Solving the enigma of granivory rates in Patagonia and throughout other deserts of the world: is thermal range the explanation?

Patricia J. Folgarait[1], J. Adrián Monjeau[2] and Marcelo Kittlein[3]

1 Centro de Estudios e Investigaciones, Universidad National de Quilmes, Avenida Roque Saenz Peña 180, 1876 Bernal, Argentina. 1 Laboratorio Ecotono, Departamento de Ecología, Centro Regional Universitario Bariloche, Universidad National del Comahue, CC 1336, 8400 Bariloche, Argentina. 3 Laboratorio de Ecofisiología, Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad National de Mar del Plata, CC 1245, 7600 Mar del Plata, Argentina.

Abstract. *In order to gain insight about why Patagonia has low levels of granivory activity, percentages of world-wide granivory rates were compared for rodents, ants, and birds in seven desertic areas of the world. Using a series of multivariate analyses, we classified and ordinated these areas according to percentages of granivory rates, environmental features of the sites, and granivore biodiversity. Granivory activity was clearly separated into two groups, one representing the Northern Hemisphere which comprised Sonora, Great Basin, and Israel, and another, representing the Southern Hemisphere with Monte, Patagonia, South Africa, and Australia. The ordination analyses did not discrimínate any clear groups using the combined environmental variables. Separate correlations between the ordination axes of granivory and each environmental variable, and granivore richness, showed that only thermal range (the difference between the extreme annual mean temperatures) successfully correlated with the differences ín overall granivory between deserts and hemispheres. Our results show that all sites from the Northern Hemisphere, which had a very high continentality (high land/ocean ratio), and therefore high thermal range, were the ones with greater levels of granivory. A linear regression analysis showed that 72 % of the variation in overall granivory, mainly driven by rodent activity, was explained by thermal range. We propose that the only strategy that can evolve in environments with high thermal range ís granivory, as seeds are the only high quality food that can be stored. We propose that the combination of strong selective pressures with the chance that a certain taxa has for being at a certain place and time determines the relative importance of different taxa as granivores. Murid rodents had arrived earlier in the Northern Hemisphere than ín the Southern, and therefore, had greater opportunity to develop the granivore syndrome. Ants -which are as old as rodents at some of the studied sites but are poikilotherms- cannot deal as efficiently as rodents with very harsh environments. Birds, finally, avoid bad situations by migrating to more favourable habitats, and therefore circumvent those selective pressures with their great vagility. The more beningn the environment (lower thermal range due to low land/ocean ratios, as in the Southern Hemisphere), the less selective pressure for granivory, a reason that can also account for the high number of omnivores in South America and Australia, and the low granivory rates in Patagonia.*

Introduction

Deserts throughout the world are subjected to similar abiotic selective pressures mainly driven by a shortage of moisture (Brown et al. 1979, Mares 1983). Solutions to cope with these environmental constraints are limited to few possible adaptations, therefore it is reasonable to expect biotic convergence among desertic areas of the world. These patterns can be recognized at the community-level despite local differences in the assemblages, which in general differ in the evolutionary histories of the taxa involved (Kerley and Whitford 1994).

Among the adaptive responses evolved in desertic areas, granivory is a very common trophic strategy. Deserts are environmentally less predictable than forests or grasslands, in part due to the lower amount of water received, also associated with higher variability (Hoffman and Cowling 1987), but most importantly, due to the effect that a change in moisture economy has on the biota of desertic areas (Monjeau et al. 1997). As a consequence, resources are not guaranteed year-round. Because foliage and animal prey cannot be stored (Kerley and Whitford 1994), desert granivores buffer this lack of resource predictability by storing seeds (Morton 1993) which also represent food with high-energy content.

In the last two decades, significant efforts have been made to understand the similarities and differences among the guild structure of desert granivores, and the resulting convergences and difergences in granivory rates (Mares et al. 1977, Mares and Rosenzweig 1978, Morton 1979, 1985, 1993, Brown et al. 1979, Parmenter et al. 1984, Mares 1985, Kelrick et al. 1986, Brown and Ojeda 1987, Kerley 1991, Kerley and Whitford 1994, Folgarait and Sala submitted). World-wide comparisons of seed removal by rodents, ants, and birds have shown large-scale similarities within hemispheres (Kerley 1991), with rodents as the most important granivore group for the Northern Hemisphere and with ants as the most important for the Southern Hemisphere. However, an exception is Patagonia, where no strict granivores exist, and ants do not seem to be the dominant group (Folgarait and Sala submitted). From analyzing these studies, it also becomes apparent the low granivory level exhibited by south american sites, in particular by Patagonia. Mares and Rosenzweig (1978) have predicted compensation in seed removal levels of granivory activity across different granivore taxa in the sense that if rodents are not important then ants should compensate for them. However, their data have shown no compensation by ants in the Monte Desert (South America) in comparison to levels of seed removal by rodents in Sonora (North America).

Several hypotheses have been discussed to explain the observed differences among desertic areas: differences in rain predictability (Westoby 1980, Morton 1985), in climate (Kerley 1991), in continentality (Vuilleumier 1971, Morton 1979, Morton and Baynes 1985, Kerley and Whitford 1994), in edaphic conditions leading to different seed production (Morton 1985), or to withstand different levels of seed burial (Westoby et al. 1982), in plant adaptations against seed predation (Pulliam and Brand 1975, Brown and Ojeda 1987), in lineage identities or taxonomic resemblance (Mares 1993, Kelt et al. 1996), in species diversity at the local or regional scale (Morton 1993, Westoby 1993), in the presence of granivore specialists (Mares and Rosenzweig 1978), in the probability of speciation (Kelt et al. 1996), in the differential palaeoclimatic impact on cladogenesis by allopatric speciation (Mares 1983), in the reduction in seed production followed by the extinction of local granivore specialists (Mares and Rosenzweig 1978, Marone and Horno 1997), in the age of deserts (Orians and Solbrig 1977), in the amount of time since a desert was colonized by a taxon and whether this has been long enough for a granivorous guild to evolve (Mares and Rosenzweig 1978, Morton and Baynes 1985), and in the differential large-scale influence due to el Niño Southern Oscillation (ENSO) phenomenon (Canby 1984, Allan 1991, Kerley 1992, Kerley and Whitford 1994).

