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ENSO RELATED FLUCTUATIONS OF RAINFALL AND THEIR CONSEQUENCES FOR SOME RODENT POPULATIONS IN NORTH CENTRAL CHILE.

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ENSO Relación entre las fluctuaciones de las precipitaciones y sus consecuencias para algunas poblaciones de roedores en el Norte de Chile Central.

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ABSTRACT: El Niño Southern Oscillation (ENSO) is evaluated for its effects on rainfall in semi-arid Chile. Daily precipitation records are used to identify biologically important rainfall events. Events are evaluated by crossing theory to derive estimates of the probability distributions of the number of events, dates of their annual first and last occurrence, and length of the critically important biologically wet season for three phases of ENSO. Biologically important rainfall events are most frequent during warm phases and least frequent during cold phases. Cold phases produce the earliest onset of the wet season, while neutral phases delay it. The importance of variation in rainfall and its association with rodent populations is discussed extensively.

Keywords: ENSO, crossing theory, precipitation, Chile rodent reproduction.

RESUMEN: La Oscilación El Niño del Sur (ENSO) es evaluado por sus efectos sobre las precipitaciones en zonas semiáridas de Chile. Se utilizan registros de precipitación diaria para identificar eventos biológicamente importantes. Los eventos son evaluados por la teoría de cruce, para obtener estimaciones de la probabilidad de distribución del número de eventos, las fechas de su primera y última ocurrencia anual y la duración de la estación de lluvias de importancia biológica crítica en tres fases de ENSO. Las precipitaciones biológicamente importantes son más frecuentes durante las fases cálidas y menos frecuentes durante las fases de frío. Las fases frías producen el inicio de la temporada de lluvias, mientras que las fases neutra, las retrasa. La importancia de la variación de las precipitaciones y su asociación con las poblaciones de roedores se discute ampliamente.

Palabras claves: ENSO, teoría de cruce, precipitación, reproducción de roedores Chile

INTRODUCTION

Western South American flora and fauna are strongly affected by an oceanic-atmospheric phenomenon known as El Niño Southern Oscillation (ENSO), which may lead to marked changes in available resources. Rodent populations display breeding dynamics in phase with ENSO. For example, a warm phase of ENSO coincides with Pearson's (1975) report of a leaf eared mice (*Phyllotis darwini* (Waterhouse)) being both pregnant and lactating at the same time, while other individuals were reproducing at ages of less than one month. During 1972-73 and each successive El Niño event, dramatic increases in small mammal populations of north central Chile have been documented (Pefaur, Yáñez & Jaksic 1979, Jiménez, Feinsinger & F.M. Jaksic 1992, Jaksic, Yáñez & Fuentes 1992, Meserve, Yunger, Gutierrez, Contreras, Milstead, Lang, et al. 1995).

In semi-arid regions, increases in rainfall facilitate mass germination of winter annuals in events knows as the “greening of the desert." Beatley (1969) found that rainfall accumulations in excess of 25 mm in autumn led to mass germination of winter annuals in the Mojave Desert. Sudden surges in primary productivity provide the link between enhanced precipitation and successful rodent reproduction (Beatley, 1966; Pearson, 1975). The reproductive output of rodents increases in concordance with their ingestion of green vegetation (Reichman & Van De Graaff, 1975).

In Chile, increased availability of resources and preferred seasonal foods (e.g. green foliage) lead to better fitness of animals (Pefaur & Campusano 1985); and small mammal population expansions have been associated with variations in annual and seasonal rainfall totals (Pefaur et al. 1979, Meserve at al. 1995, Lima & Jaksic 1998). Sigmodontidae rodents whose populations peaked after the 1987 El Niño event included *Akodon olivaceus* (Waterhouse) and *P. darwini,* along with three caviomorph rodents (*Abrocoma bennetti* (Waterhouse), *Chinchilla lanigera* (Molina) and *Octodon degus* (Molina) (Jiménez et al. 1992, Meserve et al. 1995). Jiménez et al. (1992) attribute population changes to increased rains, and Jaksic et al. (1992) exclude predator/ prey interactions for the observed fluctuations in rodent populations. Meserve & Glanz (1978) proposed that the availability of water and appropriate vegetation are limiting controls on small mammal reproduction in the area. Inter-annual variations in the length of the rainy season, and thus the period of availability of green vegetation, may permit multiple breeding cycles in some years for rodents that reach sexual maturity quickly (Table 1) (Beatley 1969; Meserve et al. 1995).

