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Comparative Ecology of the Caviomorph Rodent *Octodon degus* in Two Chilean Mediterranean-type Communities

Ecología comparativa del roedor caviomorfo *Octodon degus* en dos comunidades mediterráneas de Chile

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RESUMEN

El degu (*Octodon degus*) es el roedor caviomorfo más común que se encuentra en las comunidades de tipo mediterráneo de Chile. Entre 1973 y 1976 se desarrollaron dos estudios sobre el degu; uno de ellos se centró en la zona norte de Chile (Fray Jorge) y el otro en una sabana mediterránea de Chile central (La Dehesa). Aun cuando no fueron simultáneos, en ambos estudios se utilizaron similares metodologías y análisis, permitiendo de este modo la comparación de resultados sobre tendencias poblacionales, reproducción, hábitos alimenticios y características de asociación al hábitat. Se observaron densidades máximas de 59-65 individuos/há en octubre-noviembre como resultado del reclutamiento de juveniles a la población en ambos sitios. Los decrecimientos poblacionales durante los meses de verano se debieron fundamentalmente a la desaparición de los juveniles. El apareamiento se desarrolló principalmente en agosto-octubre, con la concepción en mayo-junio; un segundo episodio reproductivo, que refleja la presencia de estro postparto, ocurrió en la población de La Dehesa en diciembre-enero. El tamaño de la camada fue idéntico en ambas poblaciones. Los períodos reproductivos de los machos en La Dehesa, basados en el tamaño testicular, fueron en mayo-septiembre. Las dietas de ambas poblaciones difirieron con los degus de Fray Jorge alimentándose principalmente de follaje, semillas y tejidos conectivos de arbustos, mientras que los de La Dehesa se alimentaron de follaje y semillas de hierbas dicotiledóneas y monocotiledóneas. Las características de asociación al hábitat también fueron diferentes; los degus de Fray Jorge no aparecieron asociados significativamente con las estaciones de elevada cobertura arbustiva, cosa que sí ocurrió con los degus de La Dehesa. Puesto que los degus aparentemente carecen de especializaciones fisiológicas o morfológicas marcadas para ambientes estacionalmente o permanentemente áridos, su similitud demográfica en ambos sitios –a pesar de la diferencia en los períodos reproductivos, hábitos alimenticios y asociación al hábitat– enfatiza la adaptabilidad de este roedor caviomorfo a regímenes climáticos divergentes.

Palabras claves: *Octodon, degus,* caviomorfo, roedor, ecología, demografía, reproducción, dieta, hábitat, Chile, ecosistemas mediterráneos.

ABSTRACT

The degu (*Octodon degus*) is the most common caviomorph rodent found in Chilean mediterranean-type communities. Between 1973 and 1976, two studies of the degu were conducted, one in a semiarid scrub community in northern Chile (Fray Jorge), and the other in a mediterranean savanna in central Chile (La Dehesa). Although nonconcurrent, the studies used similar methodologies and analyses, thus allowing comparison of results on population trends, reproduction, dietary habits, and habitat association patterns. Maximum densities of 59-65 individuals/ha were observed in October-November as a result of juvenile recruitment into the trappable population at both sites. Population decreases during the summer months were due mainly to the disappearance of these individuals. Reproduction was principally in August-October with conception in May-June; a second episode reflecting the presence of a post-partum estrus occurred in the La Dehesa population in December-January. Litter size was identical in the two populations. Male reproductive periods in La Dehesa based on testis size were in May-September. Diets

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of the two populations were distinct with Fray Jorge degus feeding mainly on shrub foliage, seeds, and conductive tissue, whéreas La Dehesa degus fed on forb and grass foliage and seeds. Habitat association patterns were also different with Fray Jorge degus showing no significant associations with trap stations having high shrub cover in contrast to La Dehesa degus. Because degus apparently lack strong physiological or morphological specializations for seasonally or continually arid environments, the significant similarity in demography at the two sites despite differences in reproductive periods, dietary habits, and habitat association patterns emphasizes the adaptability of this caviomorph rodent to divergent climatic regimes.

Key words: *Octodon degus:* Caviomorph, rodent, ecology, demography, reproduction, diet, habitat, Chile, mediterranean ecosystems.

INTRODUCTION

Relatively few long-term studies are available for South American caviomorph rodents with some notable exceptions (e.g. *Lagidium,* Pearson (1948); *Lagostomus,* Llanos & Crespo (1952); *Ctenomys,* Pearson (1959) and Pearson et al. (1968); *Microcavia,* Rood (1970); *Hydrochaeris,* Ojasti (1973)[1]; *Proechimys,* Fleming (1971). Our knowledge of most caviomorphs is thus largely limited to that from faunal surveys, isolated observations, and laboratory studies. In view of the fact that caviomorphs make up 45.5% of the rodent genera and 32.5% of the rodent species in the Neotropics (including Middle America and the West Indies; Hershkovitz 1972), it is important to increase our knowledge of this poorly-studied group.