Despite the considerable efforts above mentioned no general theory has yet emerged, neither to explain the South American (Monte and Patagonia) enigma, nor to explain the world-wide pattern of granivory rates, probably because each hypothesis provided special, partial-case or local explanations about granivory. The challenge of this paper is an attempt to contribute to the understanding of world wide patterns of granivory in deserts reviewing the current literature and analyzing the hypotheses and evidences using a non experimental, statistical, and holistic approach, adscribing to the view that Brown and Maurer (1989) coined as macroecology. This macroecological approach is based on the conviction that there may be patterns operating at large scale, emerging as whole-system properties, that cannot be addressed simply by extrapolating from the results of local experimental studies. This general explanation could be found by using a multivariate and biogeographical approach. From this perspective, we sieved the available mentioned hypotheses selecting questions that can be subjected to statistical analyses:

1) Can environmental features combined together explain world-wide patterns of granivory rates?

Table 1. Site characteristics for each of the seven desertic areas used in this study to compare granivory rates. Variables and units: Elevation (m), SR: solar radiation (kcal/ CM^{-2} y^{-1}), EAMT: extreme annual mean temperature (ºC), TR: thermal range (°C), MAP: mean annual precipitation (mm), CV: coeffiicient of variation of annual precipitation (%), PGS: number of potential (or locally known) granivore species. R= rodents, A= ants, B= birds.

Site^	Latitude	Elevation	SR†	EAMT†	TR	MAP	(CV) †	PGS*
North America *Great Basin*	41 ºN	2103	140	- 8 17	25	226 (mainly winter)	20	R= 3 A= 1 B= 7
North America *Sonora*	31 ºN	739	170	10 31	21	267 (summer and winter)	35	R= (4) A= (7) B= 7
Israel *Negev*	31 ºN	370	180	5 36	31	101 (winter)	35	R= (4) A= (1) B= ?
Australia *New South Whales*	24-29 ºS	~150	160	10 30	20	160-205 (summer or no seasonality)	30	R= 1 A= 8 B= 6?
South Africa *Karoo*	33 ºS	~900	170	10 30	20	180-200 (winter)	30	R= (1) A= (1) B= (3)
Argentina *Monte*	27 ºS	~ 1000	160	10 25	15	290 (summer)	40	R= 3 A= 3 ? B= 6
Argentina *Patagonia*	45 ºS	~450	120	3 17	14	142 (winter)	20	R= 3 A= 5 B= 7

^ Data were taken from the following sources: *Great Basin* from Kelrick et al. 1986, *Sonora* and *Monte* from Mares and Rosenzweig 1978, *Negev* from Abramsky 1983, *New South Whales* from Morton 1985, *Karoo* from Kerley 1991, *Patagonia* from (Folgarait and Sala, in prep.t data taken from Goodall and Perry 1979. * part of data taken from Reichman 1979, Mares et al. 1985, Brown and Ojeda 1987, Kerley 1992, Medel and Vásquez 1992, Morton 1993, Monjeau et al. 1994, Lozada et al. 1996, Folgarait and Sala in prep.

2) Can each of the environmental features considered separately explain world-wide patterns of granivory rates?
3) Are granivory rates from different taxa independent from each other or do they show any kind of compensation?
4) Can granivore biodiversity from each taxa affect overall granivory rates?

Materials and Methods

Percentages of granivory rates by ants, rodents, and birds at each site were obtained from the literature (Abramsky 1983, Parmenter et al. 1984, Kerley 1991, Mares and Rosenzweig 1978, Morton 1985), supplemented with our own unpublished data (Folgarait and Sala submitted). From all the data gathered about granivory throughout the world, we selected those seven desert regions for which we found simoultaneous measurements of granivory rates for ants, rodents and birds (only in the case of Israel, no bird studies were carried out). In the case of Patagonia, granivory rates are for all insects, not only ants. We only compared data collected during the summer in order

to keep constant the season effect. Data were transformed into appropriate comparable units as percentages of grams of seeds consumed per 30 trays and per day.

Environmental features and granivore biodiversity for each desert were taken from the literature (see Table 1). Latitude, elevation, solar radiation, extreme annual mean temperatures, thermal range (difference between extreme annual mean temperatures), annual precipitation and its variability, and number of granivore species were used in our statistical analyses as potential predictors of granivory.

Data analyses

Granivory data were used in order to classify sites in multivariate analyses using the Euclidean distance algorithm in the clustering procedure (Systat, Wilkinson 1993). Because Israel has no data on birds, the program skipped the Israel/bird cell in the calculation of Euclidean distance among localities, meaning that Israel was compared with other sites only for its ant and rodent data. We also used a bootstrapping technique that allowed the objective identification of statistically significant groups of sites (Strauss 1982, Jaksic and Medel 1987, 1990). The bootstrap procedure randomized the original data matrix of percentage of granivory rates. We chose to use the randomization algorithm RA 1 (Lawlor 1980). RA 1 hardly retains the original structure of the matrix as each observed value (even zeroes) is replaced by a randomly generated number. With the Euclidean distances calculated, a matrix of sites was made and a cluster built using the UPGMA algorithm (Systat, Wilkinson 1993). This procedure was repeated a 1000 times for each of the new matrices generated with the boostrapping technique (using a program made with Visual Basic for Excel 5.0, Microsoft Corp., Redmond, WA, USA). Each iteration gave 6 node values, then from the resulting distribution of 6000 pseudovalues (nodes), the program gave a cutoff threshold of statistically significant distant values. Given the low numbers of OTUs (in this case sites), we have chosen the 10 percentile (p=10) of the distribution of node values; therefore, groups of desert sites obtained at lower distance values than the cutoff ($p < 0.10$) were considered significantly different.