Pefuar et al. (1979) observed that *P. darwini*, *Oryzymys longicaudatus* (Bennett) and *A. olivaceus,* which reach sexual maturity at a few months, attained “pest levels” in north central Chile as a result of the 1972 El Niño event (Fuentes & Campusano 1985). Thus, not only multiple litters but also multiple generations lead to exponential growth rates in years with extended wet seasons and heightened resources. Populations are known to decline when the area experiences droughts coincident with La Niña, the cold phase of ENSO. Researchers do not understand the long-term effects of these rapidly expanding populations on sympatric species, like the endangered chinchilla. Nonetheless, the availability of resources affects all individuals in the ecosystem.

Because the distribution of precipitation within a single wet season is associated with changes in habitat quality and mammalian populations of this semi-arid ecosystem, it is important to understand variations in this aspect of rainfall regime, not merely seasonal or annual totals. The objective is to detect and quantify variations in the characteristics of biologically important rainfall events (define as 25 mm or more precipitation within a three-day period) that influence small mammal populations in north central Chile. The frequency and timing of these events are investigated, leading to the development of probability distributions of the timings of the first and last such events, and the length of the intervening rainy season, all of which are related to ENSO phase. Variations in reproductive parameters, such as size of litter, gestation period and sexual maturity, of two different types of rodent species (Sigodontinae & Caviomorph), explain why some small mammals undergo population explosions where others show only slight increases. These, in combination with an understanding of the significance of precipitation, are of utmost importance for conservation and management (e.g. the endangered chinchilla) as indicated by an analysis of the dates of rodent conceptions, inferred from trapping records, and the precipitation data.

Table 1. Reproductive parameters for Caviomorph and Sigmodontine rodents in the study area.

	Abrocoma bennetti (*)	*Chinchilla lanigera* (**)	*Octodon degus* (**)	*Oryzymys longicaudatus* (***)	*Phyllotis darwini* (*)	*Akodon olivaceus* (*)
Gestation (days)	?	111(w)	90(w)	?	34 (h)	?
Litter size	1-6(r)	2(r)	1-10 (w)	3-9 (r)	2-7(e)	4-8(e)
1st Repro. (months)	?	8(w)	6(w)	few(r)	1(p),2(e)	2(r)
Litters/year	2(r)	2(h)	2(r)	3-5(r)	multiple (r)	2-3(r)
Distribution	C(r)	C(j)	C(r)	AC(r)	ACP(r)	AC(r)

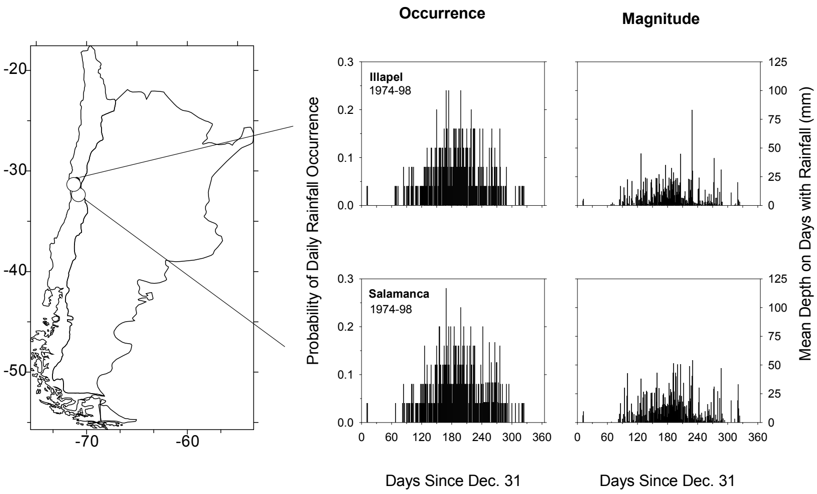
Sources: (*) Waterhouse; (**) Molina; (*** Bennett); e: J. F. Eisenberg unpub. data; h: Hayssen et al. 1993; j: J.E. Jiménez

1995; r: K. H. Redford and J. F. Eisenberg 1992; w: B. J. Wier 1974; Unknown parameters are denoted by a question mark. A: Argentina; C: Chile; P: Peru.