The degu, *Octodon degus* (Molina 1782), is one of Chile's most common rodents and inhabits a wide range of plant formations from introduced pine plantations and mediterranean scrub zones in central Chile to semiarid regions in the north (approximately a 7° latitudinal range; Woods & Boraker 1975). In agricultural regions the degu is considered a serious pest although its habit of occupying degraded pasturelands and marginally cultivated areas seems more a consequence of invasion by native shrubby species such as *Acacia caven, Puya* spp., *Lithraea caustica,* and *Baccharis* spp. due to overgrazing, burning, and fuel removal than a causative factor. The degu has received considerable attention particularly in aspects of reproduction (Weir 1970, 1974, Contreras & Rosemann 1982, Rojas et al. 1977, Contreras & Bustos-Obregón 1977, Morales & Leyton 1977, Morales et al. 1982[2]), physiological ecology and activity (Rosenmann 1977, Rosenmann et al. 1981), and natural history and behavior (Fulk 1976, Yáñez & Jaksić 1978, Reynolds & Wright 1979). A few long-term studies and experiments have been conducted on field populations (e.g. Fulk 1975, Glanz 1977a, Fuentes & Le-Boulengé 1977, LeBoulengé & Fuentes 1978, Jaksić et al. 1981a, Meserve 1981a, 1981b, Meserve et al. 1983) with emphasis however on community interactions. Finally, this species has been the object of some medical attention because of the presence of cataracts and symptoms similar to diabetes mellitus in laboratory colonies (Weir 1970, Woods & Boraker 1975).

Between 1973 and 1976, we conducted independent field studies of degu at two widely separated localities representing climatic extremes within the species' geographic range. Although performed nonconcurrently and with slightly different methodologies, the results from these studies provide considerable information on the population biology, reproductive trends, and other ecological aspects of the degu. This paper reports the results of these studies with emphasis on the comparative ecology of this species.

Study Sites and Methodology

The first study was conducted between November 1973 and January 1975 in Parque Nacional Fray Jorge (71°40'W, 30°38'S), IV Región de Coquimbo, Chile, about 250 km N Santiago. The geographical region is on the northern fringe of the Chilean mediterranean zone ("Norte Chico") and the study site was located in a valley ("Quebrada de las Vacas", 200 m

1) OJASTI J (1973) Estudio biológico del chigüire o capibara. Fondo Nacional de Investigaciones Agropecuarias (Caracas, Venezuela) pp. 1-275.

2) MORALES B, C UNDA & MA ROJAS (1983) Evolución de la fotosensibilidad de la hembra de *O. degus.* Archivos de Biología y Medicina Experimentales 16 (2): 223.

elev.) on the east side of the coast range (500 m elev.). The plant formation is termed the *Porlieria chilensis-Proustia pungens-Adesmia bedwelli* association for its most characteristic shrubs (Muñoz & Pisano 1947) and is dominated by drought-deciduous and evergreen shrubs, a sparse herbaceous understory, and open sandy substrate. A line transect analysis of the vegetation (10 m transects at each of 48 live-trap stations 20 m apart) in November 1973 and September 1974 revealed the above-ground projected shrub cover to be 59.6%, the ground-level grass and forb cover to be 21.7%, and the remaining ground-level cover to be litter, roots and shrub trunks (32,3%), and bare ground (46.0%, Meserve 1981a). The climate here is semiarid mediterranean with warm dry summers and short wet winters (di Castri 1973). Mean annual precipitation is 127 mm, but in the years of this study (1973-1974), total rainfall was 80.4 mm and 40.3 mm, respectively. Ninety percent of the rain falls between June and September, but considerable additional moisture may be provided by frequent fogs and resultant dew formation (Kummerow 1966).

Live-trapping was initiated at Fray Jorge in November 1973 on a 1.4 ha grid with 48 stations 20 m apart (6 x 8 configuration) for four nights bimonthly with two Sherman traps per station until January 1975. Animals were marked by ear-tagging and standard data on weight, sex, reproductive condition, and age collected during handling. Snap-trapping on lines in similar adjacent habitat was used to obtain stomachs for dietary analysis and autopsy information.

The second study was conducted between March 1975 and November 1976 in a partially grazed *Acacia caven* savanna, La Dehesa (El Monasterio) located 20 km NE Santiago (70°33'30"W, 33°20'S, 900 m elev.). The site was located on the north side of Cerro Manquehue in the "Depresión Intermedia" approximately 40 km E of the coast range. The plant assemblage is dominated by drought-deciduous and evergreen shrubs including *Acacia caven, Quillaja saponaria* and *Lithraea caustica* with a dense understory of grasses and forbs particularly in spring-summer months. Total above-ground projected shrub cover as determined by line transect analysis in September-November 1975 (10 m transects at each of 49 live-trap stations 15 m apart) was 20.5%; ground-level cover consisted of grasses and forbs (primarily *Bromus* spp. and *Erodium cicutarium,* 78.5%), roots and shrub trunks (10.4%), and bare ground (11.1%). The climate is typically mediterranean with a mean annual precipitation of 345 mm falling over a somewhat longer period than that at Fray Jorge (90% between May and October). During the years of this study (1975-1976) precipitation was considerably below average (149 mm and 189 mm, respectively).

