et al. 1986, 1989, Mittelbach et al. 1988, Oksanen & Oksanen 2000).

Experimental food addition positively affected numbers and biomass of most core/quasi-core species (i.e., *O. degus*, *Phyllotis*, *A. olivaceus*) during dry periods, but not during El Niño/high rainfall periods (Meserve et al. 2001). Within the context of a 3-trophic level system (vegetation, rodents, predators), food limitation implies density-dependence resulting in strong oscillations (Turchin & Batzli 2001). Further, a relationship between productivity and food chain length has been implicated at Aucó (Arim & Jaksic 2005, Arim et al. 2007), which has a similar small mammal and predator assemblage. Thus, predators may be responding to rainfall and productivity indirectly; prey abundance and functional responses among predators also are involved (Farias & Jaksic 2005).

Additionally, spatial dynamics are important in understanding population and community processes in this system (Milstead 2000, Milstead et al. 2007), possibly including source-sink dynamics (sensu Pulliam 1988, Watkinson & Sutherland 1995, Dias 1996). Spatial factors are known to be important in small mammal population cycles (Lidicker 1991, 1995) but, unlike arvicoline population cycles, oscillations at our site seem more affected by extrinsic (abiotic) factors rather than intrinsic regulation.

Given these observations and the overall complexities of this system, we have recently adjusted our focus to include three other areas of research in Fray Jorge. In combination with long-term monitoring, these will allow us to better identify the importance of key components as well as address heretofore unexamined questions.

1) Modeling small mammal population dynamics

We recently applied demographic modeling to provide deeper insight to our long-term small mammal data set (Previtali 2006). Our database is unique in extending over three trophic levels (plants-rodents-predators), spanning several El Niño/high rainfall events, and combining both observational and experimental approaches. Given the remarkable fluctuations that small mammal populations at Fray Jorge have undergone over 20 years, and the general agreement that both endogenous and exogenous factors are important in explaining population structure and change, a basic question is: What is the relative role of endogenous (feedback structure) vs. exogenous (ENSO-driven rainfall) factors in determining small mammal numerical fluctuations?

We have documented important features in common among the population dynamics of the three small mammal species analyzed to date – *O. degus*, *Phyllotis*, and *A. olivaceus*. Population changes of the latter two species were driven by the combined effect of both intrinsic (density dependent) and extrinsic (climatic) factors (Lima et al. 2006), more especifically by intraspecific competition and current and lagged rainfall. However, climate influenced dynamics for these species through very different mechanisms. Whereas rainfall had a simple additive effect for *A. olivaceus*, the best model for population growth of *Phyllotis* was a version of the Ricker model, with rainfall influencing carrying capacity non-additively, acting as the denominator in the ratio with population size (Lima et al. 2006).

Recently we applied more descriptive parameters (e.g., predation and food resources) to model variation in the population rate of change of *Phyllotis* and *O. degus* (Previtali et al. 2009). Dynamics of both species were driven by a non-additive interaction of intraspecific competition and resource availability consistent with earlier predictions (Lima et al. 2006). However, resource availability was better represented by the combined effect of seed density and plant cover for *Phyllotis,* and by rainfall for *O. degus* (Previtali et al. 2009). Although earlier work suggested influences of predation on *O. degus* (e.g., Lagos 1993, Lagos et al. 1995, Meserve et al. 1993b, 1996), the longer time series analyzed indicated that predation is not a key driver of population dynamics of degus or *Phyllotis.* Thus, bottom-up forces had strong impacts on these two species. For both, the per capita population growth rate was negatively associated with the ratio of population density over current resources, and provided the greatest explanatory power for this variable (Previtali et al. 2009). A secondary influence was the additive lagged effect of the previous year's resource availability.

In summary, the dynamics of three dominant small mammal species at our site (*A. olivaceus*, *Phyllotis*, and *O. degus*) are driven by climate-mediated variation in resources, and this leads to three new questions that we are addressing with these data. First, what are the underlying mechanisms? Second, what will be the dynamical consequences of altered rainfall patterns caused by GCC? Third, are species similarly influenced by climatically-mediated resource availability and are the general patterns similar to those documented already?

We also are expanding the analysis to examine aspects of these dynamics at shorter time intervals; rather than a single observation per year, we are investigating patterns associated with intra-annual variation in resources. This finer scale will provide insights to processes occurring at shorter time scales, while enabling us to obtain a more accurate estimate of lags in population responses to endogenous and exogenous factors (cf., Lewellen & Vessey [1998]).

We are appling stochastic stage-structured models to *O. degus* to make predictions of prospective trends in the population rate of change. We incorporate stochasticity to these models as variation in annual precipitation, reflecting predicted increases in mean and variance of annual rainfall in response to GCC (more frequent El Niño events, occasionally strong La Niña events). We are developing models using the mean and variance of demographic parameters (survival and fecundity) estimated from 18 years of data (through 2006; Previtali et al. 2010), and are validating the models by comparing predicted population size with those observed since 2006. This approach has been used to understand the effects of climatic variation on the dynamics of *Peromyscus maniculatus* (Reed et al. 2007).