LOCATION

The towns of Illapel (31°38'S, 71°11'W, 290 m), and Salamanca (31°46'S, 70°58'W, 510 m) are located in the transverse mountains of north central Chile, connecting the coastal ranges to the Andes. Precipitation occurs from May to August (Figure 1), the austral winter; followed by a prolonged dry season lasting from October to April (Waylen & Caviedes, 1990, Waylen, Caviedes & Juricic 1993) Plant communities are a mixture of xeric semiarid species and mesic mediterranean species (Sarmiento, 1975, Jiménez, 1993). All areas of north central Chile report expanded habitat resources in years with abundant rains.

Fig. 1. Chilean study sites are located on the map to the left.
Probability of daily rainfall occurrences and their mean magnitudes at Illapel (top) and Salamanca (bottom)



METHODS

Three types of data are used in this analysis: ENSO phases, small mammal trapping records, and daily precipitation. Values of the Southern Oscillation Index (SOI), an indicator of ENSO phases and a quarterly classification of ENSO conditions based on sea surface temperatures (SST) are derived from data available through the National Oceanic and Atmospheric Administration (NOAA 1999a; NOAA 1999b). Small mammal trapping records from Auco, 14 km north of Illapel, were those that Jiménez et al. (1992) used to document abundance of rodents in the study area during and after the 1987 El Niño. Daily precipitation records (1974-98) from *Ministerio de Obras Publicas, Dirección General de Augas* for the towns of Illapel and Salamanca provide the basis for the statistical analysis of rainfall.

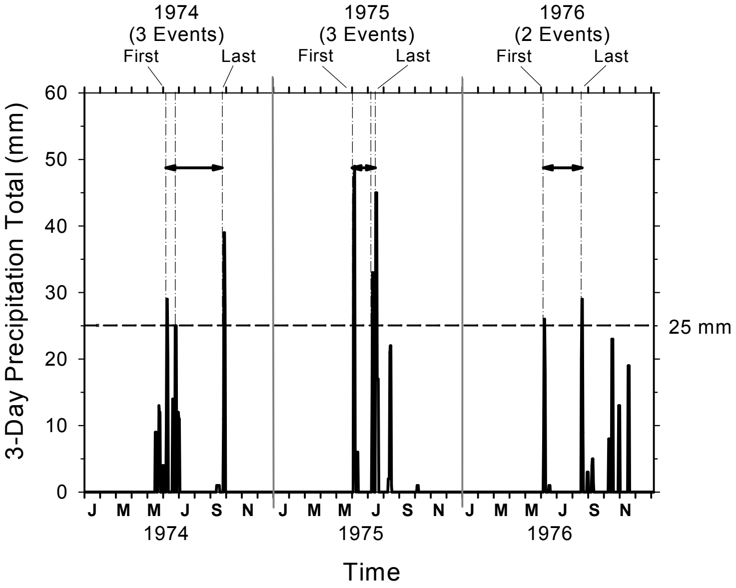
ENSO and rainfall event classification

Each historic daily precipitation series is combined into 3-day running totals of rainfall. All periods during which this new series exceed the 25 mm critical level (a biologically important event) are recorded for further analysis (Figure 2). Daily precipitation records are grouped into events, and a new data set consisting of the first and last dates of rainfall events in a rainy season, and the duration of their intervening period, is created. Two measures of the phase of ENSO are employed. Values of the Southern Oscillation Index (SOI) are used for simple correlations of annual precipitation characteristics (NOAA 1999a). In the study of precipitation events, events are divided based on the ENSO phase prevailing at their time of occurrence. A quarterly, “a priori,” tripartite classification of ENSO conditions (El Niño, Neutral and La Niña) based on sea surface temperatures (SST) in the equatorial Pacific, is used for this purpose (NOAA 1999b). For example, a rainfall event which began on July 8, 1975 in Illapel, occurs in the third quarter of 1975, which corresponds to a La Niña phase, so that rainfall event would be studied along with other cold phase events.