A 0.8 ha live-trapping grid with 49 stations 15 m apart (7 x 7 configuration) was established in March 1975 and trapped for four nights monthly to bimonthly with two National live traps per station until November 1976. Similar mark-and-recapture techniques as employed at Fray Jorge were used and snap-trapping was conducted on removal lines in similar nearby habitat to obtain stomachs and autopsy material.

The results here are concentrated on four aspects that were investigated at both Fray Jorge and La Dehesa; 1) population trends; 2) reproduction; 3) dietary habits; and 4) habitat associations. Population densities were determined from minimum number known alive estimates with adjustment for grid size and differences in trap spacing. A border strip equal to one half the average movement between captures calculated seasonally was added to the grid perimeter for density determinations (Brant 1962). Degus have been generally reported to be bimodally diurnal or crepuscular in activity (Fulk 1976, Rosenmann et al. 1981). Since Fulk (1975) had not found degus to be common at Fray Jorge and maximum diurnal temperatures occasionally reached 35°C in summer months, diurnal trapping was not conducted until March 1974. Thereafter, at least one day of diurnal trapping was conducted during each census with twice-daily checks of traps. Trapping at La Dehesa was conducted consistently during both diurnal and nocturnal periods. Reproductive trends were studied using both live-trapping and snap-trapping results. Because male degu like all caviomorphs lack a true scrotum, assessment of their breeding activity cannot be obtained from external examination of live-trapped individuals (Weir 1970, 1974, Contreras & Bustos-Obregón 1977, Contreras & Rosenmann

1982). Measurements of testis size (width x length) was taken only at La Dehesa from autopsied males. Since female degu seem to lack a clear estrous cycle and the vagina closes soon after mating (Weir 1970, 1974), assessment of reproductive condition of live-trapped individuals was limited to notation of pregnant or lactating individuals using palpation and visual examination. Embryo and fresh uterine scar counts were made from autopsied females. Given the long gestation time of degus (90 days) and the bimonthly census intervals at Fray Jorge, it is likely that some pregnant females were missed in live-trapping. The results of dietary analyses have been reported previously (Meserve 1981a, Meserve et al. 1983), but it is useful here to compare the range of food types and proportions in the diets of degus from the two sites. Dietary analysis was conducted according to Hansson (1970) and Meserve (1981a) using percent cover of identified plant fragments on microscope slides as a measure of dietary composition by volume. Finally, we considered habitat associations using capture records of degus at each site and the results of line transect analyses characterizing the cover of each trap station. Stations were grouped into roughly equal categories of 0-20%, 21-40%, 41-60% and 61-100% shrub, grass and forb, and bare ground cover; in some cases, categories were combined to increase cell sizes. Then, a goodness of fit test (X^2) was conducted comparing proportions of stations in each cover category and proportions of trap records for degus at those stations (Meserve 1981b). A critical level of $P < 0.05$ was used to accept or reject the null hypothesis of no positive association between captures and station cover characteristics.

RESULTS

Population Trends

Figure 1 shows the trap-revealed population densities for *Octodon degus* at Fray Jorge and La Dehesa during 1973-1976 along with precipitation trends during the respective trapping periods. As indicated, precipitation was considerably lower than normal in all years. Further, precipitation

