Geobios 48 (2015) 239–248

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Original article

Lama Guanicoe (Müller, 1776) body size in continental Patagonia and Tierra del Fuego☆

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ARTICLE INFO

Article history:
Received 4 June 2014
Accepted 15 February 2015
Available online 11 April 2015

Keywords:
Guanaco
Osteometry
Body size
Environmental variables
Latitudinal gradient
Bergmann's rule
South America

ABSTRACT

Lama guanicoe (Müller, 1776) is one of the most important South American large mammal species for both biologists, ecologists and archaeologists, and body size of modern and prehistoric populations of guanaco has been one of the most studied parameters. In this paper, we evaluate the latitudinal differences in body size of different modern populations of guanaco from Argentinean Patagonia based on osteometric data of their long bones. The osteological sample is made of 110 fully-fused individuals drawn from three different guanaco populations from continental and insular Patagonia covering the latitudinal interval from S40° to S54.5°. Quantitative data for the four long bones selected are analyzed with univariate and multivariate parametric statistical techniques. Apparently consistent with Bergmann's rule, results show that guanaco specimens from S53–54.5° are bigger on average than those from S48–52° which are, in turn, bigger than those from S40°. We observe a high and significant covariation between different environmental variables (maximum temperature, net primary production, and winter precipitation) and body size of the guanaco populations. Nevertheless, when the temporal factor is incorporated into the analysis of this geographical gradient of body size the scenario becomes more complex. We conclude that the current clinal pattern observed in Patagonia is the result of several microevolutionary and biogeographic processes related to an adjustment of body size to different environmental and ecological drivers and to the consequences of isolation in Tierra del Fuego that occurred around the Pleistocene-Holocene transition.

1. Introduction

The body size of modern and prehistoric mammals is one of the most relevant and studied biological parameters in macroecology, biogeography, paleobiology, paleoecology, paleontology, zooarchaeology and conservation biology, as it correlates with many ecological, morphological, physiological and behavioral traits. Performance of the locomotor system is related to body size, which in turn entails important consequences for the adaptive strategies of individuals, their relation with the environment, and interaction with other species and populations (competition, predator-prey relationships, etc.) and hence, for their evolution (Margalef, 1955; McNab, 1971; Peters, 1983; Calder, 1984; Damuth and MacFadden, 1990; Scott, 1990; Ashton et al., 2000; Meiri and Dayan, 2003; Meiri and Thomas, 2007; Olden et al., 2007; Greve et al., 2008).

In this paper, we evaluate latitudinal differences in body size of different guanaco modern populations (*Lama guanicoe* Müller, 1776) of Argentinean Patagonia from osteometric data of their long bones. Body sizes are impossible to determine directly even on modern osseous remains, but we can derive them from the measurements of long bones or their epiphyses, whose dimensions are highly correlated with overall body size (Damuth and MacFadden, 1990; Scott, 1990).

The latitudinal variation in species body size has been the subject of intense investigation for more than 170 years (Bergmann, 1847; Brown, 1995; Blackburn et al., 1999; Gaston and Blackburn, 2000; Rodríguez et al., 2006; Meiri and Thomas, 2007), with disparate results. Wild organisms do not respond directly to latitude but to various climatic parameters correlated with latitude. For this reason, it is necessary to investigate the climatic parameters involved, to determine whether they vary independently or not, and finally to

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http://dx.doi.org/10.1016/j.geobios.2015.02.007
0016-6995/

identify which of them influence guanaco's body size variations. For that reason, guanaco's body size variations are evaluated according to different environmental, ecological and biogeographical variables related to each of the three Patagonian studied samples (Table 1).

2. *Lama guanicoe* importance, history and distribution

The guanaco is a mammal species of great ecological and archaeological importance in South America. It is archaeologically significant since it was the main prey for human populations from the latest Pleistocene (10-12 ka BP) onwards (Mengoni Goñalons, 1999; Massone, 2001; De Nigris, 2004; Fernández, 2010; Santiago, 2013). Microevolutionary and biogeographic studies about this taxon are crucial to better know their environmental adaptations and the impact of the interaction of *Lama guanicoe* with its main predator: man. Indeed, the behavioral plasticity and flexibility of guanaco's populations have ensured their adaptation and survival in a variable and changing environment for thousands of years (Franklin, 1982). Since prehistoric times, the guanaco has been the most abundant camelid with the largest geographical range in South America. It occurs in the Andean region from northern Peru (S8°) to the Tierra del Fuego Island (Argentina) and Navarino Island (Chile) (S55°), and from sea level to 4500 m asl. Nevertheless, this large geographic distribution is not continuous: it is homogeneous from S55° to S30° (i.e., from Tierra del Fuego to south Mendoza), and then gradually decreases northwards (S29°–S8°) where guanaco populations become very small and isolated (Baigún et al., 2008).

Pre-Colombian guanaco populations' size has been estimated from about 30 to 50 million of individuals (Raedeke, 1979). These populations declined after the European colonization and the introduction of domestic sheep since the 1800s. The principal cause of the continuous and severe decrease of guanaco populations is related to interference competition at interspecific level due to the intensification of sheep overstocking (Raedeke, 1976; Franklin, 1982; Baldi et al., 2004, 2010). At present this species occupies only 40% of its original distribution, and 94–96% of the current population is found in Argentina (Franklin, 1982; Baigún et al., 2008). *Lama guanicoe* is not currently under extinction threat (it is categorized as "Least Concern"; IUCN, 2013; Ojeda et al., 2012), but some sub-populations are at risk at the local or regional level because of habitat degradation due to livestock interference, harassment of farmers, furtive and legal hunting, attacks by feral dogs, and lack of management plans to ensure their conservation (Raedeke, 1976; Cunazza et al., 1995; Baldi et al., 2004, 2010).

3. *Lama guanicoe* morphology

The guanaco shows no marked sexual dimorphism. In living populations it is only possible to identify the sex of individuals by observing their genitals or behavior (Franklin, 1983; Merino and Cajal, 1993). At an osteological level the absence of sexual dimorphism on the appendicular skeleton of this species was confirmed. In adult guanacos sexual dimorphism can only be determined by the size and shape of canines and pelvises (Kaufmann, 2009; Kaufmann and L'Heureux, 2009).