Statistical properties of rainfall

Crossing theory provides the theoretical basis for the analysis of the statistical properties of the biologically important events identified in the daily precipitation records (Nordin & Rosbjerg 1970). Here we use the critical crossing level or threshold of 25 mm or more precipitation occurring within three days for statistic analysis. During each ENSO phase, the observed frequency of events is calculated separately. Theoretically the number of such events will become Poisson distributed as the defining rainfall level (25 mm in this case) becomes rare compared to the average level (mean three day rainfall total) of the process (Figure 2).

Fig. 2. Example of three-day precipitation totals at Salamanca showing the critical level of 25 mm and defining critical events, their first and last occurrence and the intervening rainy season.



The distribution of the number of crossings (m) up to some point of time (t) in the year can be represented (Waylen, 1988, Waylen & LeBoutillier, 1989) as:

$$P[m(t)] = \frac{\exp[-\lambda(t)].\lambda(t)^{m(t)}}{m(t)!} \tag{1}$$

Where: λ(t) is the observed average number of events up to the time (t). Given the additive properties of the Poisson probability distribution (Haan, 1977), it is possible to sum the mean number of events in each season used by the classification to obtain the average number of events per year.

Clearly, from Figures 1 and 2, the timing of the events is strongly seasonal, but may be represented by the normal distribution

$$G(\phi) = \int_{-\infty}^{\phi} \frac{1}{\sigma\sqrt{2\pi}} \exp[-(s-\mu)^2 / 2\sigma^2] ds \qquad (2)$$

Where: μ is the mean date of events and σ the standard deviation. The empirical exceedance, probabilities of observed dates is calculated using the Weibull plotting position:

q/(n+1) (3)

Where q is the rank of the observed event (earliest event equals rank 1, latest equals rank n).

The time dependent function, λ(t), may then be estimated as follows:

$$\lambda(t) = \Lambda \bullet G(\phi \leq t) \qquad (4)$$

Where Λ is the mean number of events per year

The probability distribution of the first event in a year can be calculated as:

$$F(t) = 1 - \exp[\lambda(t)] \qquad (5)$$

and the distribution of dates of last events, H(t), as:

$$H(t) = 1 - \exp\{-[-\Lambda - \lambda(t)]\} \qquad (6)$$

(Waylen & LeBoutillier, 1989)

The duration of the period between the first and last event of a year can be viewed as the critical period for germination, and, using the respective distributions (equations 5 and 6), it becomes possible to calculate the probability distribution of the length (l) of a wet season, Y(l)

$$Y(l) = \sum_{i=1}^{365-l} F(i) \bullet H(i+l) \qquad (7)$$

F is the probability that the first event will occur on day i and H is the probability that the last event will occur on exactly *l* days later, on day *i+l*.

Comparisons of the fitted and derived distributions to the observed data are conducted using the Kolmogorov-Smirnov test at the 0.20 significance level (Haan, 1977) to reduce the chances of making a type II error. Differences in the means and variances of the dates of events under each of the three ENSO phases were investigated through the use of F- and t-tests. These were carried out at the 0.05 significance level.

Reproductive characteristics

The small mammal trapping records began in July 1987 and ceased in December 1989 (Jiménez, 1990). We estimated dates of conception of chinchillas and leaf-eared mice based on juvenile weight at trapping, linear growth curves, and each species' reproductive characteristics. The age of an immature individual can be calculated from their mass at time of capture based on linear growth curves. A disadvantage of the linear growth curves is the assumption of equal weight gain (Zullinger et al. 1984).

Neonatal weight of chinchillas is 35 grams (Weir, 1974) and lactation is considered to cease once an individual has achieved one-half adult weight. (J. F. Eisenberg, pers. com.) Mean adult weight for all non-pregnant adults was 410 grams (N= 24). Thus, weaning occurs at about 205g body weight. Length of lactation was between six and eight weeks and the animal has a gestation period of 111 days (Redford and Eisenberg, 1992). Estimated weights at birth and at the end of lactation were graphed. The age of a juvenile when trapped was estimated for 42, 49 and 56 day lactation periods creating three possible dates of conception. The breeding season for chinchillas in Chile has been reported as biannual with its onset in the austral spring (Hayssen, Tienhoven & Tienhoven, 1993).