We next used non-metric multidimensional scaling (MDA, Systat, Wilkinson 1993) to ordinate desert sites based on percentage of granivory rates and environmental variables of the sites. MDA is appropriate for non-normally distributed data (Jongman et al. 1987). According to Rohlf et al. (1982), MDA has the advantage of representing interpoint distances more faithfully than does its parametric analog, Principal Component Analysis. We superimposed on the results of the MDA, the cluster of sites based on the previous classification analysis of percentage of granivory rates by using circles of confidence at $p<0.10$. In this way, we looked at the correspondence between classification and ordination of our granivory data on one hand, and on the other we were able to explore the matching between the ordination based on environmental features with the groups obtained by the classification on the basis of percentage of granivory. Because MDA does not provide p values, we next used a non-parametric test to compare the site loadings (from each of the ordination axes) among the previously recognized groups by the cluster analysis.

Given the two ordinations of desert sites generated by the MDA, we made Spearman rank correlations between ordination axes based on environmental features with the ordination axes based on percentage of granivory rates. Next, through pairwise Spearman correlations between site loadings of each dimension and each variable shown in Table 1, we gained insight about how each abiotic and biotic variable could explain granivory differences among deserts. In order to perform these multiple comparisons, we corrected the alpha level using Bonferroni's adjustment method (Neter et al. 1985) as to maintain an experiment-wise error rate $< 10\%$. We made 10 correlations for all comparisons (alpha=0.10/10=0.01) except for the ones between taxa of granivores, for which we made 2 comparisons (alpha =0.10/2=0.05), and the ones between taxa of granivores and their sum, correlated with each environmental variable separately, for which we made 4 comparisons per variable (alpha=0.10/4=0.025). Finally, we made regression analyses in order to predict granivory based on the observed values of the independent variables that we found important in our analyses.
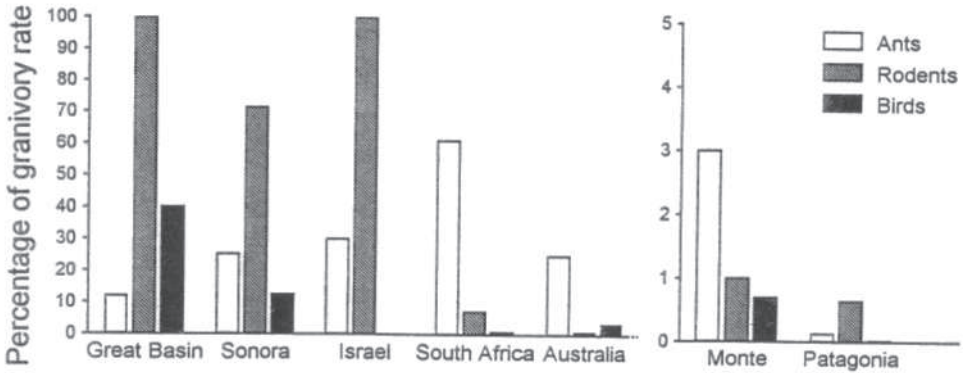
Figure 1. Percentage of grams of seeds consumed per 30 trays per day by ants, rodents, and birds in seven desert sites throughout the world. In each case, trays were accesible only to animals of one of the three taxa. White bars show the percentage of granivory rates by ants, dashed bars by rodents, and black bars by birds. Note that the scale of the y-axe differs between south american deserts and the others.
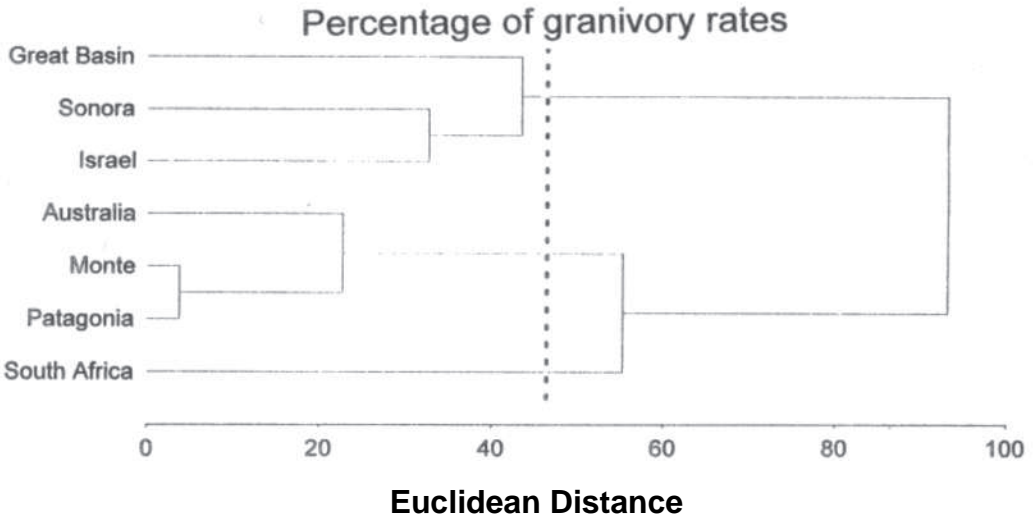

Euclidean Distance

Figure 2. UPGMA distance dendrogram from cluster analysis of seven desert sites based on percentage of granivory by ants, rodents, and birds. The vertical broken line was obtained from a bootstrap procedure and indicates that groups of sites to the left of the line are significant at P < 0.10.