Guanaco is one of the largest and heaviest native wild terrestrial quadruped mammals in South America (Merino and Cajal, 1993). Individual weight varies according to the area and time of year of registration. On the Tierra del Fuego Island where the largest specimens occur, their weight ranges between 100 and 150 kg (Franklin and Fritz, 1991) with an average weight of 119.7 kg (Raedeke, 1976). In continental Chilean Patagonia, weight ranges between 100 and 120 kg (Franklin, 1982), and in continental Argentinean Patagonia females range between 75 and 120 kg (Sarasqueta, 2001). The records of the weights of the cattle at birth are also variable, ranging from 8 to 15 kg (Franklin, 1982) and 10 to 12 kg (Raedeke, 1976) for continental and insular Chilean Patagonia, respectively, or from 9.6 to 11 kg (Sarasqueta, 2001). This variability may be explained by differences in ecological and geographical factors where these populations were living (e.g., climate or vegetation), conditioning their physical status and nutritional level. Nutrition and genetics are considered to be the ultimate factors that influence the adult body size (Raedeke, 1979).

Body length recorded on the continent is 185 cm (excluding the tail), whereas it ranges between 188.4 cm and 191.5 cm on the Tierra del Fuego Island (Cabrera and Yepes, 1940; Raedeke, 1976). The shoulder height is 110–115 cm (Raedeke, 1979; Franklin, 1982) and the height of hind legs of Tierra del Fuego individuals is 51.2 cm for males and 50 cm for females (Raedeke, 1976). Prior studies have shown a chronological variation of the *Lama guanicoe* body size from 12 to 0.5 ka BP in continental Patagonia (L'Heureux, 2008, 2009).

4. Material and methods

Body size of guanaco's modern populations was inferred from long bones length. The osteological sample was composed by fully-fused individuals drawn from three different guanaco populations from continental and insular Patagonia (provinces of Rio Negro, Santa Cruz, and Tierra del Fuego; southern Argentina) covering the latitudinal interval between S40° and S54.5° (Fig. 1; Table 1). Samples were analyzed from:

- Rio Negro Province, northern Patagonia: Cinco Chañares (S40° 36', W65° 28'; Kaufmann, 2009);
- Santa Cruz Province, southern Patagonia: Belgrano lake (S47° 52′, W72° 08′), Cardiel lake (S48° 21′, W71° 11′), San Martin lake (S49° 06′, W72° 22′), Roca lake (S50° 33′, W72° 45′), Pali Aike Lava Field (S51° 35′, W69° 53′), and Gap canyon (S52° 07′, W68° 33′) (L'Heureux, 2008, 2009; L'Heureux and Borrero, 2002);
- Tierra del Fuego, insular Patagonia: Las Mandibulas lagoon (S53° 30′, W68° 31′), Estancia Maria Luisa (S54° 30′, W66° 17′), Valentin bay, Mitre peninsula (S54° 50′, W65° 30′), Estancia Remolino (S54° 51′, W67° 52′), and Cambaceres bay, Beagle Chanel (S54° 45′, W67° 18′) (Herrera, 1988; Vázquez, 2006).

The sample was collected between 2007 and 2010 during archaeological field works in Patagonia. Osteological collections held in museums of natural sciences of Argentina were also reviewed. A total sample of 110 MNI (Minimum number of individuals *sensu* Lyman, 2008) was studied. In all cases the carcasses were found incomplete and only the unweathered

Table 1
Environmental and ecological variables describing the three sampled province and biozone of Patagonia.

Sample origin	Latitude	Biozone	Temperature (Celsius)		Precipitation			Aerial net primary productivity (ANPP)
			Maximum	Minimum	Summer	Winter	Annual mean	
Rio Negro	S40°	Monte shrub steppe	40.4	−6.3	43.9	26.7	31.8	600
Santa Cruz	S48–52°	Grass steppe	29.7	−11.2	27.1	16.3	22.7	900
Tierra del Fuego	S53–54.5°	Forest-steppe ecotone	24.2	−7.0	38.9	18.0	30.6	1110

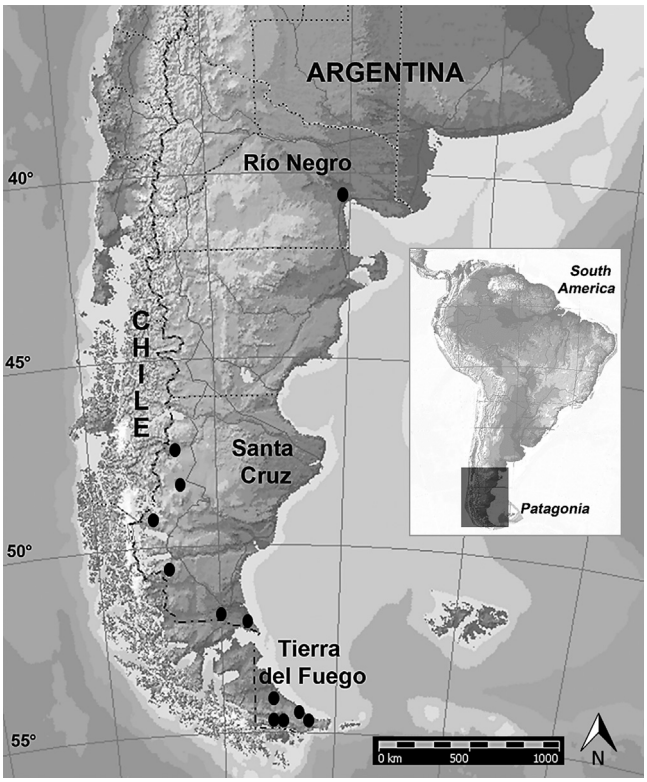

Fig. 1. Location of the guanaco samples from Rio Negro, Santa Cruz, and Tierra del Fuego (Patagonia, Argentina).

appendicular bones were collected (or with low stages of weathering; *sensu* Behrensmeyer, 1978). We do not know the exact cause of death of each individual, since they were collected in the field once dead, already skeletonized or in most cases with little tissue attached; although it is known that the causes of guanaco's death in southern Patagonia are varied and include poaching, entrapment in fences, heavy snow storms and very cold winters. For continental Patagonia the predation by pumas should also be considered (on the Tierra del Fuego Island there are no pumas). There are no statistics about this, and in the present work we assume that on average none of these causes of death predominates nor biases the study sample towards a particular type of animal (e.g., sick animals, etc.).

Sample controls were focused on preventing the morphological variation related with age. Sexual dimorphism was ruled out because it has been proven no such dimorphism occurs in the size and shape of the appendicular skeleton in this species (Kaufmann and L'Heureux, 2009). The age estimation was performed following the epiphyseal fusion schedule proposed by Kaufmann (2009) for guanaco populations of Rio Negro, Patagonia. All the bones analyzed in this study have completed their stages-fusion. Therefore the individuals analyzed had at least 36–48 months at the time of death and were adults (the guanaco tend to reach skeletal maturity at 36 months). Hence, there was no sex or age bias in this sample.