We look forward to applying similar quantitative approaches to other species in the assemblage, in particular *Thylamys* and *A. longipilis*, insectivorous species with very different dynamics (Meserve et al. 1995, 2003). The former is a "core species" but exhibits strong intra-annual fluctuations, whereas the latter is an "opportunistic species" that disappears from the thorn scrub during dry periods but maintains populations in the fog forests and immigrates to the thorn scrub during El Niño/high-rainfall events. Whereas climate and food availability have been implicated as important demographic drivers in *Thylamys* (Lima et al. 2001b), those of *A. longipilis* appear dominated by higher-order processes, at least in southern Chile (Murúa et al. 2003). The pattern of fluctuations observed for *A. longipilis* at Fray Jorge, with slow increases after rainy years followed by slow declines, is typical of second-order dynamics, although influences from cyclic external factors (e.g., oscillating climatic forces) can generate apparent second-order patterns in a first-order dynamics (Berryman & Lima 2007). We are investigating dynamics of *A. longipilis* using approaches similar to those recently applied to other species in Fray Jorge (Previtali et al. 2009), involving time series analyses to investigate temporal changes in rodent densities and in the relationship between R_t and time-lagged densities. In light of predictions of more frequent and intense El Niño events, these analyses are important in forecasting changes that may occur in the Fray Jorge small mammal community.

Finally, we also look forward to analyses on the opportunistic species *Oligoryzomys longicaudatus*, although their low and sporadic numbers make such analyses challenging if not impossible. Ultimately, these analyses will include all core species (*O. degus*, *Phyllotis*, *Thylamys*) as well as a quasi-core species (*A. olivaceus*), and an opportunistic species (*A.

longipilis; sensu Meserve et al. [2003], Milstead et al. [2007]) in the small mammal assemblage. We anticipate that characterizing demographic patterns and driving factors in this manner will lead to a more comprehensive understanding of the dynamics of key small mammal species at our site, and allow us to make predictive assessments of likely responses by these key elements of the fauna in response to climate change, and extrapolate them to predictions at the community level.

2) Importance of other consumer groups – birds

Until recently, our efforts have concentrated on documenting important linkages between several major subsets of the organismal components of our study system – small mammals, plants (herbage, seeds), and vertebrate predators. Another major consumer group that likely has important links to their predators and/or prey is songbirds, and we initiated studies on these in 2002. Surprisingly little work has been pursued on avian ecology in northern Chile, and hence, we initiated basic censuses as well as documented foraging ecology for select species. Most recently we have begun characterizing plumages in birds at Fray Jorge to distinguish sexes and age classes externally; with this information we hope to initiate formal monitoring of avian productivity and survivorship (e.g., MAPS - Monitoring Avian Productivity and Survivorship; DeSante et al. 2008) in the near future.

Birds are the primary granivores at Fray Jorge, followed by small mammals (especially when populations are high); ants are only trivial consumers (Kelt et al. 2004a, 2004b, 2004c). This contrasts with high seed consumption rates by ants (and small mammals) in Northern Hemispheric arid zones (e.g., Brown et al. 1979, Davidson et al. 1980, 1984, 1985, Brown 1987), but supports other studies refuting suggested low granivory overall in South America (Mares & Rosenzweig 1978, Brown & Ojeda 1987, Medel & Vásquez 1994, Medel 1995, Vásquez et al. 1995). Moreover, an extensive seed bank and large guild of granivorous birds has been documented in South American arid zones (e.g., Marone & Horno 1997, López de Casenave et al. 1998, Marone et al. 1998, 2000, Gutiérrez & Meserve 2003). Unlike the documented numerical responses of small mammals to El Niño events, we lack such information for birds. We do know that there are strong seasonal increases in avian populations due to immigration from the Andean foothills and/or southern Chile in the austral winter, and recently, we confirmed transient populations of birds migrating through the park in spring (A. Engilis, unpublished data). Thus, we have focused our work on documenting avian responses to ENSO-induced fluctuations in resource levels, including seasonal and annual demographic fluctuations as well as variation in reproductive patterns and productivity (fledgling success).

In 2002, we verified that variable-radius point counts were the most appropriate means of monitoring avian numbers, and in 2004 we initiated triannual surveys on eight 1 km transects comprising four stations ca. 250 m apart crossing the study area. Transects are oriented east-west and are arranged at 1 km intervals (north-south) to span Quebrada de Las Vacas. Using detection curves we determined that a count of eight minutes was optimal for surveying the scrub habitat of the park. We conducted counts during the post-breeding period (Feb.-Mar.), mid-winter (July-Aug.), and during peak breeding season (Oct.-Nov.). All counts were conducted from daybreak to no later than 1,000 hrs on days lacking moderate or strong winds; we conducted all surveys twice (on separate days) to minimize any spurious results. Thus, each survey included 32 point counts sampled twice for a total of 512 min. We determined detectabilities and abundance for key species using DISTANCE (Buckland et al. 2001, Thomas et al. 2006). Surveys conducted during the breeding season are not complete (only three years analyzed and a fourth year only recently obtained) and thus are not included here. To date we have recorded 49 bird species (Table 1), with a mean of just over 30 species per census (Fig. 4).

Considering only birds detected within 50 m of the survey point, over half of our detections comprised only five species (Fig. 5) – chincol (*Zonotrichia capensis* [Muller, 1776]; 18 %), yal (*Phrygilis fruticeti* [Kittlitz, 1833]; 12 %), canastero (*Asthenes humilis* [Cabanis, 1873]; 8 %), tapaculo (*Scelorchilus albicollis*

TABLE 1

List of all bird species recorded on point counts in Bosque Fray Jorge National Park with annotations of occurrence by session during 2004-2008. In the table, the proximity of the bird to the survey point is indicated as 1 = 25 m radius, 2 = 50 m radius, 3 = 500 m radius, 4 = no limit.

Lista de todas las especies de aves registradas en puntos de conteo en el Parque Nacional Bosque Fray Jorge con anotaciones de ocurrencia por sesión durante 2004-2008. En la tabla, la proximidad del ave al punto de censo se indica como 1 = 25 m de radio, 2 = 50 m de radio, 3 = 500 m de radio, 4 = sin límites.