Neonatal weight is not available for *P. darwini*, however Lima and Jaksic (1998) estimated that a newborn reaches 20 grams in 20 days. Gestation period is approximately 34 days and litter sizes range from 2-7 (Redford & Eisenberg, 1992). The animal reaches sexual maturity at 60 days and is close to adult mass by this time (J.F. Eisenberg, pers. com.). Some populations have been reported to reach sexual maturity at young ages and to breed year round during ‘favorable seasons’ (Pearson, 1975). Linear growth curves for two scenarios were constructed for *P. darwini*. Both use a base weight of 20 grams on day twenty and either 45 grams or 50 grams at sixty days.

By using graphs, we estimate the age, in days, of an individual. The appropriate length of gestation (days) is added to the estimated age (days) of each animal, thereby providing possible dates of conception.

RESULTS

Rainfall variations

The study area experiences considerable interannual variability in precipitation (Table 2). Regression of annual precipitation on the SOI indicates a statistically significant (0.05 level) negative correlation at no lag period [warm phases of ENSO (low SOI values) lead to increased annual precipitation]. At a three-year lead period, a significant positive correlation exists, which possibly indicates the tendency for opposing phases of ENSO to follow shortly after one another (Waylen & Caviedes, 1990). A similar procedure based on seasonal (quarterly) precipitation totals and SOI, at lag zero, shows that variations in SOI account for 25% of the interannual variation in precipitation during April, May and June and 37% during July, August and September.

Table 2. Annual precipitation (mm) characteristics for each site from 1974 to 1998.

Site (year)	Mean (mm)	S.D. (mm)	Min (year)	Max
Illapel (1987)	165.4	122.6	15.8 (1998)	513.4
Salamanca (1987)	248.7	178.6	44.6 (1998)	800.5

As expected, a higher frequency of biologically important rainfall events is experienced during El Niño years and the fewest number under La Niña. (Table 3) Regardless of ENSO phase, Salamanca has more biologically important precipitation events. This is due to factors such as higher elevation and the concomitant increased adiabatic cooling of air masses. (Barros & Lettenmaier, 1994).

Table 3. Annual mean number and total number of observed critical events reported by ENSO phase and based on the historical record. (1974-1998)

Phase	Illapel	Salamanca
El Niño	2.41 (n=23)	3.59 (n=34)
Neutral	1.61 (n=18)	2.38 (n=27)

La Niña	0.73 (n=3)	1.60 (n=6)

Similar quarterly patterns of occurrences occur at both sites under varying ENSO phases (Table 4). Event frequencies peak during the normal wet season with few, if any, events during the first and last quarters of the year. During neutral years, peak frequencies occur during the third quarter as opposed to the second during warm phases. During cold phases, Illapel experiences a peak in the second quarter, whereas Salamanca peaks in the third. In no season was the fitted Poisson distribution of events per season significantly different from the observed frequencies.

Table 4. The mean number of events observed per season based on the historic record. (1974-1998)

	Season	El Niño	Neutral	La Niña
	JFM	0.000	0.000	0.000
Illapel	AMJ	1.330	0.636	0.400
	JAS	1.000	0.833	0.333
	OND	0.083	0.143	0.000
Salamanca	JFM	0.000	0.000	0.000
	AMJ	2.222	0.818	0.600
	JAS	1.200	1.417	1.000
	OND	0.167	0.143	0.000