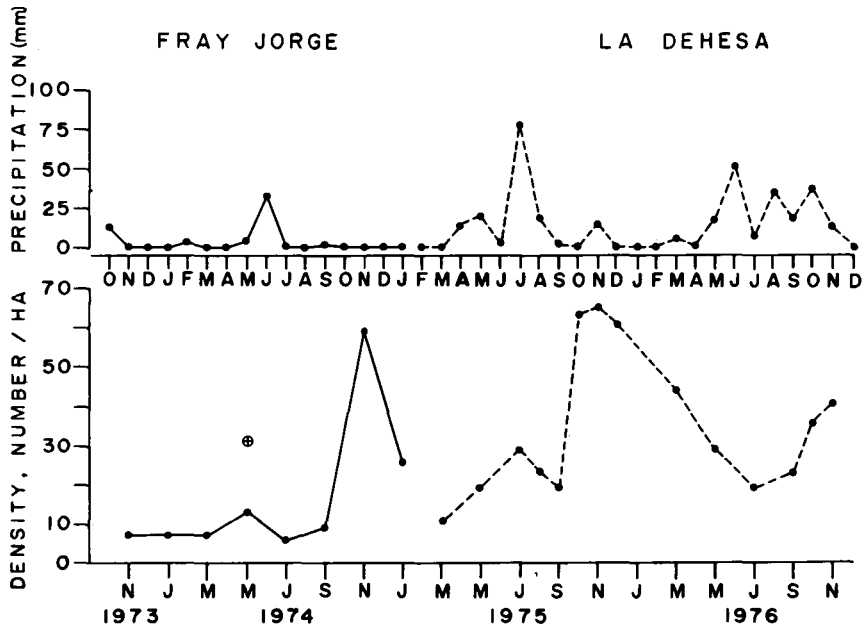

Fig. 1: Minimum number known alive densities in number/ha of *Octodon degus* (bottom), and precipitation trends (top) at two Chilean localities during 1973-1976. See text for explanation of single point during May 1974 at Fray Jorge.

Cantidad mínima estimada de *Octodon degus*, en número por hectárea (abajo) y tendencia de la precipitación (arriba) en dos localidades chilenas durante 1973-1976. Véase el texto para la explicación del punto aislado durante mayo de 1974 en Fray Jorge.

at Fray Jorge was 46 to 79% less than that at La Dehesa. Despite this, maximum population densities at both sites were similar (59-65 individuals/ha) and periods of increase were in the same months (October-November) due primarily to the recruitment of juvenile degu into the trappable populations. Based on laboratory data and field growth curves (Reynolds & Wright 1979, R.E. Martin, unpubl. data), a weight of 150 g was used to delineate juveniles of the year from adults; animals caught from previous censuses at initial weights greater than 150 g were excluded even if they subsequently decreased below this weight. In Fray Jorge, 93.3% and 81.3% of the individuals caught in November 1973 and November 1974, respectively, were juveniles. For La Dehesa, the corresponding figures in November 1975 and November 1976 were 57.0% and 49.2%, respectively. Decreases following maximum densities were due largely to the failure of juvenile degu to remain in the trappable population. At Fray Jorge, only 34.1% of the juveniles survived at least two months between November 1974 and January 1975; the corresponding figure for the interval between October and December 1975 at La Dehesa was 59.7%. The isolated point in Figure 1 for May 1974 in Fray Jorge includes the results of a single diurnal trap check in which 41 new adult individuals were recorded. Because only six of these individuals were subsequently recaptured in later censuses, it was concluded that this was a spurious density estimate due to the inclusion of peripheral nonresident animals that were attracted onto the grid by baited traps or were at higher risk of capture due to longer movements during a period of intensive sexual activity (see next section).

Reproduction

Figure 2 presents the percentages of pregnant and lactating females at Fray Jorge and La Dehesa based on live-trapping evidence and autopsy results. At Fray Jorge, a pregnant female was recorded in July 1974 and both pregnant and lactating females in September 1974. Otherwise, there was no evidence for reproduction by females in any other month. At La Dehesa, pregnant and lactating females were present

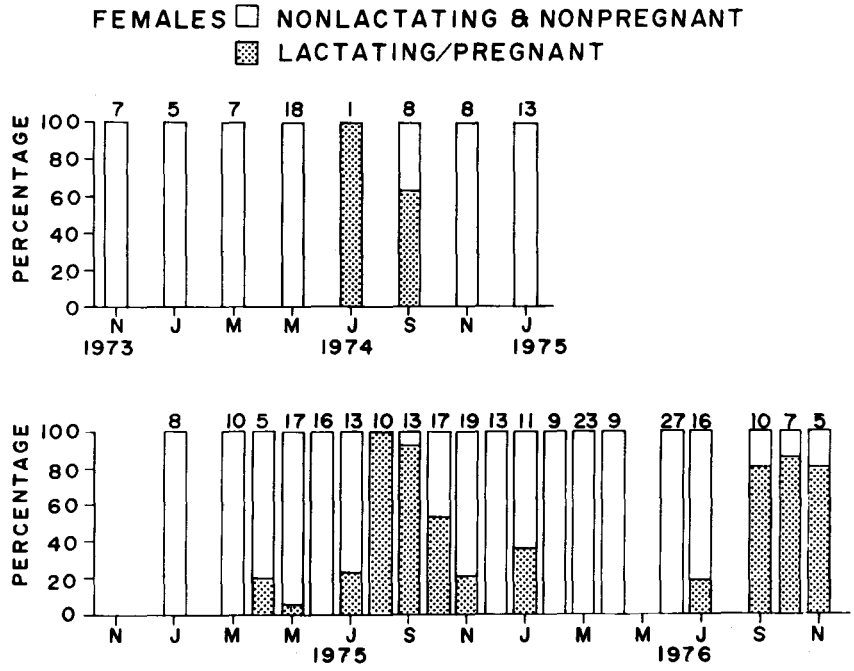

Fig. 2: Percentages of pregnant and lactating female *O. degus* at Fray Jorge (top) and La Dehesa (bottom) during 1973-1976. Numbers over bars indicate sample sizes.