Family	Species	Chilean name	EnglishName	2004		2005		2006		2007		2008	
Familia	Especies	Nombre chileno	Nombre inglés	Smr Ver	Wtr Inv	Smr Ver	Wtr Inv	Smr Ver	Wtr Inv	Smr Ver	Wtr Inv	Smr Ver	Wtr Inv
Tinamiidae	*Nothoprocta perdicaria*	Perdiz chilena	Chilean tinamou		2	1	1	1	1	1	4	4	4
Odontophoridae	*Callipepla californica*	Codorniz	California quail	1	2	1	1	1		1	1	2	2
Threskiornithidae	*Theristicus melanopsis*	Bandurria	Black-faced ibis						4				
Accipitridae	*Buteo polyosoma*	Aguilucho	Variable hawk	4	4	3	2		4	4			
Accipitridae	*Circus cinereus*	Vari	Cinereus harrier	4									
Accipitridae	*Geranoaetus melanoleucus*	Águila	Black-chested buzzard-eagle	4	4	4	4	4	4	4	4		
Accipitridae	*Parabuteo unicinctus*	Peuco	Harris' hawk	1	4	4	4	4		2	2		
Falconidae	*Falco peregrinus*	Halcón	Peregrine falcon						4		4		4
Falconidae	*Falco sparverius*	Cernícalo	American kestrel						4	4			4
Falconidae	*Milvago chimango*	Tiuque	Chimango caracara	3	3		4	4	2	4	2		4
Charadriidae	*Vanellus chilensis*	Queltehue	Southern lapwing								4		
Columbidae	*Columba araucana*	Torcaza	Chilean pigeon							1	4		
Columbidae	*Zedaida auriculata*	Tórtola	Eared dove			2	4			2	4		2
Strigidae	*Asio flammeus*	Nuco	Short-eared owl	4									
Strigidae	*Athene cunicularia*	Pequén	Burrowing owl		2	2	2	1	2	2	1		
Strigidae	*Glaucidium nanum*	Chuncho	Austral pygmy-owl	1	1	2	4	1			4		2
Camprimulgidae	*Caprimulgus longirostris*	Gallina ciega	Band-winged nightjar			4	4	1		1			
Trochilidae	*Patagona gigas*	Picaflor grande	Giant hummingbird	1	3	4	4		4	3	4	4	4
Trochilidae	*Sephanoides sephanoides*	Picaflor chico	Green-backed firecrown	2	1	4	1	4	1	1		1	1
Picidae	*Colaptes pitius*	Pitio	Chilean flicker							4			
Picidae	*Picoides lignarius*	Carpinterito	Striped woodpecker	1	1	2	4	1	1	1	1	1	2

Furnariidae	*Asthene humilis*	Canastero	Dusky-tailed canastero	1	1	1	1	1	1	1	1	1	1
Furnariidae	*Geositta cunicularia*	Minero	Common miner				2		1				1
Furnariidae	*Geositta rufipennis*	Minero cordillerano	Rufous-banded miner						2				
Furnariidae	*Leptasthenura aegithaloides*	Tijeral	Plain-mantled tit-spinetail	1	1	1	1	1	1	1	1	1	1
Furnariidae	*Upucerthia dumetaria*	Bandurilla	Scale-throated earthcreeper		1				2		1		2
Rhinocryptidae	*Pteroptochos megapodius*	Turca	Moustached turca	1	2	1	1	1	1	2	1	1	1
Rhinocryptidae	*Scelorchilus albicollis*	Tapaculo	White-throated tapaculo	1	1	1	1	1	1	1	1	1	1
Rhinocryptidae	*Scytalopus fuscus*	Churrin	Dusky tapaculo	2	1	2	4	4	3	2	4	2	4
Tyrannidae	*Agriornis livida*	Mero	Great shrike-tyrant	2	1	3	1	1	2	4	2	1	
Tyrannidae	*Anairetes parulus*	Cachudito	Tufted tit-tyrant	1	1	1	1	1	1	1	1	1	1
Tyrannidae	*Coloramphus parvirostris*	Viudita	Patagonian tyrant								4		4
Tyrannidae	*Elaenia albiceps*	Fio Fio	White-crested elaenia					4					
Tyrannidae	*Muscisaxicola macloviana*	Dormilona tontita	Dark-faced ground-tyrant										2
Tyrannidae	*Xolmis pyrope*	Diucón	Fire-eyed diucon	2	2		1	1	2	2	1	1	1
Hirundinidae	*Tachycineta meyeni*	Golondrina chilena	Chilean swallow	1	4	4		4	4	2	4	4	4
Troglodytidae	*Troglodytes musculus*	Chercán	Southern house wren	1	1	1	1	1	1	1	1	1	1
Mimidae	*Mimus tenca*	Tenca	Chilean mockingbird	1	1	1	1	1	1	1	1	1	1
Turdidae	*Turdus falklandii*	Zorzal	Austral thrush		2		4		3			4	2
Emberizidae	*Diuca diuca*	Diuca	Common diuca-finch	1	1	1	1	1	1	1	1	1	1
Emberizidae	*Phrygilus alaudinus*	Platero	Band-tailed sierra-finch	3	1	2	1	2	4	2	1	1	1
Emberizidae	*Phrygilus fruticeti*	Yal	Mourning sierra-finch		1	1	1		1	2	1	2	1
Emberizidae	*Phrygilus gayi*	Cometocino de Gay	Grey-hooded sierra-finch				1		1	1	1	2	4
Emberizidae	*Sicalis luteola*	Chirihue	Grassland yellow-finch							4		4	
Emberizidae	*Zonotrichia capensis*	Chincol	Rufous-collared sparrow	1	1	1	1	1	1	1	1	1	1
Fringillidae	*Carduelis barbata*	Jilguero	Black-chinned siskin			4	4		4				
Icteridae	*Curaeus curaeus*	Tordo	Austral blackbird	1	2	2	2	2	2	3	4	2	2
Icteridae	*Molothrus bonariensis*	Mirlo	Shiny cowbird							2			
Icteridae	*Sturnella loyca*	Loica	Long-tailed meadowlark	1	2	1	1	1	1	1	1	2	1
Fringillidae	*Carduelis barbata*	Jilguero	Black-chinned siskin			4	4		4				