In this traditional osteometric study longitudinal and transverse ratio variables were measured with digital caliper (accuracy: 0.01 mm) and an osteometric board. All measurements were taken by a single individual (GLL). Four long bones were considered for analysis: the humerus (130 complete; 136 proximal epiphyses; 164 distal epiphyses), the metacarpals (112 complete; 128 proximal epiphyses; 112 distal epiphyses), the femora (103 complete; 119 proximal epiphyses; 124 distal epiphyses) and the metatarsals (81 complete; 86 proximal epiphyses; 84 distal epiphyses). Sample sizes for each bone (complete; distal epiphysis; proximal epiphysis) and for each region are given in Table 2. A set of measurements especially adapted to the anatomy of the guanaco was used (Fig. 2; L'Heureux, 2008) and obtained from different previous osteometric standards (Von den Driesch, 1976; Kent, 1982; Speth, 1983; Menegaz et al., 1988).

The resulting quantitative data was evaluated by province and latitude and analyzed with univariate and multivariate parametric statistical techniques (Principal Component Analysis and One-Way ANOVA). A post-hoc analysis was performed when necessary (Tukey test). The analyses were performed using raw data for each variable and the geometric mean (GM). The GM was considered as the best estimator of overall bone size. All analyses were performed with the software PAST v. 2.17 (Hammer et al., 2001) and SYSTAT 13. The type I error risk was set at 0.01 ($P < 0.01$) for statistical significance.

To determine whether the body size of guanaco varies in association with, or dependence of latitude, we evaluated bone size

Table 2
Descriptive summary statistics of Geometric Mean (GM) values for bones of the three sampled populations of guanacos. Data for complete humerus (HU), femur (FE), metacarpal (MC), and metatarsal (MT) bones and their proximal (PX) and distal (DS) epiphysis.

	HU	PX HU	DS HU	FE	PX FE	DS FE	MC	PX MC	DS MC	MT	PX MT	DS MT
Rio Negro												
Number of cases	38	40	43	36	43	43	38	40	40	34	34	34
Minimum	45.01	47.82	36.03	35.95	30.98	36.01	26.65	21.24	22.27	23.37	18.83	20.83
Maximum	51.38	57.11	41.32	43.12	38.02	43.45	30.21	25.12	25.07	26.46	21.78	23.43
Median	48.02	52.24	38.31	38.70	33.26	39.55	28.54	23.41	23.81	25.00	20.56	22.09
Std. Error	0.29	0.32	0.24	0.28	0.22	0.27	0.15	0.14	0.13	0.13	0.12	0.12
Std. Dev	1.77	2.05	1.56	1.66	1.44	1.75	0.89	0.89	0.81	0.78	0.70	0.71
Santa Cruz												
Number of cases	32	33	34	20	27	24	25	28	25	16	18	16
Minimum	46.85	50.36	37.46	38.01	31.38	38.60	28.19	23.15	23.40	24.54	19.84	21.72
Maximum	54.00	57.90	42.64	42.90	37.21	43.41	31.56	26.55	26.67	27.37	22.61	24.71
Median	49.43	53.61	39.87	40.66	34.68	41.35	29.92	24.92	25.04	26.27	21.68	23.14
Std. Error	0.37	0.38	0.27	0.28	0.32	0.24	0.21	0.19	0.18	0.22	0.20	0.21
Std. Dev	2.08	2.198	1.58	1.27	1.65	1.17	1.03	0.99	0.89	0.86	0.85	0.83
Tierra del Fuego												
Number of cases	60	63	87	47	49	57	49	60	47	31	34	34
Minimum	47.98	51.01	37.85	39.25	33.35	40.27	29.86	23.86	24.61	26.16	20.69	20.97
Maximum	54.68	59.45	45.20	44.73	37.82	46.70	34.01	29.81	28.32	28.45	23.75	25.86
Median	51.07	55.69	40.99	41.87	35.688	42.59	31.40	25.44	26.61	27.21	21.94	24.53
Std. Error	0.21	0.24	0.16	0.17	0.15	0.18	0.13	0.14	0.13	0.12	0.14	0.13
Std. Dev	1.66	1.88	1.48	1.19	1.05	1.37	0.87	1.11	0.90	0.65	0.79	0.75