Porcentajes de hembras preñadas y lactantes de *O. degus* en Fray Jorge (arriba) y La Dehesa (abajo) durante 1973-1975. Los números sobre las barras indican los tamaños muestrales.

as early as April and as late as January although the peak in numbers and proportions of reproductive females was in August-October 1975 and September-November 1976. All individuals captured in October-November 1975 and October 1976 were lactating. The additional lactating individuals in January 1976 and the fact that three out of four reproductive individuals in November 1976 were pregnant females indicates the presence of a second although smaller episode of reproduction in La Dehesa degus. Rojas et al. (1977) and Fulk (1976) also noted a second parturition in central and northern Chilean degus in December-January, and Weir (1970, 1974) indicated the presence of a post-partum estrus in which females do not regularly mate. Based on a gestation period of 90 days and a weaning period of 4-6 weeks (Weir 1970, 1974), juvenile degu first captured in October-November were probably conceived in May-June and born in August-September. A post-partum estrus with subsequent conception in August-September would yield a second litter born in December-January. Interestingly, the first-mentioned conception date coincides with the observed increase in numbers of adults captured on both sites (Fig. 1) and may represent a period of intense sexual activity. This also may explain the large number of new adults captured at Fray Jorge in May 1974 most of which were not subsequently recaptured. Litter size based on embryo or recent placental scar counts of autopsied females was identical for Fray Jorge individuals ($\bar{X}=5.33 \pm 1.21$, 1 SD, $n=6$) and La Dehesa individuals ($\bar{X}=5.33 \pm 1.00$, $n=9$). Figure 3 shows the trends for testis size of La Dehesa males. Testis size was greatest between the months of May and September with the increase in 1976 occurring a month earlier (in April) than in 1975. The initiation of maximal testis growth coincides with the projected first conception of La Dehesa females in May-June and 1975 males still had large testes at the projected second conception date following parturition in August-September. Although comparable information is lacking for Fray Jorge males, snap-trapped males were frequently found to have ejaculated semen in July 1974.

Dietary Habits

The diets of degus in both areas were determined from stomach analysis (La Dehesa) and a combination of stomach and fecal analysis (Fray Jorge). Samples were obtained in most months in which live-

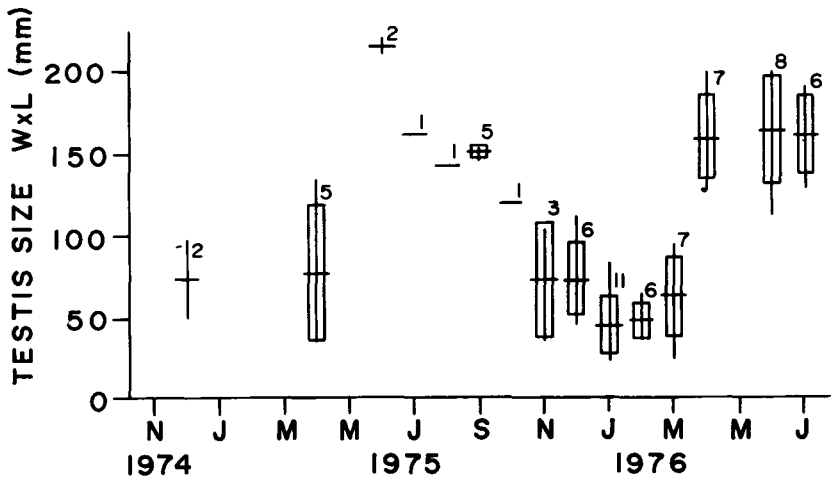

Fig. 3: Testis size (width X length, mm) for autopsied male *O. degus* at La Dehesa during 1974-1976. Horizontal lines indicate the mean, vertical lines the range, and open vertical bars the interval mean ± 1 SD. Numbers over the bars are sample sizes.

Tamaño testicular (ancho por largo, en mm) para machos autopsiados de La Dehesa durante 1974-1976. Las líneas horizontales indican la media, las líneas verticales el rango y las barras verticales abiertas, un error estándar de la media. Los números sobre las barras son los tamaños muestrales.