[Kittlitz, 1830]; 8 %), and diuca (*Diuca diuca* [Molina, 1782]; 7 %). Summer and winter data reflect marked changes in faunal composision. In summer over 50 % of detections were of chincol (21 %), canastero (14 %), chercán (*Troglodytes aedon* Vieillot, 1809; 9 %), and tapaculo (9 %); in winter these included yal (21 %), chincol (19 %), diuca (8 %), and tapaculo (7 %). Species abundance relationships are typical for such assemblages, with few species comprising the majority of observations, and a large tail of rare species observed one to a few times (Fig. 5).

Six species were observed only once within a 50 m radius. Of these, three (aguilucho [*Buteo polyosoma* (Quoy & Gaimard, 1824)], torcaza [*Patagioenas araucana* (Lesson, 1827)], picaflor gigante [*Patagona gigas* (Vieillot, 1824)]) are commonly seen at Fray Jorge; the former two were documented frequently at greater distances, and the latter was observed frequently but not documented on point counts. Three other singleton species are commonly observed in northern Chile. Two of these, the minero (*Geositta cunicularia* [Vieillot, 1816]) and the dormilona tontita (*Muscisaxicola macloviana* [Garnot, 1829]), are uncommon in the park because these species do not frequent scrublands, but prefer open and barren ground outside the park. The third, the mirlo (*Molothrus bonariensis* [Gmelin, 1789]), frequents agricultural areas and is rarely observed in the park.

Our data confirm that temporal patterns are species-specific, and that overall, the avian assemblage undergoes dramatic seasonal fluctuations (Table 1). Some species are highly seasonal in their abundance (e.g., yal, present only in winter), whereas others are not clearly seasonal (e.g., diuca, tenca [*Mimus thenca* (Molina, 1782)], cachudito [*Anairetes parulus* (Kittlitz, 1830)]), and some (e.g., chincol) appear highly seasonal in most years but notably aseasonal in others (Fig. 6). Detectability is a function of bird behavior and varies across species as well as seasons; most songbirds are much more detectable in the breeding season when they are vocalizing to defend breeding territories or attract mates. This does not explain the dramatic seasonality of yal, however, which generally leave the park in summer, presumably for areas in the Andes or in southern Chile. Chincol at our site also are more abundant in winter (presumably due to the arrival of non-breeding individuals), so we believe the patterns represented in Fig. 6 are valid. On the other hand, to our knowledge tijeral (*Leptasthenura aegithaloides* [Kittlitz, 1830]), cachudito, and canastero are residents in the park, and the very different numbers in summer and winter requires further investigation. We speculate that in winter

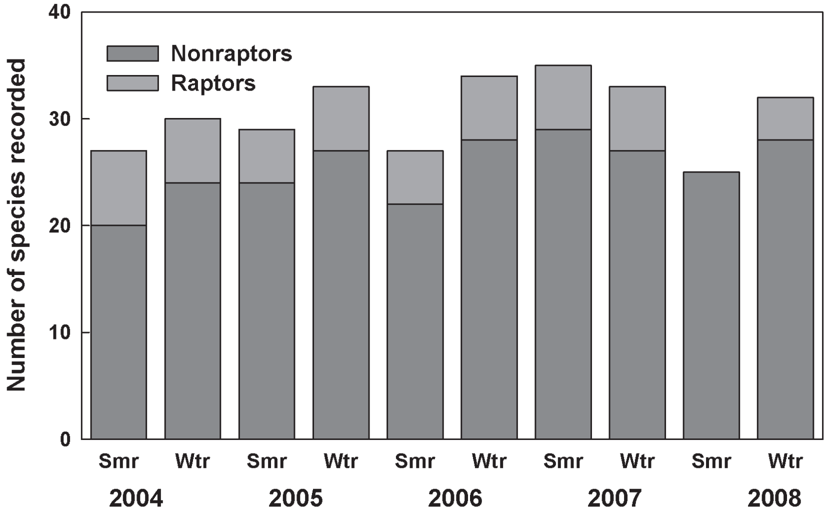

Fig. 4: Number of species separated by raptors vs. nonraptors. Figure includes all birds noted, including “flybys”, potentially at great distances.

Número de especies separadas por rapaces vs. no rapaces. La figura incluye todas las aves divisadas, incluyendo “bandadas”, potencialmente a gran distancia.

these insectivores may band to form mixed-species flocks, call less, and thus may be encountered less frequently. Tencas also are year-round residents in the park, and patterns for this species were similar in both seasons, with a gradual increase from 2004 throughout 2005/06 followed by some variability in numbers in subsequent seasons. These more regular patterns may be explained by the Tenca's mutualistic relationship with the endophytic mistletoe, *Tristerix aphyllus* (Martínez del Río et al. 1996). Their patterns of distribution in the park are predictable due to their association with cactus that play host to the mistletoe. Tenca have been observed maintaining territories through the winter and to vocalize year-round (A. Engilis, unpublished data). We currently are quantifying densities for other species and we look forward to comparing ecologically related (e.g., trophic) groups of species.