Results

Percentages of granivory rates from the deserts surveyed showed that Great Basin, Sonora, and Israel had a remarkable dominance of rodents in the granivorous guild, whereas in Australia, South Africa, and Monte, ants exhibited greater percentages of seed removal in comparison to other granivores (Figure 1). Monte and Patagonia, the two South American desertic areas, showed a lower granivory activity in comparison to other semidesertic sites.
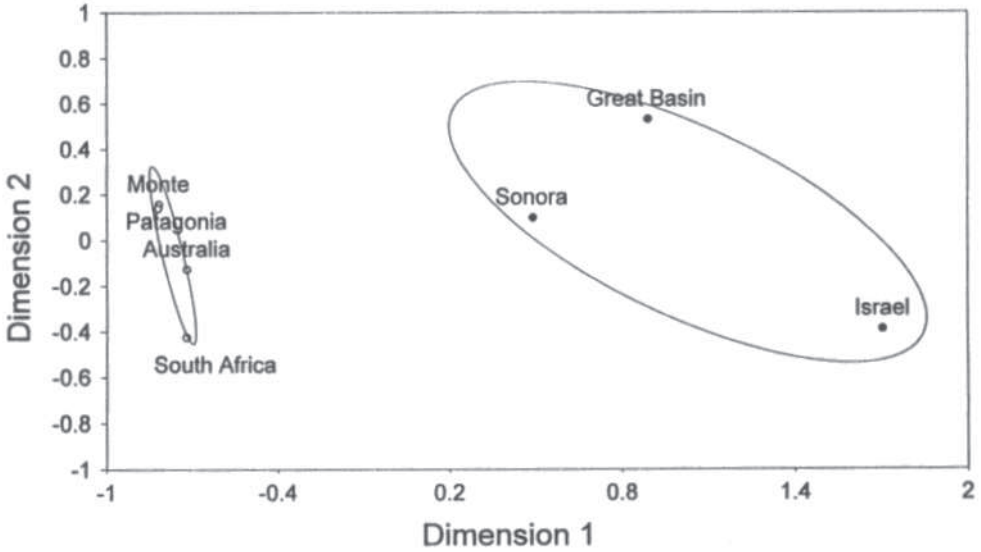
Figure 3. Non-metric multidimensional scaling of desert sites based on percentage of granivory by ants, rodents, and birds. Ellipsoids indicate 90% confidence areas for the "North" and "South" groups identified by the clustering procedure, each represented by solid and empty dots, respectively.
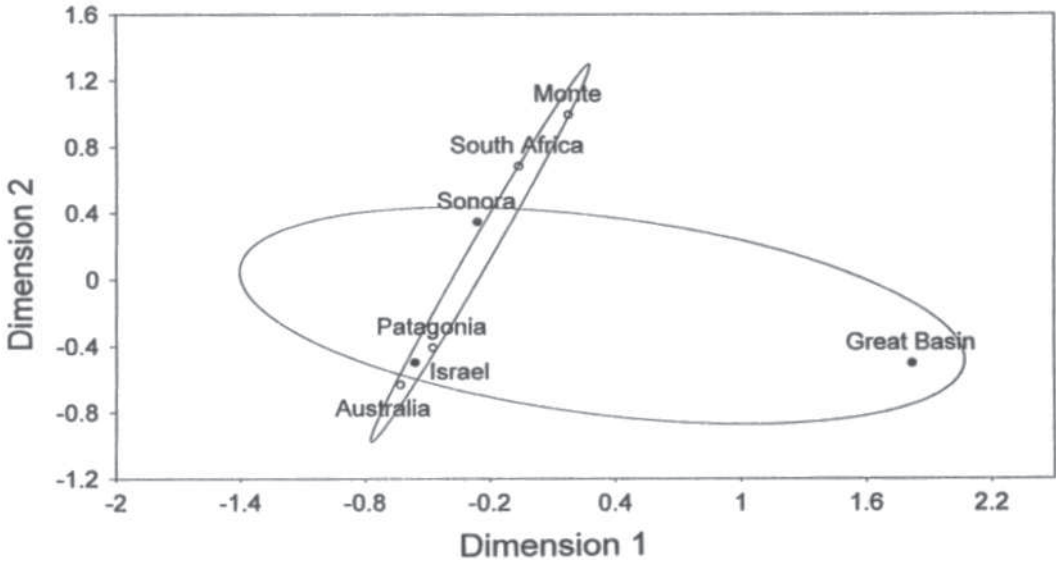

Figure 4. Non-metric multidimensional scaling of desert sites based on environmental variables. Ellipsoids indicates 90% confidence areas for the "North" and "South" groups identified by the clustering procedure, each represented by solid and empty dots, respectively.

Cluster analysis on percentage of granivory resulted in two discrete groups of sites clearly discriminating between Northern and Southern Hemispheres (Figure 2). The bootstrap procedure determined a cutof of 0.46 (p < 0.10); therefore, two statistically significant groups were found, one including Great Basin, Israel, and Sonora, and another joining Australia with Monte and Patagonian deserts. Despite being closer to the Southern Hemisphere sites, South Africa did not show a

statistically significant linkage with them. The two localities from southern South America, Monte and Patagonia, are more alike than any other pair of localities.

Showing consistency with the cluster analysis, two discrete groups were also obtained as a result of the ordination in the MDA multidimensional space (Figure 3). In the "north" group, the Sonora and Great Basin are closer to each other than to Israel in comparison to results from the cluster analysis. Regarding the "south" group, South Africa appeared borderline in the confidence elipsoides. A Mann-Whitney U-test rejected the null hypothesis of similarity between the previously determined groups "north" and "south" for the dimension 1 (p<0.03). In contrast, dimension 2 seemed to contain no discriminant information between these two groups (p < 0.72).

Up to this point in our analysis, classification and ordination techniques showed a clear and statistically significant separation between North and South sites based on granivory data. MDA results on the basis of environmental characteristics of desert sites (Figure 4) showed no consistency with the ordination obtained on the basis of granivory. Moreover, a Mann-Whitney U-test did not reject the null hypothesis of similarities between North and South sites either in dimension 1 or in dimension 2. This result suggested that differences in overall environmental features of desert sites do not explain differences and similarities in granivory.

The correlation analyses between the loadings of the sites ordered by percentage of granivory rates (Figure 3), and the loadings of the sites ordered by environmental characteristics (Figure 4), and between each of the environmental variables (Table 1), showed four results:

a) There were no significant correlations between the ordination axes obtained with the environmental data and the ordination axes obtained with percentage of granivory rates; therefore, the answer to question 1 is that environmental features combined were not correlated with percentage of granivory.

b) There was a strong positive correlation (R=0.99, p < 0.00001) between the ordination axes 1 of granivory and thermal range; therefore, the answer to question 2 is that thermal range was the only variable correlated with overall granivory as represented by ordination vectors.

c) There were no significant correlations between the percentages of granivory exhibited by each taxon; therefore, the answer to question 3 is that there was no apparent compensation among taxa in levels of seed removal.

d) There were neither correlations between species richness shown by each taxon with the ordination axes of granivory, nor with the percentage of granivory exhibited by each taxon; therefore, the answer to question 4 is that species richness did not explain granivory patterns.