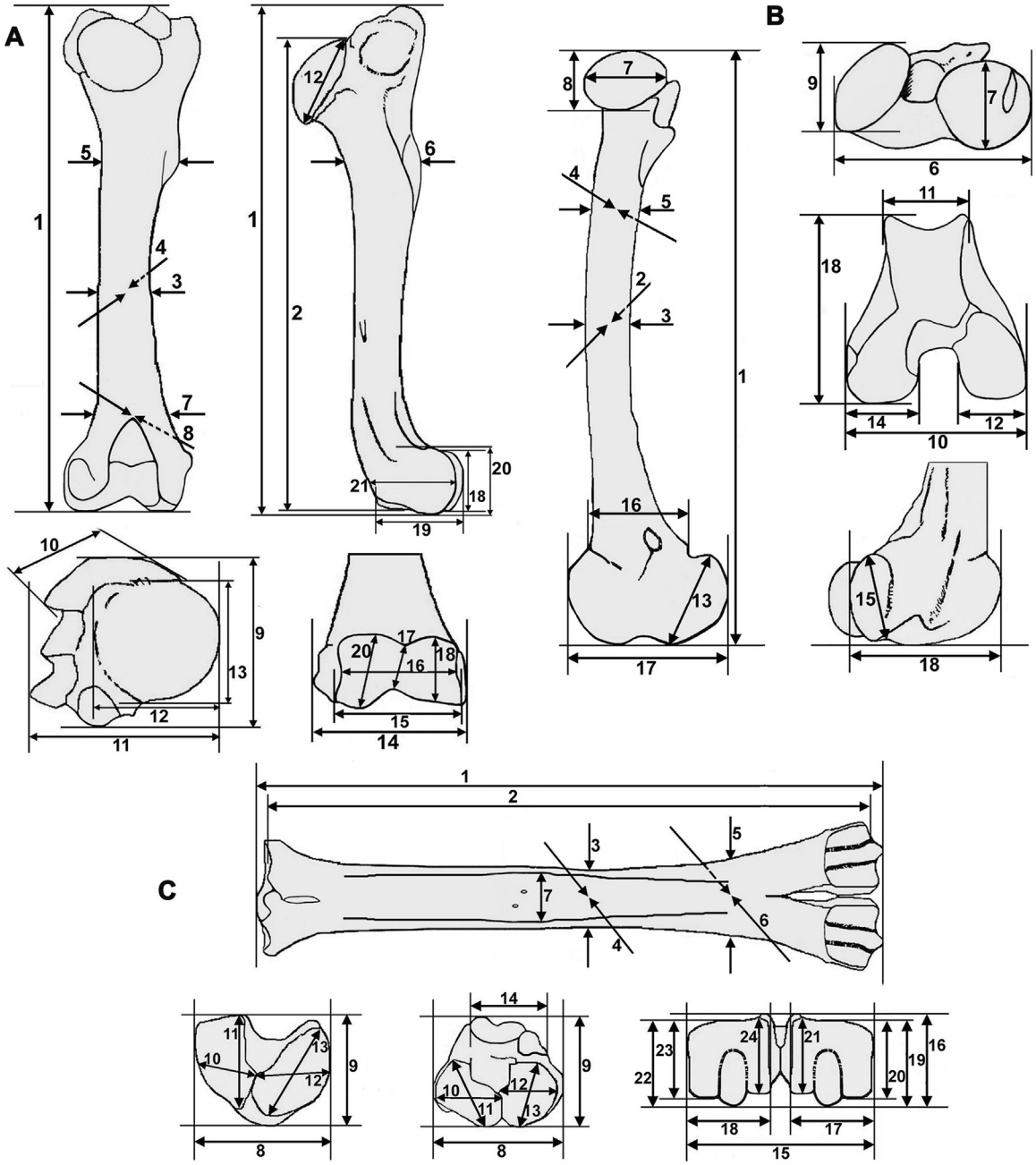

Fig. 2. Measurements obtained on humerus (**A**), femur (**B**), and metapodials (**C**). Measures for humerus (A): **1-**GL: Greatest length; **2-**GLC: Greatest length from caput (head); **3**-SD: Smallest breadth of diaphysis; **4-**DDm: Depth of the diaphysis; **5-**GBD: Greatest breadth of the diaphysis; **6-**GDD: Greatest depth of the diaphysis; **7-**BDd: Distal breadth of the diaphysis; **8-**DDd: (smallest) Depth of the distal diaphysis; **9-**Bp: (greatest) Breadth of the proximal epiphysis; **10-**GDT: Depth of greater (lateral) tuberosity; **11-**GDp: Greatest depth of the proximal epiphysis; **12-**DH: (greatest) Depth of head; **13-**BH: (greatest) Breadth of head; **14-**Bd: (greatest) Breadth of the distal epiphysis; **15-**BT: (greatest) Breadth of the trochlea; **16-**BT: (smallest) Breadth of the central trochlea; **17-**HTl: (smallest) Height of the central trochlea; **18-**HTm: Height of the (medial) trochlea; **19-**DTm: Depth of the (medial) trochlea; **20-**HTl: Height of the (lateral) trochlea; **21-**DTl: Depth of the (lateral) trochlea. Measures for femur (B): **1-**GL: Greatest length; **2-**GLC: Greatest length from the caput femoris (head); **3-**SD: Smallest breadth of diaphysis; **4-**SD: Smallest depth of the diaphysis; **5-**SBLtr: Smallest breadth of the diaphysis (bellow of lesser trochanter); **6-**DDLtr: Smallest depth of the diaphysis (bellow of lesser trochanter); **7-**Bp: (greatest) Breadth of proximal epiphysis; **8-**BHN: Breadth of head and neck; **9-**DC: (greatest) Depth of the caput femoris (head); **10-**GHH: Greatest height of the head; **11-**SDN: Smallest craniocaudal depth of neck; **12-**DGTr: Greatest craniocaudal depth of the greater trochanter; **13-**Bd: (greatest) Breadth of the distal epiphysis; **14-**GBT: Greatest breadth of the trochlea; **15-**GBmC: Greatest breadth of medial condyle; **16-**GLmC: Greatest length of the medial condyle; **17-**GBlC: Greatest breadth of lateral condyle; **18-**GLlC: Greatest length of lateral condyle; **19-**Dds: Depth of the distal metaphyseal; **20-**GDm: Greatest depth (medial) of the distal epiphysis; **21-**GDl: Greatest depth (lateral) of the distal epiphysis. Measures for metapodials (C): **1-**GL: Greatest length; **2-**GLl: Greatest length of the lateral part; **3-**SD: Smallest breadth of the diaphysis; **4-**DDm: Depth of the diaphysis; **5-**BDD: Breadth of the (distal) diaphysis; **6-**SDD: Smallest depth of the diaphysis; **7-**GBDG: Greatest breadth of the posterior groove of the diaphysis; **8-**Bp: (greatest) Breadth of the proximal epiphysis; **9-**Dp: (greatest) Depth of the proximal epiphysis; **10-**GBFl: Greatest breadth of the articular (lateral) facet; **11-**LFl: Greatest length of the articular (lateral) facet; **12-**GBFm: Greatest breadth of the articular (medial) facet; **13-**LFl: Greatest length of the articular (medial) facet; **14-**BPml: Breadth of the proximal (posterior) section of metatarsal; **15-**BDPp: Breadth of the proximal (posterior) process of metatarsal; **16-**LDPp: Length of the proximal (posterior) process of metatarsal; **17-**Bd: (greatest) Breadth of the distal epiphysis; **18-**GDp: Greatest depth of the distal epiphysis; **19-**WCM: Breadth of the medial condyle; **20-**WCL: Breadth of the lateral condyle; **21-**DVM: Depth of the (medial) sagittal ridge; **22-**DEM: Depth of the medial trochlea; **23-**DIM: (internal) Depth of the medial trochlea; **24-**DVM: Depth of the (lateral) sagittal ridge; **25-**DEL: Depth of the lateral trochlea; **26-**DIL: (internal) Depth of the lateral condyle.

according to different environmental and ecological variables related to each sampling area. Environmental variables studied were: (i) mean maximum and minimum temperatures, (ii) mean precipitation (summer/winter and annual), and (iii) aerial net primary productivity (ANPP) (Table 1). Temperature and precipitation data correspond to the period from 1987/1991 to 2007; they have been obtained from the National Weather Service of Argentina (http://www.smn.gov.ar). We used the climatic data from the weather station closest to the place where the samples were collected. The values of ANPP (kg/ha.year) were defined based on functional biozones of Patagonia *sensu* Paruelo et al. (1998). Analysis of association and dependence between guanaco body size and environmental variables was performed using the software SAM v4.0 (Spatial Analysis in Macroecology; Rangel et al., 2010).