Species diversity (Shannon-Wiener index, H'; Fig. 7) tended to be higher in summer than winter (mean H' = 1.56 vs. 1.45; t = 1.88, P = 0.0621). Whereas this parameter varied significantly across all surveys (F = 291, P < 0.0001), a second order regression with time explained little of the variance (r^2 = 0.18; Fig. 7).

As indicated above, we are now quantifying external indicators of reproductive activity and using these to characterize reproductive patterns and determine age of individual birds more precisely. In 2008, we used mist-netting, marking, and photography to document plumages on 20 species in the park. These data will be supplemented with examination of museum specimens to develop a manual for

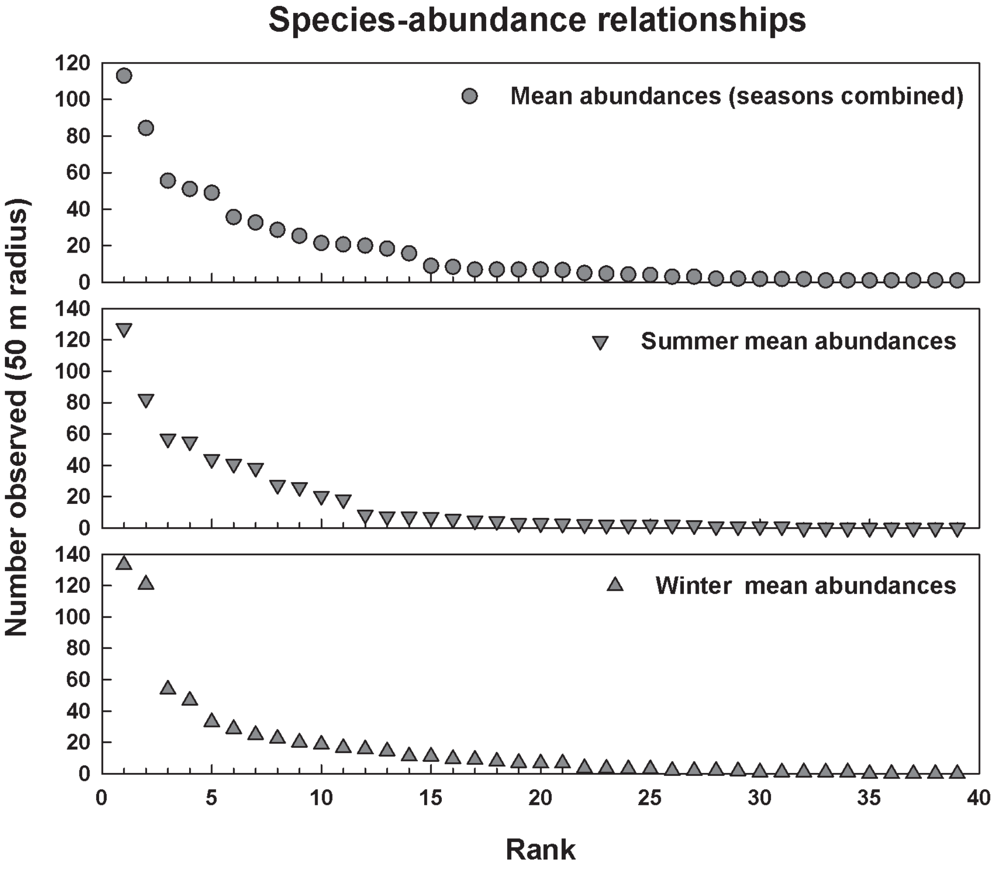

Fig. 5: Rank species abundance curves for all bird data, and summer and winter separately in Bosque Fray Jorge National Park.

Ranking de curvas de abundancia de especies para todos los datos de aves, separadamente para verano e invierno en el Parque Nacional Bosque Fray Jorge.

ageing and sexing key avian species of Chilean matorral. Such data are entirely absent for species in our assemblage, but will allow us to quantify recruitment (and hence productivity) at a population level, which is more readily accomplished than individual-based recruitment (e.g., fledgling success at focal nests) and avoids problems associated with disturbing nests and possibly providing cues to nest predators. Tracking avian densities and productivity will allow us to quantify responses to resource availability (e.g., precipitation and seed availability in control plots), allowing comparison with our long-term data on mammals. Natural history and descriptive ecology provide the foundation on which more conceptual research can be pursued; to this end, we quantified foraging behavior of the Cachudito in coastal steppe matorral in Fray Jorge (Engilis & Kelt 2009). Population densities are higher at Fray Jorge than reported elsewhere in Chile and Argentina, and both abundance and ease of observation allowed us to document 94 foraging bouts (77 in summer, 17 in winter) and 709 prey captures. Cachuditos foraged frequently in pairs, leapfrog style, maintaining contact with soft "perrreet" calls. Eighteen agonistic encounters (15 in summer, three in winter) consisted of rapid calling and displacement behaviors, apparently related to territoriality; once an intruder moved away, the defending pair resumed foraging. Cachuditos generally foraged in shrubs proportional to their availability, although our data suggest some preference for *Adesmia*, *Baccharis*, or *Porlieria* (76 % of observations but only 58 % of cover based on line transects). They located prey (insects) visually, and made an average of 3.1 attacks per minute, capturing prey by perch gleaning (47 % of captures), hover gleaning (31.5 %), and flycatching (21.5 %).