In order to see if granivory rates exerted by each taxon also correlated with thermal range, we performed Spearman correlations and found that only rodents correlated significantly with thermal range (R=0.83, p<0.019). This result means that overall levels of granivory across desertic sites are driven mainly by rodents.

A Mann-Whitney U-test rejected the null hypothesis of similarity in thermal ranges between the previously determined groups "north" and "south" (p<0.03). Deserts from the Northern Hemisphere have significantly broader thermal ranges than deserts from the Southern one.

We finally built a linear regression model to predict granivory rates (Figure 5). The dependent variable was normally distributed (Shapiro-Wilk Test, W=0.906, p > 0.386), the North and South groups showed homoscedasticity (Barlett Test, Fratio=0.26, DF=1, p > 0.612), and the residuals were not correlated (r=0.506, p > 0.246). The regression was able to explain 74 % of the variation in overall granivory rates based on thermal range (y=9. 1 IX - 119.45; r^2=0.74, p<0.0125).
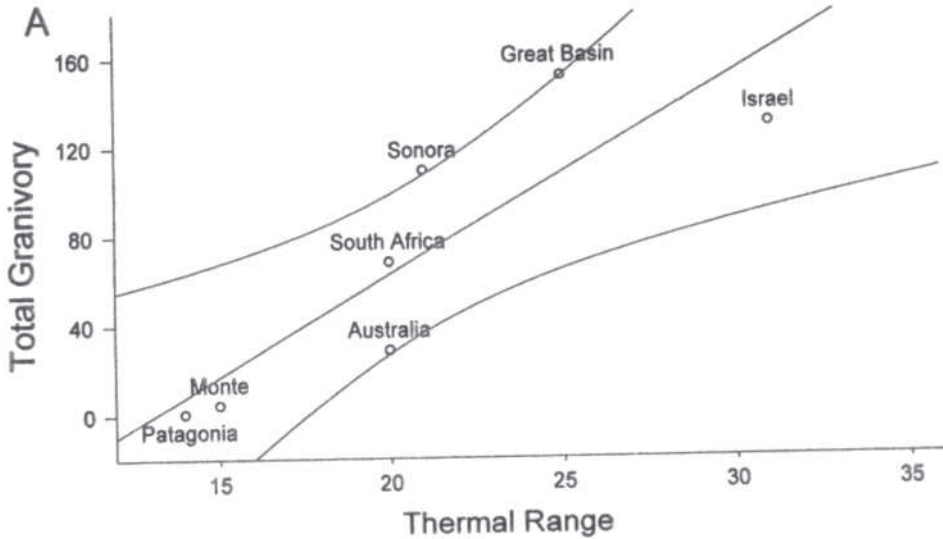
Figure 5. Linear regression model for total granivory as a function of thermal range; y=9.11x - 119.45, r^2 =0.74, P=0.012. A). Regression line and 95% predicted confidence limits for the seven desert sites analyzed. Dots represent the observed total granivory rates for each site.

Discussion

We have found that thermal range was able to explain the rates of granivory across seven desertic areas of the world, sheding light within a global context to the hitherto unexplained South America enigma and the Patagonian case. We also found that neither the levels of granivory, nor the identity of the most important granivore group, were convergent throughout the world.

Neither the species richness of each granivorous group nor the richness of the granivore guild explained differences in granivory. The lack of correlation between the number of species and the percentage of granivory rates suggests that a greater number of granivorous species in a given desert is not a necessary condition in order to observe high levels of granivory activity. However, we believe that independently of the type of evolution that had occurred (anagenetic or cladogenetic sensu Mares 1983), and therefore the resultant granivore diversity found locally, what may have been important is the level of specialization shown by the granivore community whether made by one or ten species. In spite of the presence of rodents that consume seeds as a main part of their diets in the two South American deserts studied here (Kelt et al. 1996, Guthmann et aí.1997, Monjeau 1989, Pearson 1995) the general pattern is that there are no obligatory granivorous species in these deserts. On the other hand, both, at the Great Basin with few rodent species, and at Sonora with high richness of rodents, great amounts of seeds are removed by highly specialized granivores. The species number may play a different role in the granivory system by affecting niche partitioning (i.e. based on seed size or habitat selection) and then community structure, but not by changing drastically the levels of granivory.

In order to understand why southern South America have low proportion of granivores we need to discuss several questions exploring differences among deserts from the Northern and Southern Hemispheres.
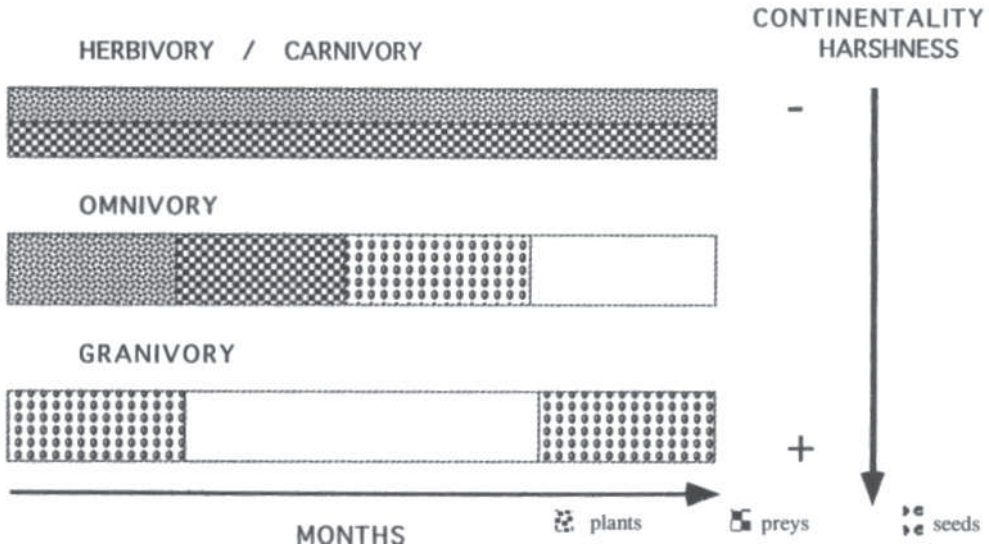
Figure 6. Main feeding strategies that should be favoured by natural selection in relation to the environment; the greater the continentality, the harsher the desert will be, and therefore, there will be months per year with no food available (empty boxes). If the food supply is constantly available, either herbivory or carnivore should evolve. If different food is available at different times of the year, omnivory should be favoured. If food is scarce or not available during part of the year, granivory should be favoured. Given a certain selective regime, serendipity will determine which group will play the major role in the granivore guild in each desertic area.