5. Results

5.1. Latitudinal variation of guanaco bone size

For all bones (humerus, femur, metacarpal and metatarsal) the first principal component (PC) of the PCA reflected an ordering from smaller to bigger size of the Rio Negro's sample on the left (S40°) to the Tierra del Fuego's sample on the right (S53°–54.5°), in agreement with the latitudinal increase of the location of the guanaco samples (Fig. 3). This pattern was observed irrespective of the fact whether the whole bone or just the epiphyses were considered, but on the distal epiphysis this trend was even more remarkable. Humerus' variables with highest loading on the first PC were the 16, 15, 9, 2 and 1 (in decreasing loading order); for the distal femora they were 20, 21 and 18; for the distal metacarpal they were 21, 26, 23 and 24; and for the complete metatarsal they were 21, 24, 22 and 20 (Fig. 2). The first three components explain 71.59% of the total variation for the complete humerus, 88.95% for the distal femora, 90.12% for distal metacarpal, and 75% for the complete metatarsal.

From these results it is clear that *Lama guanicoe* displayed a great body size variability at both intrapopulational and intraspecific levels. In Fig. 3, an important superposition is observed in the distribution of bone sizes in the Santa Cruz sample (intermediate latitude) with the bones of the Rio Negro and the Island, meaning that in spite of marked clinal differences of sample averages, similar individual sizes can be found at different latitudes.

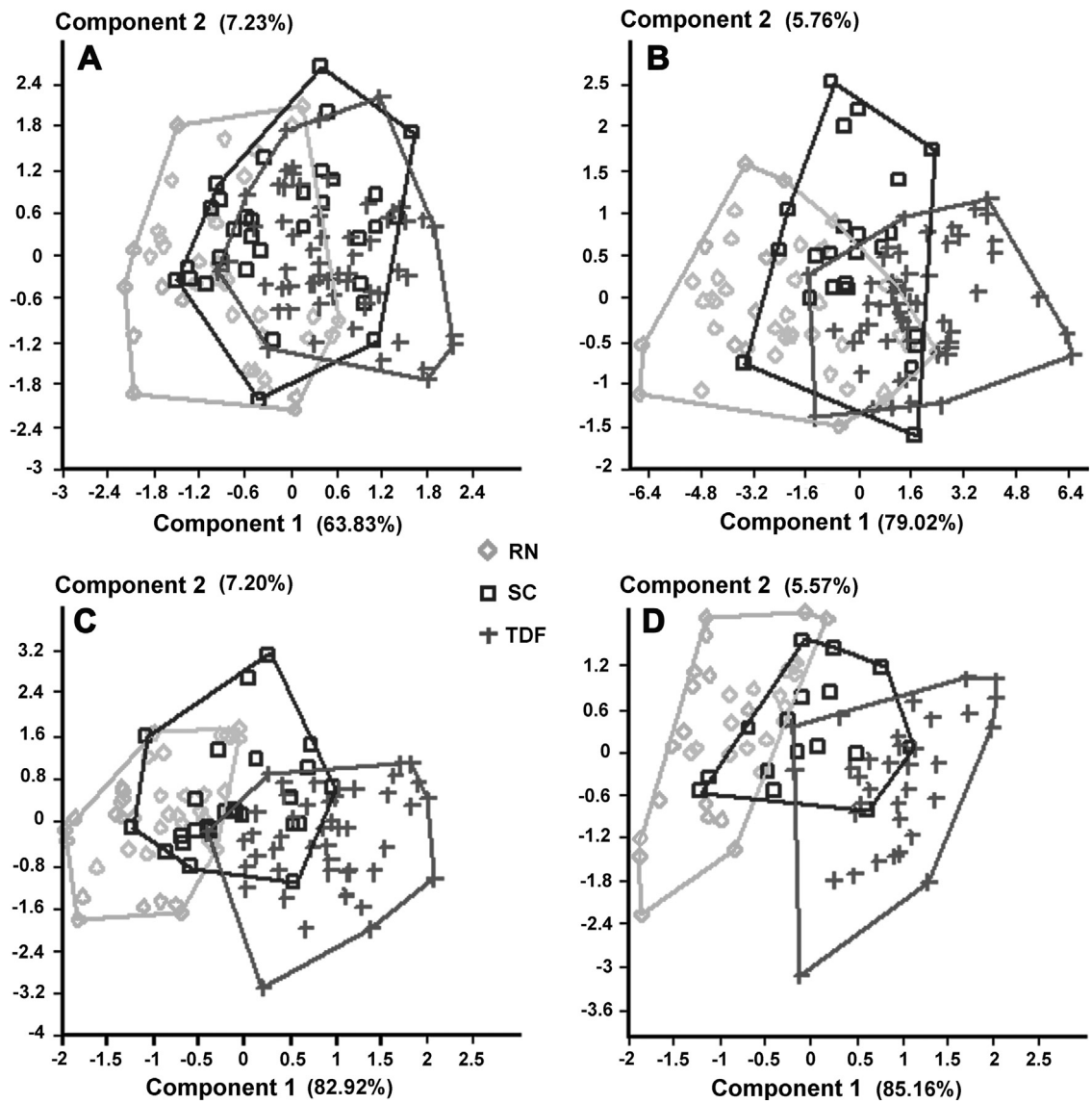

Fig. 3. PCA analysis performed on sizes of complete humerus (**A**; SEM = 0.088), distal femur (**B**; SEM = 0.09), distal metacarpal (**C**; SEM = 0.094), and complete metatarsal (**D**; SEM = 0.109). Percent values refer to the % of total variance explained by each Principal Component.

Table 3
Average Geometric Mean (GM) values for bones of the three sampled populations of guanacos. Data for complete humerus (HU), femur (FE), metacarpal (MC), and metatarsal (MT) bones and their proximal (PX) and distal (DS) epiphysis from Rio Negro (RN), Santa Cruz (SC), and Tierra del Fuego (TDF).