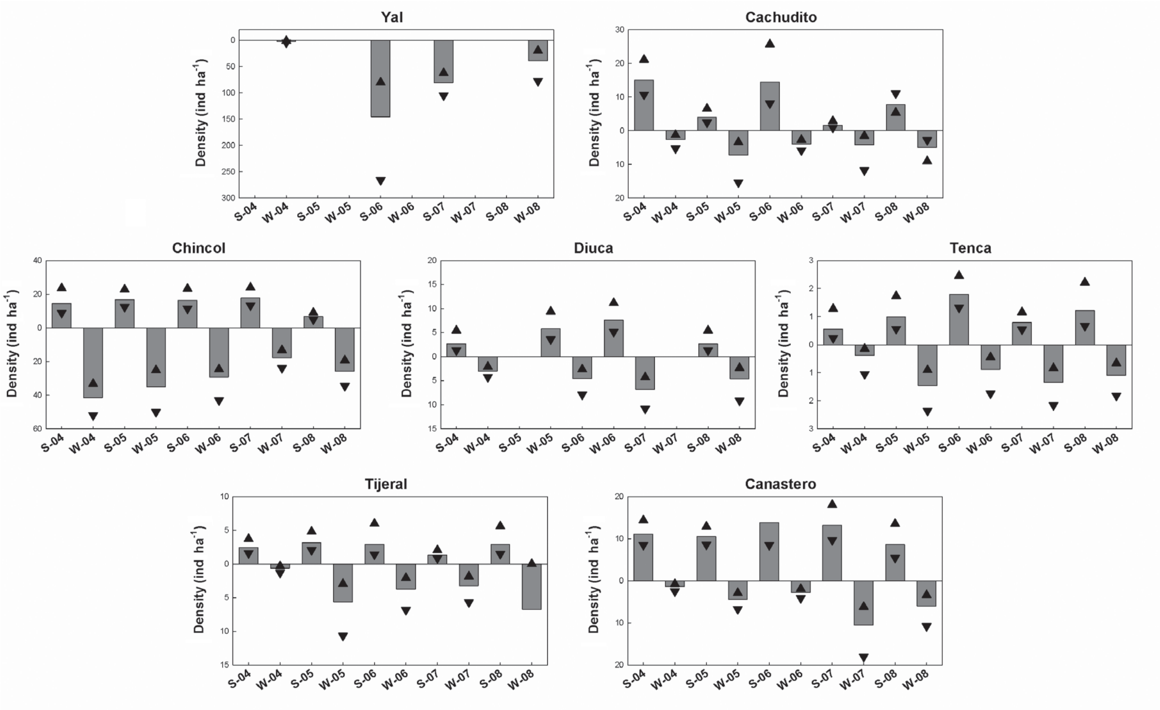

Fig. 6: Temporal patterns in seven bird species at Fray Jorge over four years. Values for summer are above the horizontal line, whereas those for winter are presented below the horizontal line. Densities (bars) and confidence limits (▲ and ▼) were calculated using Program Distance (Laake et al. 1993).

Patrones temporales de siete especies de aves en Fray Jorge en cuatro años. Valores por verano están presentados arriba de la línea horizontal, mientras que estos por invierno están presentados debajo de la línea. Densidades (barras) y límites de confianza (▲ y ▼) se calcularon usando el programa Distance (Laake et al. 1993).

3) Impacts of introduced vs. native species in the context of changing environmental conditions

Introduced plants comprise 18 % of the Chilean flora, including 27 % of herbaceous plants. Some naturalized species (e.g., *Erodium*, *Medicago polymorpha*, *Malva nicaensis*) constitute up to 45 % of the vegetation in Chilean matorral (Arroyo et al. 2000, Figueroa et al. 2004). Changes in the proportions of exotic species have been attributed to the effects of exotic grazers (Holmgren 2002) and fire (Sax 2002, Kunst et al. 2003; but see Holmgren et al. 2000a, 2000b). In Fray Jorge, where fire and most livestock have been absent at least since 1944, exotic plants comprise up to 21 % of the herbaceous species, and 19 % of the seed bank species (Gutiérrez & Meserve 2003). In contrast to plants, only 24 of 610 vertebrate species in continental Chile (4 %) are introduced (Jaksic 1998a, Iriarte et al. 2005). However, the negative impacts of introduced murid rodents (*Rattus rattus* [Linnaeus, 1758], *R. norvegicus* [Berkenhout, 1769], *Mus musculus* Linnaeus) and lagomorphs (*Oryctolagus cuniculus* [Linnaeus, 1758], *Lepus europaeus* Pallas, 1778) have been well-documented (murids, Lobos et al. 2005, Milstead et al. 2007; lagomorphs, Jaksic 1998b). Jaksic (1998b) described positive effects of rabbits and hares on indigenous vertebrate predators including pumas, diurnal hawks, and owls, but also noted that predators apparently neglected to utilize these until the late 1980's. In Fray Jorge, rabbit and hare populations were relatively low until recently (Meserve et al. pers. observ.) simultaneous with the prolonged El Niño/ high rainfall event in 2000-2002 and a sharp decrease in the numbers of foxes caused by an outbreak of parvovirus, rabbit and hare numbers increased dramatically in the park. Experimental work immediately S of Fray Jorge demonstrated significant effects of rabbit and hare exclusion, including a 90 % increase in survival of *Prosopsis chilensis* (an arborescent shrub largely extirpated from arid northern Chile), increases in tall native grasses (e.g., *Bromus berteroanus*), and decreases in native and exotic prostrate ephemerals (Gutiérrez et al.