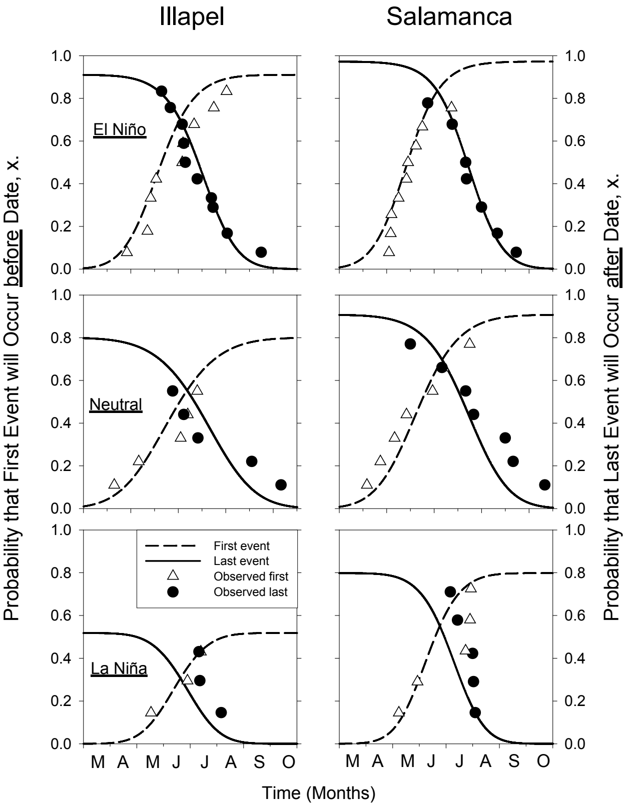
The normal distributions fitted to the starting dates of critical precipitation events under each set of conditions were not significantly different from the empirical frequencies. Parameters of the appropriate normal distributions are listed in Table 5. Both Illapel and Salamanca experience their earliest mean date of events while under the influence of La Niña and the latest in neutral years. The greater variation in mean dates between ENSO phases (over 3 weeks) occurs at Illapel. The largest variation in dates (standard deviation) occurs during neutral years and least during La Niña. Use of F- and t-test reveals no statistically significant difference between either set of parameters regardless of site or ENSO phase. The high observed variances, regardless of ENSO phase, account for the failure to detect significant differences in mean dates.

Table 5. Mean and standard deviation of the dates of critical events. Figures in parentheses indicate days since December 31.

	Event Type	Illapel	Salamanca
Mean date of event	El Niño	July 01 (182)	July 03 (184)
	Neutral	July 10 (191)	July 09 (190)
	La Niña	June 18 (169)	June 22 (173)
Standard deviation (days)	El Niño	41.18	43.45
	Neutral	52.48	47.98
	La Niña	30.29	30.71

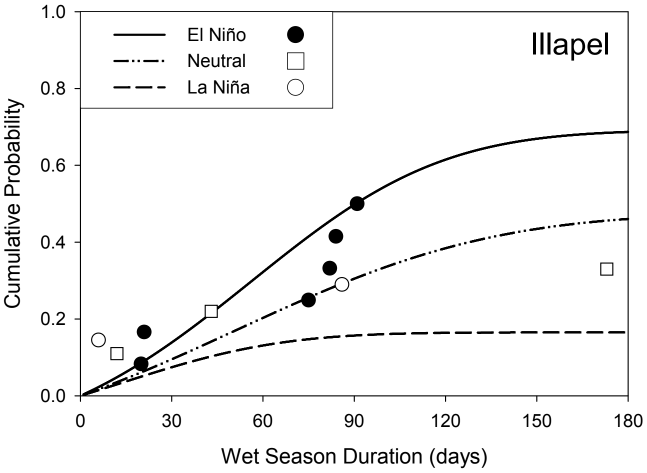
Using the parameters discussed above the first and last dates of precipitation events for each phase were not different from their expected distribution (Figure 3). The probabilities do not reach 1, because there a possibility of no events occurring in any one year (i.e., no first or last event). The probability of this eventuality is the complement of the respective cumulative probabilities at the end of the year. In Salamanca, the probability of at least one event (as indicated by the cumulative probabilities of first or last dates) is greatest during El Niño. For Illapel, there is a slightly higher probability of at least one event occurring earlier during neutral years than El Niño years. The latest predicted dates for first events occur during La Niña phases. The last events of the year occur earlier in La Niña and later in El Niño conditions. After October, neutral years have a higher probability of events occurring later in the year for both areas.

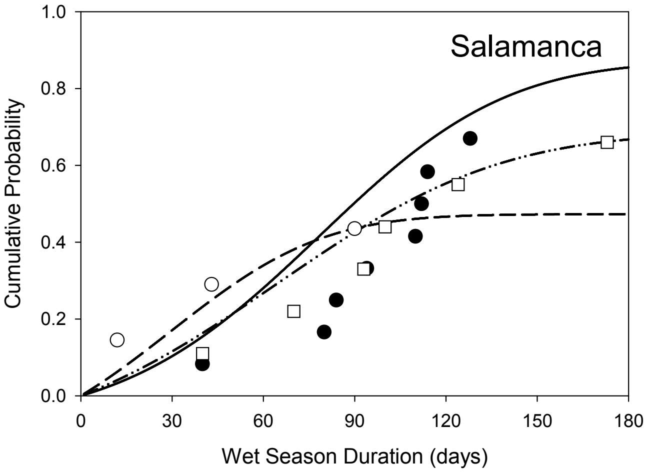
Fig. 3. Predicted cumulative probabilities (lines) and observed (symbols) dates of first (dashed line) and last (solid line) rainfall events for Illapel (left) and Salamanca (right).