Humerus				
Sample	Latitude	Complete	PX	DS
RN	S40	48.07	51.85	38.50
SC	S48–52	50.10	54.07	40.05
TDF	S53–54.5	51.38	55.58	41.03
Femur				
Sample	Latitude	Complete	PX	DS
RN	S40	39.01	33.34	39.62
SC	S48–52	40.82	34.75	41.44
TDF	S53–54.5	42.01	35.69	42.92
Metacarpal				
Sample	Latitude	Complete	PX	DS
RN	S40	28.67	23.35	23.78
SC	S48–52	29.82	24.73	25.06
TDF	S53–54.5	31.42	25.58	26.54
Metatarsal				
Sample	Latitude	Complete	PX	DS
RN	S40	25.06	20.56	22.09
SC	S48–52	26.17	21.68	23.20
TDF	S53–54.5	27.24	22.15	24.48

We provide some basic summary statistics in Tables 2 and 3. An univariate statistical analysis was performed using the geometric mean (GM) of all measurements for each bone element to compare bone sizes among populations (Table 3). Complete bones and their epiphysis were evaluated using this procedure. The magnitude of the differences between the GM sizes was variable; in some elements it was greater than others (Table 3). The One-Way ANOVAs performed on the GM of each bone show significant statistical differences between samples (complete bones and their proximal and distal epiphyses; Table 4). Tuckey's post-hoc analyses show that significant differences ($P < 0.01$) take place between all three samples (Table 4), illustrating the same clinal variation from small (S40°) to large sizes (S53–54.5°) for both complete bones and their epiphyses (Fig. 4). The GM of bone sizes of Rio Negro are significantly smaller than the GM registered in the guanacos of Santa Cruz, which in turn displays GM values significantly smaller than those of Tierra del Fuego (Table 4).

5.2. Bone size, latitude, and environmental and ecological variables

The maximum temperature, the winter precipitation and ANPP significantly covary with latitude (Table 5). In contrast the mean values of summer precipitation and minimum temperatures are not associated with latitude in Patagonia.

The sizes of the humerus and femur are positively correlated with ANPP ($r = 1$) and negatively with the maximum temperature ($r = -0.99$) and winter precipitation ($r = -0.99$ for humerus; $r = -0.85$ for femur), these three correlations being statistically

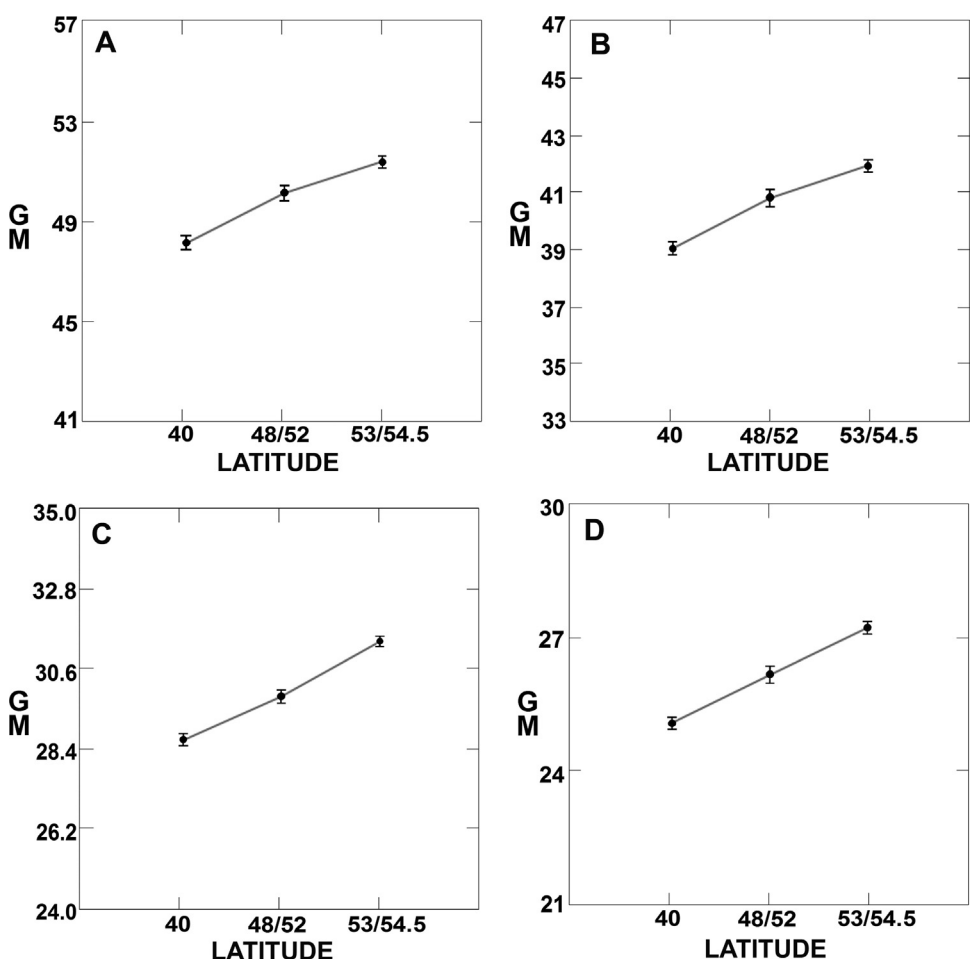

Fig. 4. Clinal size variations for Patagonian guanacos. Analyses performed on the average GM values of complete humerus (**A**), complete femur (**B**), complete metacarpal (**C**), and complete metatarsal (**D**). SEM values for each GM are provided in Table 2.

Table 4
One-Way ANOVAs performed on the GM values of each bone and associated post-hoc analyses. Bold values are statistically significant ($P < 0.01$). RN: Rio Negro; SC: Santa Cruz; TDF,:Tierra del Fuego.

	Analysis of Variance (ANOVA)				Tuckey's post-hoc			
Bone	Source	DF	F-Ratio	*P*-value		RN	SC	TDF
Complete Humerus	Latitude	2	39.372	< **0.001**	RN	–		
	Error	127			SC	< **0.001**	–	
					TDF	< **0.001**	**0.003**	–
Proximal Humerus	Latitude	2	41.935	< **0.001**	RN	–		
	Error	133			SC	< **0.001**	–	
					TDF	< **0.001**	**0.001**	–
Distal Humerus	Latitude	2	39.964	< **0.001**	RN	–		
	Error	161			SC	< **0.001**	–	
					TDF	< **0.001**	**0.005**	–
Complete Femur	Latitude	2	46.423	< **0.001**	RN	–		
	Error	100			SC	<< **0.001**	–	
					TDF	<< **0.001**	**0.007**	–
Proximal Femur	Latitude	2	35.74	< **0.001**	RN	–		
	Error	116			SC	<< **0.001**	–	
					TDF	<< **0.001**	**0.010**	–
Distal Femur	Latitude	2	58.734	< **0.001**	RN	–		
	Error	121			SC	<< **0.001**	–	
					TDF	<< **0.001**	< **0.001**	–
Complete Metacarpal	Latitude	2	97.913	< **0.001**	RN	–		
	Error	109			SC	< **0.001**	–	
					TDF	< **0.001**	< **0.001**	–
Proximal Metacarpal	Latitude	2	56.979	< **0.001**	RN	–		
	Error	125			SC	< **0.001**	–	
					TDF	< **0.001**	**0.001**	–
Distal Metacarpal	Latitude	2	110.45	< **0.001**	RN	–		
	Error	109			SC	< **0.001**	–	
					TDF	< **0.001**	< **0.001**	–
Complete Metatarsal	Latitude	2	68.488	< **0.001**	RN	–		
	Error	78			SC	< **0.001**	–	
					TDF	< **0.001**	< **0.001**	–
Proximal Metatarsal	Latitude	2	68.488	< **0.001**	RN	–		
	Error	78			SC	< **0.001**	–	
					TDF	< **0.001**	< **0.001**	–
Distal Metatarsal	Latitude	2	85.969	< **0.001**	RN	–		
	Error	81			SC	< **0.001**	–	
					TDF	< **0.001**	<**0.001**	–