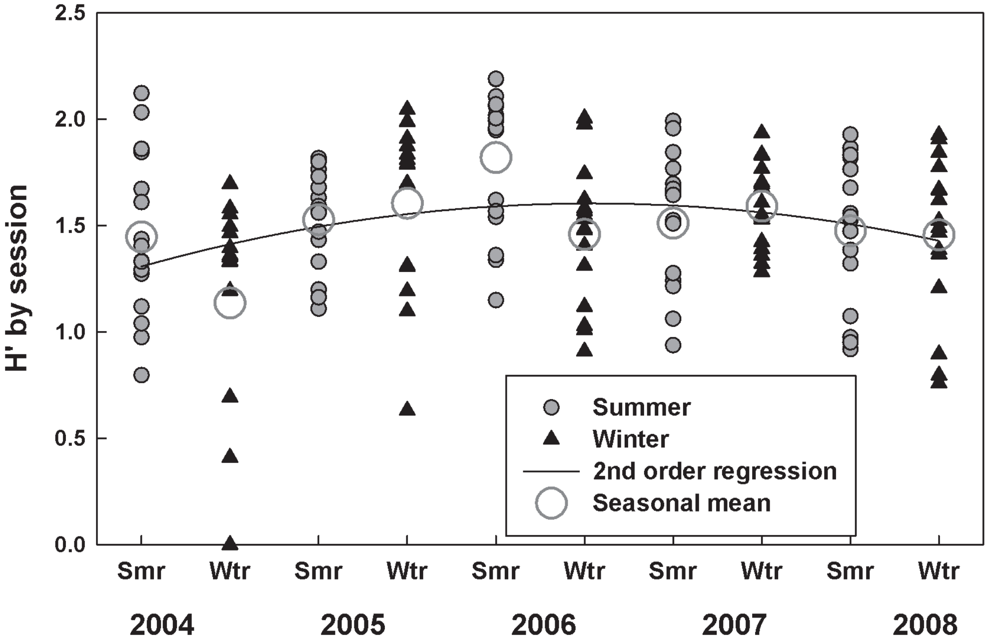

Fig. 7: Bird species diversity (H') for summer and winter periods over five years at Bosque Fray Jorge National Park. The quadratic regression ($H' = 1.18 + 1.39x - 0.01x^2$) is highly significant ($F_{10,150} = 291$, $P < 0.0001$) but explains little of the variation ($r^2 = 0.058$).

Diversidad de especies de aves (H') para los períodos de verano e invierno en cinco años en el Parque Nacional Bosque Fray Jorge. La regresión cuadrática ($H' = 1.18 + 1.39x - 0.01x^2$) es altamente significativa ($F_{10,150} = 291$, $P < 0.0001$) pero explica poco de la variación ($r^2 = 0.058$).

2007). Additional exclusion of herbivores under conditions of simulated high rainfall increased overall plant productivity, and favored native species (Manrique et al. 2007). Access by lagomorphs reduced native grass biomass and facilitated invasive grasses; thus, lagomorph herbivory may affect plant community structure and composition by influencing competitive dynamics between native and exotic plant species.

As noted earlier, we converted D-P grids to –SM treatments in 2001. To investigate the potential effects of introduced herbivore/folivores in the thorn scrub community in Fray Jorge, we initiated an additional series of exclusions using former degu exclusions (–D+P) plus four new experimental grids in 2007 (see Fig. 1); as noted above, there have been few discernible changes in the vegetation or seed bank attributable to the exclusion of degus here. We converted two former –D+P grids (randomly selected) plus two new experimental grids to lagomorph exclusion grids (–L) by removing existing fencing and installing ca. 1.5 m h chain link fencing buried ca. 20 cm. The remaining two –D+P plus two food addition grids were converted to all-small mammal & lagomorph (–SM –L) exclusions by use of the –SM fencing design supplemented with a 1.5 m h chain link fencing inside it. Grid conversion was completed, and small mammal trapping and both vegetation and seed bank sampling initiated, in late 2007.

Attempts to monitor lagomorphs with spotlight surveys and live-trapping have proved unsuccessful in this densely-covered shrubland; to quantify patterns in lagomorph numbers at our site, we initiated indirect inventory techniques in August 2007. We established 54 pellet count stations (Lazo 1992, Diaz 1998, Palomares 2001, Murray et al. 2002, 2005, Mills et al. 2005) in six lines of nine stations each. Stations are ca. 100 m apart and established to sample the central grid complex. All pellets within a 1 m radius of a central stake were removed, and all new pellets are counted and removed at six-month intervals.

We predict strong vegetative responses to the combined exclusion of small mammals and lagomorphs, particularly in high rainfall years when plants show the strongest numerical increases. This may alter community composition as well as interspecific interactions among various plant groups. A mild La Niña event in 2007 made the timing of the initiation of our studies of lagomorph and small mammal + lagomorph exclusions auspicious. Based on earlier results (Gutiérrez et al 2007, Manrique et al. 2007), exclusion of larger mammalian herbivores such as lagomorphs should influence vegetation dynamics especially among the herbaceous plant guild in the thorn scrub. Further, effects of lagomorphs and smaller mammals may be cumulative in total exclusion treatments.

CONCLUSIONS

With 20 years of constant data collection, many of our initial perceptions on how components of the Chilean semiarid community function and interact have required continued revision. Whereas we initiated our work on the presumption of a strong overwhelming role of biotic interactions, abiotic factors have been shown to have a strong and often determining role. Further, models of small mammal dynamics here call for incorporation of spatial and temporal heterogeneity to understand overall assemblage dynamics. Other components of the system such as birds may also be important, but to date remain understudied. Finally, we must interpret the changes that are occurring in the system against a background of a large and influential component of invasive species as well as ongoing climatic change. The latter aspect may be the most important factor that needs to be addressed.