trapping was conducted. For purposes of comparison, the results of Meserve (1981a) and Meserve et al. (1983) were adjusted by eliminating bait and unidentified material and prorating the identified material to 100%. Identifiability was lower at Fray Jorge ($\bar{X}$=84.9 ± 1.5%, 1 SD) than at La Dehesa ($\bar{X}$=92.1 ± 2.6%) due probably to the use of fecal analysis and the higher diversity of morphological similar shrub and herbaceous species at the former site. Figure 4 presents the relative volumes for five major classes of dietary items identified in *Octodon degus* stomachs and feces during the two studies. It is immediately apparent that at Fray Jorge, shrub foliage, seeds, and conductive tissue were considerably more important in degu diets than at La Dehesa (collectively, $\bar{X}$=58.4 ± 29.2% 1 SD by volume vs. 25.6 ± 25.3%, respectively). Much of the shrub material at Fray Jorge consisted of foliage and seeds of *Chenopodium petiolare,* a suffructicose perennial with persistent foliage, which was consumed in large amounts in late fall to spring months (March-September). In only one period (November 1973) was total shrub volume less than 40%; in contrast at La Dehesa, six out of nine periods had degu diets consisting of less than 40% shrubs by volume, and five periods had less than 20% shrubs by volume. Conversely, La Dehesa degus consumed more forb and grass foliage and seeds than Fray Jorge populations ($\bar{X}$=73.8 ± 25.4%, 1 SD vs. 41.4 ± 29.3%; totals do not equal 100% due to small amounts of arthropods consumed by degus at both sites). Foliage and seeds of *Erodium cicutarium* and *Bromus* spp. were particularly important. Although herbaceous material made up a majority of the diets in at least some spring-summer months at both sites, the duration of their importance was longer at La Dehesa (April-December) probably due to the more dispersed pattern of rainfall than at Fray Jorge (Fig. 1). Shrub foliage and conductive tissue particularly of *Acacia caven* was important in late summer-fall months at La Dehesa. Total seed volumes (shrub, and grass and forb) were fairly similar at La Dehesa and Fray Jorge ($\bar{X}$= 35.6 ± 26.4%, 1 SD vs. 25.6 ± 18.3%, respectively), but most seeds at the former site were those of grasses and forbs whereas those at the latter site were primarily shrub seeds.

Habitat Associations

The results of the habitat association analysis conducted for degu captures at each site were as follows (categories of 0-10% and 11-20% bare ground cover were used in the association analysis at La Dehesa because no stations had more than 20% of this category): 1) degus at Fray Jorge showed no significant association with trap

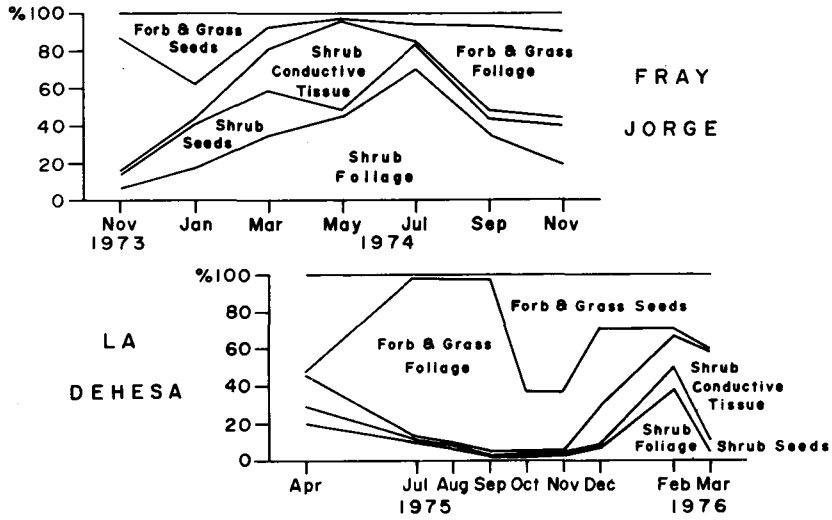

Fig. 4: Relative proportions by volume of five major classes of food items in the diets of *O. degus* at Fray Jorge (top) and La Dehesa (bottom) during 1973-1976.

Proporciones volumétricas de las cinco clases principales de ítemes alimenticios en las dietas de *O. degus* en Fray Jorge (arriba) y La Dehesa (abajo) durante 1973-1976.

stations having low or high shrub cover whereas those at La Dehesa were significantly associated with stations having > 20% shrub cover ($X^2 = 31.5$, df = 1, $P < 0.001$); 2) degus at Fray Jorge had significant association with capture stations having low forb and grass cover (< 20%, $X^2 = 57.3$, df = 3, $P < 0.001$ whereas those at La Dehesa had no significant association with low or high forb and grass cover; and 3) degus at Fray Jorge had significant association with capture stations having high bare ground cover (> 40%, $X^2 = 41.1$, df = 1, $P < 0.001$) and those at La Dehesa significant association with stations having low bare ground cover (< 11%, $X^2 = 8.2$, df = 1, $P < 0.01$).