Since it is possible to represent the probabilities of the dates of first and last events with reasonable accuracy, these are used to make predictions for the length of the wet season. (Figure 4)

Fig. 4. Predicted cumulative probabilities (lines) and observed (symbols) length of the critical rain season for Illapel and Salamanca.





The sample size is greatly reduced when only the first and last events of each year are used for analysis. In years with zero or one event, no data are available for inclusion in the analysis of durations. For example, at Illapel under La Niña conditions, only two years provided the necessary minimum of two events to define the length of the wet season. The probability of having a wet season during which at least one biologically significant event occurs, increases during El Niño. The risk of experiencing no such favorable conditions increases markedly under La Niña. (Figure 3) In general, the shortest wet seasons are experienced during cold phase years and the longest during warm phase.

During El Niño years, the probability of there being no critical precipitation season is 0.22 and 0.16 for Illapel, and Salamanca, respectively. The equivalent probabilities are greatest during La Niña, 0.82 and 0.53. Under neutral conditions the probabilities are 0.54 and 0.34. The probability of a wet season of up to 90 days is greatest during El Niño phases for sites, 0.50 Salamanca, and 0.54 at Illapel. For Illapel, this decreases to a 30% chance during neutral years and only 16% chance during La Niña years for a three-month wet season. Like Illapel, Salamanca has the greatest probability of a three-month wet season during El Niño phases. However, it has similar probability of a 90 day wet season during both La Niña and neutral phases. The predicted dates and durations are compared to the observed dates for all three sites and each set of conditions. No significant differences were detected at the .20 level using the Kolmogorov-Smirnov test, although great caution should be noted due to the very small sample sizes.

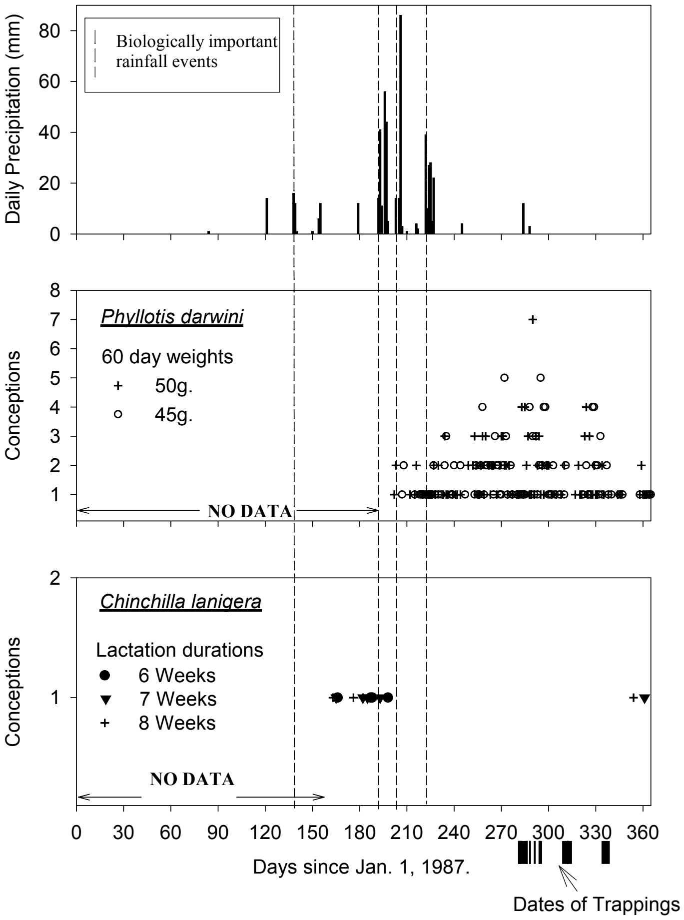
Total annual rainfall for 1987, 1988 and 1989 was 513.4mm, 57.5mm and 104.3 mm respectively. Also, 1987 was an El Niño year, while both 1988 and 1989 rainfall was less than normal due to La Niña conditions. In 1987, 4 biologically important rainfall events occurred, in 1988 there were none while two were detected in 1989.