In recent decades, rainfall had been declining in the northern Chilean semiarid zone, continuing a gradual aridity trend over the past 1,000 years (Bahre 1979, Villalba 1994). Since 2000, however, five of the past nine years have seen above average precipitation; moreover, the three largest El Niño events of the past 100 years have occurred since 1982 (Gergis & Fowler 2009). Although there has been little change in small mammal assemblage and shrub cover here over 50 years, El Niño has been shown to facilitate outbreaks of small mammals and to influence agriculture elsewhere (e.g., Pearson 1975, Péfaur et al. 1979, Fuentes & Campusano 1985, Jiménez et al. 1992, Jaksic 2001, Jaksic &

Lima 2003, Holmgren et al. 2006a, 2006b, Sage et al. 2007). Holmgren & Scheffer (2001) and Holmgren et al. (2001, 2006a, 2006b) emphasized that more frequent El Niño/ rainfall events may reverse or ameliorate the general desertification of much of north-central semiarid Chile (Bahre 1979, Schofield & Bucher 1986, Ovalle et al. 1993). Superimposed on this, increased frequency and intensity of El Niño events as a consequence of GCC may greatly alter the relative importance of biotic and abiotic interactions in semiarid systems. Increasing rainfall may have strong impacts such as altering patterns of nutrient cycling and primary productivity (e.g., Gutiérrez 1993, 2001, Jaksic 2001, Reich et al. 2006, de la Maza et al. 2009), species interactions and community diversity (e.g., Chesson et al. 2004, Holmgren et al. 2001, 2006a, 2006b), disease vectors, reservoirs, and zoonoses (Epstein 1999, 2000, Epstein & Mills 2005), and the impact of introduced species (e.g., Jaksic 1998, 2001, Logan et al. 2003).

We recognize that an alternative climate change scenario could occur in this region; our understanding of interactions between global warming and ENSO and, in turn, between ENSO and local environments, continues to improve. For example, increased rainfall during El Niño events increases productivity at lower elevations in this region, but not at higher elevations due to colder temperatures (Squeo et al. 2006). Further, the influence of fog from the Pacific Ocean, an important contributor to local moisture in this semi-arid region (Kummerow 1962, del-Val et al. 2006), is reduced during El Niño years (Garreaud et al. 2008).

Finally, we acknowledge uncertainty regarding the strength and even the reality of a causal link between the observed demographic patterns and climate change (McCarty 2001), especially due to a number of constraints that exist when attempting to anticipate the effects of climate change based on knowledge of current conditions (Berteaux et al. 2006). Nevertheless, our study contributes to the growing body of studies in this field that is helping to develop a more comprehensive understanding of the potential effects of climate change (McCarty 2001). Our study is unique in that it implicates increased rains as the climate change driver, documents clear responses in community parameters, and provides insight to climatic influences on small mammal species, all of which are seldom reported in the literature on climate change impacts.

Long-term research on small mammal assemblages in arid systems has been productive in our understanding of ecosystem processes. Recent studies have emphasized the role of local ecological compensation and “zero-sum dynamics” within the context of a regional species pool (e.g., Ernest et al. 2008). Such dynamics assume a diverse pool of species as potential colonists. Chile has relatively low beta diversity of both birds and small mammals (Cody 1975, Glanz & Meserve 1982) and as such it is unlikely that spatio-temporal signals in terrestrial ecology at our site will be similar to those documented elsewhere. To test this conjecture we are preparing to quantify ecosystem properties including energy utilization across grids and over time. In particular, we are eager to compare small mammal assemblages on predator and lagomorph removal plots with those on controls.

Many authors have stressed the importance of both spatial and temporal scale in ecology, and of the dearth of studies extending across large spatial scales or many years (e.g., Wiens et al. 1986, Giller & Gee 1987, Powell 1989, Wiens 1989, Levin 1992, Polis et al. 1996, Schneider 2001). Recently, Agrawal et al. (2007) recognized that the strength and outcomes of species interactions depends on the biotic and abiotic context in which they occur, a fact borne out clearly by results of our studies. Now the longest field manipulation in the temperate neotropics, and spanning five El Niño/high rainfall events in 20 years of study, our work has documented variable effects of biotic interactions depending on the abiotic context.

In this context, the role of long-term ecological studies such as this one assumes great importance. For example, since about 2000, we have noted a tendency for small mammal biomass in Fray Jorge to be dominated by the larger, more mesic-adapted caviomorph rodent, *O. degus* (Meserve et al. 2009); further, degus are showing greater survival and recruitment in the last 10 years (Previtali et al. 2010). Small mammal species diversity has also become more stable and less oscillatory at the site (Meserve et al. 2009). This has occurred concomitant with the increase in mean annual precipitation since 2000, and less-pronounced interannual variation (Fig. 3). Without long-term studies such as this one, we would not have been able to detect such changes, nor compare them against a background of prevailing population fluctuations in response to periodic El Niño events. Determining whether such trends signal a major shift in small mammal (and other biotic) components will only be feasible with continued maintenance of long-term monitoring efforts in this unique part of Chile.

SUPPLEMENTARY MATERIAL

The Spanish version of this article is available as online Supplementary Material at http://rchn.biologiachile.cl/suppmat/2010/1/SM_Gutierrez_et_al_2010.pdf

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