DISCUSSION

Throughout much of the degu's geographical range, it is potentially water-stressed because the mediterranean-type climate has long dry seasons and frequent summer temperatures of 30-35°C. Although the degu can concentrate its urine approximately seven times its normal osmolarity for short periods (Woods & Boraker 1975); and Rosenmann (pers. commun.) has observed a thicker medullary zone of the kidney in Fray Jorge populations (as compared to those of central Chile), it nonetheless suffers the disadvantages of being a relatively large diurnal rodent which does not employ aestivation. Further, it has an evaporative water loss rate considerably greater than that of the white rat (approximately 2 mg H_2O/g/hr) and an upper critical temperature of only 32°C above which thermoregulatory costs and evaporative water loss rates increase rapidly (Rosenmann 1977). The optimum temperature for balancing thermoregulatory costs and evaporative water loss rates appears to be 24°C, a temperature only slightly greater than that encountered in degu burrows in central Chile during summer (Rosenmann 1977, Contreras & Rosenmann 1982). Degus in the northern arid zone may be able to resist desiccation by seasonal acclimatization similar to that described for two cricetid rodents in Fray Jorge, *Akodon olivaceus* and *Phyllotis darwini* (Meserve 1978). Some indication of seasonal adjustment in body weights is evident from adult male degus trapped in different months of 1974 (Table 1). Body weights declined an average 19.8% between January and May 1974 during the driest and warmest months at Fray Jorge; subsequently, in the period of vegetative growth during and following winter rains (September-November), body weights increased 33.1% to levels at or above January weights. Subadult males such as individuals No. 6 and 9 born the previous spring experienced a smaller weight decline than older males (Table 1). Degus trapped in November 1974 and January 1975 demonstrated the initiation of a similar weight decline suggesting an earlier onset of the acclimatization effect than observed in 1973-74 (November weights for four adults males: $\bar{X} = 156.3 \pm 14.0$ g, 1 SD; their January weights: $\bar{X} = 150.6 \pm 13.1$ g).

Rojas et al. (1977) suggested that degu reproduction may be triggered by the availability of green vegetation at the time of first ovulation and conception. In their central Chilean populations studied in the same years (1975-76) as the La Dehesa population at a site approximately 10 km away, conception occurred in mid-June to mid-July and parturition in mid-September

TABLE 1

Mean body weights (g) of five male degu trapped during January-November 1974

Pesos corporales promedio (g) de cinco *O. degus* atrapados durante enero-noviembre 1974.

Number	Month			
	January	March	May	September-November
6	127	121		168
9	117		100	
88	193	173.5	152.5	155
802	140	110	105	148
803	163	131	116.7	160.7
$\bar{X} \pm$ SD	148 ± 30.5	133.9 ± 27.9	118.6 ± 23.7	157.9 ± 8.5

to mid-October with a second litter born to some females in December-January probably as a result of a post-partum estrus. These data generally agree with the results at La Dehesa although we encountered some pregnant females as early as April-May 1975 (Fig. 2) prior to the initiation of their study. This coincided with an unusually early initiation of winter rains that year (Fig. 1) and suggest that at least some reproduction by degu is triggered by precipitation. However, the major episode of reproduction coincided with maximum vegetation growth following rains in 1975. Interestingly, testis size in male degu was still quite small in April 1975 at La Dehesa (Fig. 3) suggesting that sperm production and male fertility may have preceded measurable testis growth. In Fray Jorge, reproduction was limited to one major episode in 1974 with all pregnant and lactating females occurring between July and September; no evidence of a second litter was present. Reproduction here may have also been triggered by precipitation although the total amount of moisture in May 1974 was extremely small (6.2 mm) compared to that in June (33 mm) when mating and conception probably occurred. The availability of shrubs with persistant foliage such as *Porlieria chilensis* and *Chenopodium petiolare* at Fray Jorge and their high importance in degu diets in May-July 1974 (Fig. 4) may allow them to respond directly to precipitation rather than herbaceous growth. Fulk (1976) reported the presence of a pregnant female in November 1972 and juveniles less than a month old in mid-April during a year of above-average rainfall (260 mm) further supporting the role of moisture. The variability of reproduction among degus in different years and localities argues against photoperiod playing a solitary role in triggering reproduction onset as supported by Morales et al. (1983). Given the degu's long gestation period and unpredictability of its environment, sensitivity to climatic cues may be essential to successful reproduction. Interestingly, litter size was identical for La Dehesa and Fray Jorge populations and very similar to that reported by Fulk in central Chile at La Rinconada ($\bar{X} = 5.3$, Fulk 1975). Degus in the laboratory however have considerably larger litter sizes ($\bar{X} = 6.8$; Woods & Boraker 1975).