Granivory differences and abiotic variables. Environmental variables taken together in the multivariate space did not provide any explanation that could be correlated to the observed differences in granivory between deserts from the Northern and Southern hemispheres. Even though we demonstrated a remarkable correlation between thermal range and levels of granivory, such strong correspondence was masked by the multivariate analysis, which was not able to account for the differences found in granivory rates.

Thermal range seems to be the best predictor of granivory rates in deserts. However, the process that links thermal range with granivory is not direct, and it is necessary to ask a further series of questions: how is thermal range established, how could thermal range act on an animal community, and what are the chances of having "the best granivore" present in a certain area?

Why is thermal range related with overall levels of granivory? Among the many abiotic conditions that could describe harshness of the environment, those related to thermal ranges in deserts seem to be particularly important to set the stage for high levels of selective pressure towards granivory (Figure 6). Scarcity of moisture and lack of food availability are related with extreme temperatures, and as a consequence, desert organisms may either shut down their activity at those times, may migrate, or may use the food that was collected and stored at other times. If foliage is not guaranteed year round, it is not a good adaptation to be a strict herbivore in such an environment. If insects are not available year round, natural selection will not favour a strict insectivore. In areas of great food unpredictability, but in which at certain times of the year there are some insects available, or foliage, and at others there are seeds, then omnivores should be selected. If the environment is even harsher (in a predictable manner or not), and no food is warranted year round, then strict granivores will be the best adapted animals to such conditions as they can store seeds whenever these are produced and eat them at harsh times. There is no other trophic strategy that could be used to deal with the fact that resources are completely shut down at certain times of the year. Our data support this notion. The ranking of thermal range correlates perfectly well (R=0.99, p < 0.00001) with the ranking of percentage of granivory represented by loadings in our data. This

suggests that the harsher the environment, the greater the selective pressure for granivory. In fact, our regression equation could predict the granivory activity given a level of thermal range.

In a world-wide comparison of rodent richness, Kelt et al. (1996) have found that granivore alpha richness is greater in North America and Israel while omnivores are more important in South America and Australia. Moreover, herbivores have greater diversity in South America and carnivores are extremely diverse in Australia. Our thermal range model is supported by Kelt's findings. In fact, Sonora and Great Basin in North America, together with Israel, have the greatest thermal ranges, whereas Australia and South America (Monte and Patagonia), have the lowest. Why are carnivores dominant only in Australia and not in South America, a place where mild winters are also found? In order to answer this, it is necessary to consider the earth's history. Thermal range may have been even greater during the Pleistocene glacial maxima due to the increase of the ratio between land masses/oceans (Clapperton 1993). A harsher winter climate in the Northen Hemisphere may have limited the availability of insects and foliage, and desert small mammals may have been forced to rely on seeds (Kerley and Whitford 1994). While southern South America was profoundly affected by glaciations, a tundra desert occupied most of Patagonia (Clapperton 1993), and a massive extinction of marsupials occurred during the Pleistocene (Reig 1981). Australia, on the contrary, was much less affected during the glaciations, and since then it has been maintaining milder climates, as well as a persistent marsupial fauna. These facts, probably favoured the activity of poikilothermic organisms, and the relatively high abundance of ants and termites, may explain, in turn, the dominance of marsupial carnivores which feed on them.

Our pattern of granivory rates explained by thermal range is mainly driven by rodents. Birds do not correlate well with thermal range probably because they move away from poor conditions, looking constantly for plentiful resources through migration and dispersal. Therefore, granivorous birds are not under the same set of selective pressures than the other taxa that cannot fly away from their homes; and despite being able to remove great levels of seeds they really do not constitute any single resident assemblage. Ants as poikilothermic organisms have less chance of surviving and being active in a very harsh environment, and therefore lower levels of seed removal are expected. in comparison to rodents, and this may be the reason why ant granivory did not correlate with thermal range.

Why are there differences in levels of granivory between hemispheres? The different proportion of land masses between hemispheres is apparent. The larger the land masses (i.e. Northern Hemisphere), the greater the continentality, and the broader the thermal ranges (Gates, 1993). Kerley (1990) suggested that differences in patterns of granivory could be due to continentality, although later Kerley and Whitford (1994) rejected this hypothesis when they found that only a small component of mammals were granivorous in Asian deserts. Given the fact that in our analyses species diversity did not explain granivory rates (i.e. Israel and Great Basin compared to Sonora), and given our finding that thermal range explained granivory levels, we support the continentality hypothesis. Measurements of rates of seed removal in Asia will be extremely enlightening to support or reject our model.

A more severe climate in the northern land masses may have increased the selective pressure towards strict granivory in deserts such as Sonora, Great Basin and Israel. The influence of the oceans buffers temperature differences in the Southern Hemisphere, and the position at relatively higher latitudes leads to milder climates, guarranteeing year-round the availability of insects and foliage, decreasing in turn the selective pressures towards strict granivory (Figure 6).

Why do rodents predominate in the Northern Hemisphere and ants tend to predominate in the Southern Hemisphere? Even if thermal range explains why granivory in deserts is greater in the Northern Hemisphere than in Southern Hemisphere, it does not explain why the main granivore group is represented by different taxa. Thermal range seems to be the surrogate of a more complex relationship between abiotic constraints and biotic responses, combining unique historical circumstances with differential selective pressures.

Evolution of granivory in deserts seems to contain a serendipitous factor (Roberts 1989): being there at the right time and doing the right thing can change the course of evolution. On one hand, rodents have been present in the northern masses from the Oligocene while only from the Pliocene or Pleistocene in the Southern Hemisphere (Nowak 1991). Therefore, they had more time to evolve towards granivory in the harsher, more continental, Northern hemisphere. However, if it were a question of time only, why have ants not been important everywhere or as important as rodents since they have been all over the world since the Oligocene (Holldobler and Wilson 1990)? Ants as poikilothermic organisms cannot persist well in very cold environments, even under the soil, whereas rodents, as homeotherms, have more chances to deal with those situations. This fact may explain why ants are so important in Australia, a continent with relatively mild winters (Morton 1993).