significant ($P < 0.001$) (Fig. 5). There is a low and non-significant association between the sizes of the humerus and femur with the minimum temperatures ($r = -0.26$ for humerus; $r = -0.25$ for femur), the summer precipitation ($r = -0.5$ for humerus; $r = -0.24$ for femur), and annual precipitation ($r = -0.25$ for humerus; $r = -0.41$ for femur).

The sizes of the metacarpals and metatarsals are positively correlated with ANPP ($r = 0.98$ and 0.99 for metacarpal and metatarsal, respectively), and negatively with the maximum temperature ($r = -0.96$ and -0.98 for metacarpal and metatarsal, respectively). The size of the metapodial shows a lower and non-significant correlation with winter precipitation ($r = -0.72$ and -0.78 for metacarpal and metatarsal, respectively) (Fig. 6). There is a low association between metapodials and minimum temperatures ($r = -0.04$ and -0.14 for metacarpal and metatarsal, respectively), the summer precipitation ($r = -0.20$ and -0.30 for metacarpal and metatarsal, respectively), and annual precipitation ($r = -0.03$ and -0.13 for metacarpal and metatarsal, respectively).

Table 5
Pearson's correlation table and associated significance tests. Latitude *vs.* climatic and ecological variables: mean maximum and minimum temperatures (MAX T, MIN T), mean summer and winter precipitations (SUM P, WIN P), and aerial net primary productivity (ANPP). Bold values are statistically significant ($P < 0.05$).

Latitude *vs.*	Pearson *r*	*P*-value
MAX T	−1	< **0.001**
MIN T	−0.32	0.611
SUM P	−0.47	0.436
WIN P	−0.89	**0.049**
ANPP	1	< **0.001**

6. Discussion

The results obtained clearly show that the *Lama guanicoe* individuals from Tierra del Fuego (S53–54.5°) were on average bigger than those from Santa Cruz (S48–52°) and that, in turn, the latter were bigger than those from Rio Negro (S40°). Statistically, this latitudinal variation was significant for complete humerus, femora, metapodials and their epiphyses. This latitudinal gradient is, in appearance, consistent with the expectations derived from Bergmann's (1847) rule and in accordance with other studies indicating that more than half of the species studied so far follow this biogeographical rule (Ashton et al., 2000; Meiri et al., 2004; Lomolino et al., 2006; among others). The problem with Bergmann's rule is that we observe here a high and significant

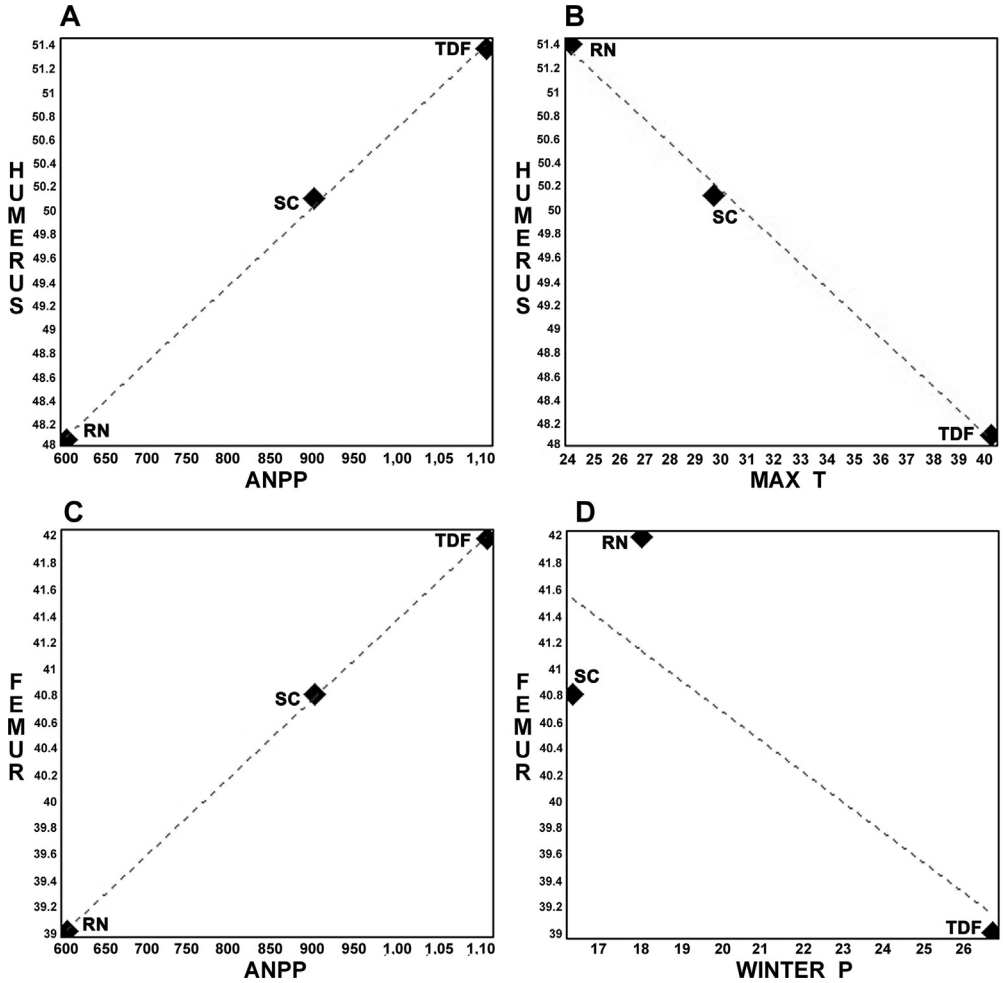

Fig. 5. Linear associations between body size of Patagonian guanacos and environmental variables. **A**: humerus on aerial net primary productivity; **B**: humerus on maximum temperature; **C**: femur on aerial net primary productivity; **D**: femur on winter precipitation.

covariation between different environmental variables that potentially influence body size (e.g., ANPP).