Degu populations at La Dehesa and Fray Jorge show distinct dietary patterns and habitat associations. Trophically, degu play an ecological role similar to that of diurnal ground squirrels and woodrats (Glanz 1977a, 1977b, Glanz & Meserve 1982). Differences in relative proportions of shrub and forb and grass foliage and seeds would have been expected at more arid vs. mesic mediterranean communities. Shrub conductive tissue has a high water content and thus would be an important moisture source in late fall months (Rojas et al. 1977); in La Dehesa this is provided by *Acacia caven* and in Fray Jorge by *Chenopodium petiolare* and *Porlieria chilensis.* In Meserve et al. (1983), significantly greater proportions of grass seeds were found in juvenile degu diets at La Dehesa in October 1975; a similar trend was not found at Fray Jorge, but overall consumption of seeds was considerably lower there and the advantages of preferential selection of high protein seeds could be outweighed by their lower water content and higher nitrogen in a more arid environment. Habitat association patterns were opposite at the two localities. Degu characteristically open up habitats and alter plant associations as a result of burrowing, runway-making activities, and selective foraging (Glanz 1977a, Fuentes & LeBoulengé 1977, LeBoulengé & Fuentes 1978). Thus, their association with low forb and grass cover, and high bare ground cover at Fray Jorge could be a consequence rather than a causative factor in their micro-distributions. The lack of association with high shrub cover stations in Fray Jorge in contrast to La Dehesa could also be due to the much greater shrub cover values at the former site (59.6% vs. 20.5%, respectively) and the greater uniformity of the vegetation. In central Chile, degu seem more numerous in relatively open disturbed sites such as at La Dehesa (LeBoulengé & Fuentes 1978, Jaksić et al. 1981a). Paradoxically, degu then are positively associated with stations having high shrub cover in habitats with lower overall shrub cover (Glanz 1977a, Jaksić et al. 1979, this study). Fuentes & LeBoulengé (1977), LeBoulengé & Fuentes (1978), and Jaksić et al. (1979, 1980, 1981b) have emphasized the importance of aerial and terrestrial predators in explaining habitat distributions of degu and other small mammals particularly in central Chile. Although diurnal aerial raptors were relatively rare in Fray Jorge, terrestrial

carnivores including *Dusicyon culpaeus* and *D. griseus* were common and have been found to be major predators of degus (Jaksić et al. 1980). In a dense shrubby habitat such as Fray Jorge, habitat associations might be weaker especially as the hunting success of a terrestrial carnivore such as *Dusicyon* would be less influenced by horizontal vegetative cover. In La Dehesa, diurnal aerial predators were common and terrestrial carnivores less common; hence shrub cover would afford more predator protection from an aerially searching raptor.

At Fray Jorge, three other small mammal species (all cricetids) were present year-around: *Akodon olivaceus, A. longipilis* and *Phyllotis darwini* (Meserve 1981b). At La Dehesa, only *P. darwini* was occasionally common. At both sites however, a second caviomorph, *Abrocoma bennetti,* was present and commonly shared burrows, runways and similar foods as degus (Meserve 1981a, 1981b, Meserve et al. 1983). Fulk (1976) and Martin & Rodriguez (unpubl. data) have noted the strong mutual association of these two species and Rosenmann et al. (1981) suggested the presence of a mutualistic relationship. The fact that *A. bennetti* and *O. degus* exhibit differences, albeit small, in a bimodally diurnal to crepuscular activity rhythm and that the diet of the former species is typically dominated by only one food item (Meserve 1981a, Meserve et al. 1983) in contrast to the degu's more diversified diet suggests that the two species could share similar resources in a overlapping, but noncompeting fashion; that is the pattern of resource utilization by *A. bennetti* fits the included niche pattern (sensu Colwell & Fuentes 1975).

In spite of the significant differences revealed here between reproductive patterns, diets, and habitat associations, and the more than three-fold difference in available precipitation, it is remarkable that degus at Fray Jorge and La Dehesa share a strong similarity in population trends (Fig. 1). Density estimates during maximum increase periods (October-November) are similar (59-65 individuals/ha) as are episodes of juvenile recruitment, subsequent population decline, and aspects of reproduction including litter size, and chronology of first conception-parturition. Maximum densities reported elsewhere (LeBoulengé & Fuentes 1978, Jaksić et al. 1981a) in central Chile range from 73 to 84 individuals/ha in October-January (with the exception of "Site A" in the first study in which densities of 259 to 192 individuals/ha were reported; all data from 1975 and 1976). Thus, in spite of the degu's unspecialized physiology and the inherent disadvantage of being a large size diurnal caviomorph, it has successfully evolved life history tactics equally compatible in central and northern Chilean arid zones. A parallel may be drawn between the adaptability of the degu in Chile and other caviomorphs inhabiting the extremely arid desert regions of Argentina including *Microcavia australis* and *Galea musteloides* (Rood 1970, Mares 1975). Thus, in regions largely devoid of highly specialized heteromyids and larger-bodied folivores such as sciurids and woodrats, caviomorphs such as the degu have successfully exploited a wide range of arid zone communities by means of a variety of behavioral, ecological, and life history adaptations.

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