Some features of desert mammal granivores like checkpouches (which allow the collection of many seeds at a time), bipedalism (which permits more efficient movements: faster, using less energy, and doing less contact with the soil), and homeothermy (which allows the continual activity of the organism even under extreme temperatures) could provide them with a competitive advantage under extreme conditions in which consumers are forced to rely on seeds. Given the circumstance of having a potential set of rodents with these features and ants (that have none of these adaptations) coexisting under harsh environments, the first ones will be able to take advantage of the granivore niche more easily.

The combination of strong selective forces and the evolutionary opportunity taken by murid rodents since the Oligocene may explain why they predominate in the Northern Hemisphere. On the other hand, milder climates in the Southern Hemisphere in combination with a later arrival of small mammals (Muridae) in the Pliocene may explain why ants could take advantage of the situation, but with a lower overall level of granivory due to the weak abiotic selective forces towards granivory. In southern South America there are no obligatory granivorous species of murid rodents despite the fact that they have been present for at least 3.5 million years (Patterson and Pascual 1972) or more (Marshall 1979, Reig 1978). This may be explained in part by the lack of strong selective pressures towards granivory, as shown by the small thermal ranges found in the deserts analysed from the southern hemisphere. South America decreases its proportion of land with respect to oceans at increasing latitudes, reaching the most extreme situation in Patagonia, the site with lowest levels of granivory activity.

References

Abramsky, *Z.* 1983. Experiments on seed predation by rodents and ants in the Israeli desert. Oecologia 57:328-332.

Allan, R.J. 1991. Australasia. *Pp.* 73-120. In: Glantz, M., R. W. Katz and N. Nichols (eds.). Teleconnections Linking Worldwide Climate Anomalies. Cambridge University Press, London.

Brown, J.H. and B.A. Maurer. 1989. Macroecology: The division of food and space among species on continents. Science 243:1145-1150.

Brown, J.H. and R.A. Ojeda. 1987. Granivory: patterns, processes, and consequences of seed consumption on two continents. Revista Chilena de Historia Natural 60:337-349.

Brown, J.H., O.J. Reichman and D.W. Davidson. 1979. Granivory in desert ecosystems. Annual Review of Ecology and Systematics 10:201-227.

Canby, T.Y. 1984. El Niho's ill wind. National Geographic 165:144-83.

Clapperton, C. 1993. Quaternary geology and geomorphology of South America. Elsevier, Amsterdam. 779 pp.

Folgarait, P.J. and O.E. Sala. In review. Granivory rates of seeds by rodents, insects, and birds in the Patagonian steppe.

Gates, D.M. 1993. Climate Change and its Biological Consequences. Sinauer Associates, Inc, Massachusetts. 280 pp.

Guthmann, N., M. Lozada, J.A. Monjeau, and K.M. Heinemann. 1997. Population dynamics of five sigmodontine rodents of northwestern Patagonia. Acta Theriologica 42:143-152.

Goodall, D.W. and R.A. Perry. 1979. Arid land ecosystems: structure, functioning and management. Vol. 1. International Biological Program 16. Cambridge University Press, Cambridge.

Hoffman, M.T. and R.M. Cowling. 1987. Plant physiognomy, phenology and demography. Pp 1-34. In: Cowling, R.M. and P.W. Roux (eds.). The Karoo Biome: a Preliminary Synthesis. Part 2- Vegetation and History. South African National Scientific Program Report No. 142.

Hölldobler, B. and E. O. Wilson. 1990. The Ants. Belknap Press of Harvard University , Massachusetts. 732 pp.

Jaksic, F.M. and R. Medel. 1987. El acuchillamiento de datos como método de obtención de intervalos de confianza y de prueba de hipótesis para índices ecológicos. Medio Ambiente 8:95-103.

Jaksic, F. M. and R. Medel. 1990. Objective recognition of guilds: testing for statistically significant species clusters. Oecologia 82:87-92.

Jongman, R.H.G., C.J.F. Ter Braak, and O.F.R. van Tongeren. 1987. Data analysis in Community and Landscape Ecology. Cambridge University Press, London. 299 pp.

Kelrick, M.I., J.A. MacMahon, R.R. Parmenter and D.V. Sisson. 1986. Native seed preferences of shrub-steppe rodents, birds and ants: the relationship of seed attributes and seed use. Oecologia 68:327-337.

Kelt, D.A., J.H. Brown, E.J. Heske, P.A. Marquet, S.R. Morton, J.R.W. Reid, K.A. Rogovin and G. Shenbrot. 1996. Community structure of desert mammals: comparisons across four continents. Ecology 77:746-761.

Kerley, G.I.H. 1990. Small mammals as granivores in the Karoo, South Africa. Ph.D. Thesis, University of Port Elizabeth. (not seen, cited in Kerley and Whitford 1994).

Kerley, G.I.H. 1991. Seed removal by rodents, birds and ants in the semi-arid Karoo, South Africa. Journal of Arid Environment 20:63-69.

Kerley, G.I.H. 1992. Small mammal in the semi-arid Karoo, South Africa: biomass and energy requirements. Journal of Arid Environments 22:251-260.

Kerley, G.I.H. and W.G. Whitford. 1994. Desert-dwelling small mammals as granivores: intercontinental variations. Australian Journal *of* Zoology 42:543-555.

Lawlor, L.R. 1980. Structure and stability in natural and randomly constructed competitive communities, American Naturalist 116:394-408.

Lozada, M., J.A. Monjeau, K.M. Heinemann, N. Guthmann and E.C. Birney. 1996. Abrothrix *xanthorhinus*. Mammalian Species 540:1-16.

Mares, M.A. 1983. Desert rodent adaptation and community structure. Pp. 30-43. In: Reichman, O.J. and J.H. Brown (eds.). Biology of Desert Rodents Great Basin Naturalist Memoirs No 7.