Dates of conception

Using the linear growth graphs, we derived possible dates of conception for 9 juvenile chinchillas and 185 juvenile leaf-eared mice. Estimated chinchilla conceptions occurred in June, July, October and December. Because of the previously discussed assumptions made about the weights of the leaf-eared mouse, it was possible to estimate dates of conception of all the juveniles that were trapped. Based on the graphs, we estimated neonatal weight between 5 and 8 grams for *P. darwini*. Dates of conception encompassed all months except February, the end of the dry season. (Figure 1)

Figure 5 shows the estimated dates of conception for juveniles and the biologically important rainfall events that occurred in 1987. All conceptions occurred after the first biologically important rainfall event. Although the trapping record is not complete for early 1987, a similar correspondence between the date of the biologically significant precipitation events and dates of conception is observed in the complete, but not as extensive, record of 1989. In 1988, under La Niña conditions, conceptions of leaf-eared mice occurred in all months except February and a chinchilla was conceived in July. It is interesting to note that although no biologically important events occurred under our criteria of 25 mm of rainfall, 24.4 mm of precipitation was recorded for July, 1988. Thus, the critical level for events biologically important rainfall events in semi-arid North Central Chile may require less rainfall than that in North America.

Fig. 5 Derived dates of conception for *Phyllotis darwini* (Waterhouse) and *Chinchilla lanigera* (Molina) graphed with the biologically important rainfall events (equal or greater than 25 mm accumulation in three days) for 1987. The various symbols represent estimates based on varying assumptions about 60 day weights and lactation durations. No data was available for small mammals during the first part of the year as indicated on the graphs.



DISCUSSION AND CONCLUSIONS

Knowledge of temporal fluctuations and variations of biologically important rainfall events aids in our understanding of the complex interactions between the physical and biological realms. ENSO has a dramatic influence on the climate of this area. As atmospheric/ocean conditions fluctuate, the number of biologically significant precipitation events and the period during which those events occur, vary greatly. The highest probabilities of experiencing a larger number of events and of a lengthy wet season are concurrent with El Niño phases. The driest conditions are experienced during La Niña phases, when fewer storms occur and the rainy season is shortened.

From one phase to the next, changes occur in species populations, biological communities, and ecosystem structure. With additional events, primary productivity increases; the quantity and quality of resources in turn affect the physical condition of animals. These biologically important rainfall events are more frequent during El Niño, and the area can support larger populations for longer periods of time during these wetter years.

Fluctuations in populations are a result of variations in birth and death rates. Focusing on potential rates of reproduction, some species are able to reproduce more frequently, and their offspring reach sexual maturity sooner than other species. Secondly, the time between litters and litter size are very distinctive characteristics for the varying types of rodent that occur in the study area. Sigmodontine rodents are able to achieve high rates of recruitment in a short time period. In a three month wet season, multiple generations of all sigmodontine rodents in the study area may be produced and reproducing. Seasons of such length are unlikely, but their probabilities are highest during El Niño events. In these years multiple generations may be reproducing offspring and their populations can reach high numbers. This is due to both biological and environmental factors such as abundant available resources and the extension of the wet season. In caviomorph rodents, selective pressures have resulted in long gestation periods, low birth rates, small litter size and delayed timing of first reproduction. The reproductive biology of caviomorphs inhibits offspring from reaching sexual maturity and being able to breed within a single wet season. Chinchillas and other caviomorphs probably have better survivorship and maybe larger litter sizes during warm phases (Eisenberg, pers. com.) Caviomorph species that have been reported to increase due to warm phases of ENSO include *O. degus* & *A. Bennetti* (Meserve et al. 1995). These two species have larger litters' sizes than the endangered *C. lanigera* (Asdell, 1964). Due to small litter sizes, age of first reproduction, as well as length of gestation, chinchillas do not experience great population fluctuations as a result of annual fluctuations in ENSO and precipitation. Litter size and survival may be improved in all these species and that could account for the increase in their populations (Jiménez et al. 1992).

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