Mares, M.A. 1985. Mammal faunas of xeric habitats and the Great American Interchange. Pp. 489-520. In: Stehh, F.G. and S.D. Webb (eds.). The Great American Biotic Interchange. Plenum Publishing Corporation.

Mares, M.A. 1993. Desert rodents, seed consumption, and convergence. BioScience 43:372-379.

Mares, M.A. and M. L. Rosenzweig. 1978. Granivory in North and South American deserts: rodents, birds, and ants. Ecology 59:235-241.

Mares, M.A., W.F. Blair, F.A. Enders, D. Gregor (Jr.), A.C. Hulse, J.H. Hunt, D. Otte, R. D. Sage, and C.S. Tomoff. 1977. The strategies and community patterns of desert animals. Pp. 107-163. In: Orians, G.H. and O.T. Solbrig (eds.). Warm Deserts: Convergent Evolution. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.

Mares, M.A., J. Morello and G. Goldstein. 1985. The Monte desert and other subtropical semi-arid biomes of Argentina, with comments on their relation to North American arid areas. Pp. 203-237. In: Evenari, M.I., Noy-Meir, and D.W. Goodall, editors. Ecosystems of the world 12 A. Hot deserts and arid shrublands, Elsevier, New York, USA.

Marone, L. and M.E. Horno. 1997. Seed reserves in the central Monte desert, Argentina: implications for granivory. Journal of Arid Environments 36:661-670.

Marshall, L.G. 1979. A model for paleobiogeography of South American cricetine rodents. Paleobiology 5:126-132.

Medel R.G. and R.A.Vázquez. 1992. Comparative analysis of harvester ant assemblages of Argentinian and Chilean Arid Zones. Journal of Arid Environments 26:363-371.

Monjeau, J.A. 1989. Ecología y distribución geográfica de los pequeños mamíferos del Parque Nacional Nahuel Huapi. Tesis Doctoral, Univ. National de La Plata, La Plata, Argentina. 253 pp.

Monjeau, J.A., N. Bonino and S. Saba. 1994. Annotated checklist of the living land mammals in Patagonia, Argentina. Mastozoologia Neotropical 1:143-156.

Monjeau, J.A., R.S. Sikes, E.C. Birney, N. Guthmann, and C.J. Phillips. 1997. Small mammal community composition within the major landscape divisions of Patagonia, southern Argentina. Mastozoologia Neotropical 4:5-16.

Morton, S.R. 1979. Diversity of desert-dwelling mammals: a comparison of Australia and North America. Journal of Mammalogy 60:253-264.

Morton, S.R. 1985. Granivory in arid regions: comparisons of Australia with North and South America. Ecology 66:1859-1866.

Morton, S.R. 1993. Determinants of diversity in animal communities of arid Australia. Pp. 159-169. In: Ricklefs, R.E. and D. Schluter (eds.). Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press, Chicago, Illinois, USA.

Morton, S.R. and A. Baynes. 1985. Small mammal assemblages in arid Australia: a reappraisal. Australian Mammalogy 8:159-169.

Neter, J., W. Wasserman, and M. Kutner. 1985. Applied linear statistical models. Irwin, R. (ed.). Homewood. 1127 pp.

Nowak, R.M. 1991. Walker's Mammals of the World, fifth edition, vol 11. The Johns Hopkins University Press, Baltimore and London. 1 127 pp.

Orians, G.H. and O.T. Solbrig (eds.). 1977. Convergent evolution in warm deserts: an examination of strategies and patterns in deserts of Argentina and the United States. Dowden, Hutchingon and Ross, Pennsylvania, USA. 333 pp.

Parmenter, R.R., J.A. MacMahon and S.B. Vander Wall. 1984. The measurement of granivory by desert rodents, birds, and ants: a comparison of an energetic approach and a seed-dish technique. Journal of Arid Environments 7:75-92.

Patterson, B. and R. Pascual. 1972. The fossil mammalian fauna of South America. Pp 247-309. In: Keast, A.F., F.C. Erk, and B. Glass (eds.) Evolution, Mammals, and Southern Continents. Albany, New York: State University of New York Press.

Pearson, O.P. 1995. Annotated keys for identifying small mammals living in or near Nahuel Huapi National Park or Lanin National Park, southern Argentina. Mastozoologia Neotropical 2:99-148.

Pulliam, H.R. and M.R.Brand. 1975. The production and utilization of seeds in plains grassland of southeastern Arizona. Ecology 56:1158-1166.

Reichman, O.J. 1979. Desert granivore foraging and its impact on seed densities and distributions. Ecology 60:1085-1092.

Reig, O.A. 1978. Roedores cricétidos de] Plioceno Superior de la Provincia de Buenos Aires (Argentina). Publicaciones de] Museo Municipal de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia" 2:164-190.

Reig, O. A. 1981. Teoría del origen y desarrollo de la fauna de mamíferos de América del Sur. Monografie Naturae, 1. Publicaciones del Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mar del Plata, Argentina. 162 Pp.

Rohlf, F.J., J. Kishpaugh, and D. Kirk. 1982. NT-SYS. Numerical taxonomy system of multivariate statistical program. State University, New York, Stony Brook.

Roberts, R.M. 1989. Serendipity: accidental discoveries in science. John Wiley & Sons, New York. 270 pp.

Strauss, R.E. 1982. Statistical significance of species clusters in association analysis. Ecology 63:634-639.

Vuilleumier, B.S. 1971. Pleistocene changes in the fauna and flora of South America. Science 173:771-780.

Westoby, M. 1980. Elements of a theory of vegetation dynamics in arid rangelands. Israel Journal of Botany 28:169-194.

Westoby, M. 1993. Biodiversity in Australia compared with other continents. Pp. 170-177. In: Ricklefs, R.E. and D. Schluter, editors. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois.

Westoby, M., J.M. Cousins, and A.C. Grice. 1982. Rate of decline of some seed populations during drought in western New South Wales. Pp. 7-10. In: Buckley, R.C. (ed.). Ant-plant Interactions in Australia Junk, The Hague.

Wilkinson, L. 1993. SYSTAT. The system for statistics. SYSTAT, Inc., Evanston, Illinois. 750 pp.