Latitude itself obviously does not influence body size, so the correlation between latitude and body size reflects selective forces that covary with latitude. Covariation between latitude and body size has been already associated with many factors that may explain this patterns: temperature, precipitation, environmental carrying capacity, net primary production during the growing season, duration of the annual productivity pulse, species richness, species density, predation, competition, and several combinations of them and others (Geist, 1987; Castro et al., 1992; Ashton et al., 2000; Meiri et al., 2004; Rodríguez et al., 2006; Yom-Tov and Geffen, 2006; Meiri and Thomas, 2007; Wolverton, 2008; Houston and Wolverton, 2011). From this point of view, we observe here that Patagonian guanaco body size records strong and significant correlations with maximum temperature, aerial net primary production, and winter precipitation, all these environmental factors covarying with latitude.

In the study area, other factors may account for part of the observed latitudinal differences, as genetic isolation in the southernmost insular environment after the opening of the Strait of Magellan during the Early Holocene (L'Heureux, 2005, 2008). It has been repeatedly shown that island mammals may have significantly different body sizes when compared to their continental counterparts (Foster, 1964; Heaney, 1978; Davis, 1983; Lomolino, 1985; Angerbjörn, 1986; Dayan and Simberloff, 1998; Lomolino et al., 2006), a biogeographic phenomenon named "the island rule" by Van Valen (1973). According to our results the latitudinal pattern observed for guanaco may also reflect the effects of insularity, with insular dwellers showing larger sizes than continental ones. In this way, the analysis of the geographical gradient of body size of guanacos in Patagonia may become more complex, and besides the Bergmann's rule, the current clinal pattern observed could be the result of different biogeographic processes (McCulloch et al., 1997; Rabassa et al., 2000; L'Heureux, 2005, 2007, 2008). Hence the traditional model of a linear relationship between body size and temperature becomes too simple. Bergmann's rule should be treated as a general empirical pattern and not as an exclusive explanation: it is a biogeographical "rule" that does not necessarily have to be invariably true (it is not a "law") and describes a common intraspecific size pattern in endotherms (Mayr, 1956; Dayan et al., 1991; Blackburn et al., 1999; Meiri, 2011; among others).

We conclude that the body size of guanacos in Patagonia may follow the principle of Bergmann's rule only from a discrete and synchronic point of view, and could be valid to explain the morphological pattern of modern guanacos only for continental Patagonia. However, if we consider different potential ecological drivers in addition to temperature, the aerial net primary productivity and winter precipitation appear to closely determine the latitudinal variations in guanaco body size. Last, when we analyze continental Patagonia and Tierra del Fuego Island altogether, the isolation process should also be considered.

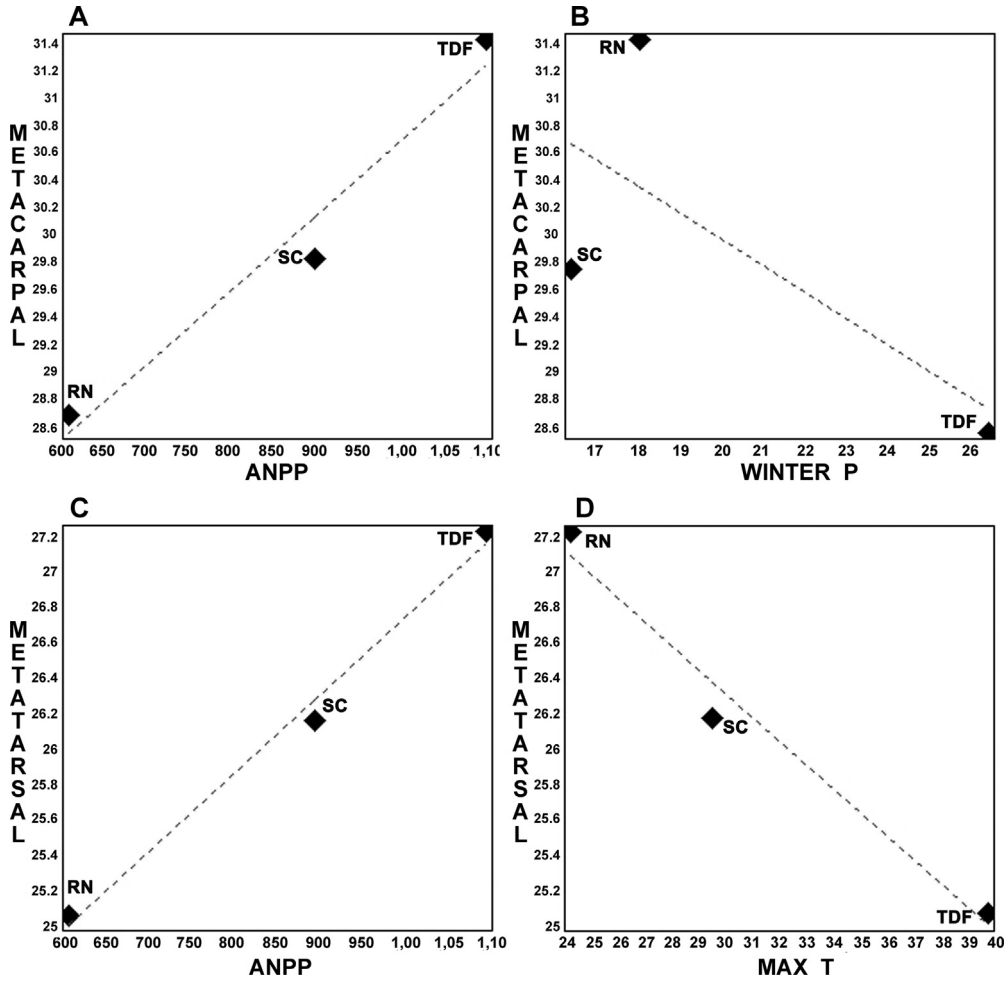

Fig. 6. Linear associations between body size of Patagonian guanacos and environmental variables. **A**: metacarpal on aerial net primary productivity; **B**: metacarpal on winter precipitation; **C**: metatarsal on aerial net primary productivity; **D**: metatarsal on maximum temperature.

Acknowledgements

We thank C. Kaufmann, J. Belardi, I. Cruz, N. Franco, E. Piana, L. Orquera and M. Vázquez for allowing us the access to their samples, and to R. Barberena, K. Borrazzo and L. Borrero for their efforts in collecting guanaco bones in the field. We thank also the INAPL and the Mastozoology Division (FCNyM, UNLP; Argentina) for research collaboration. We thank Dr. Katherine Moore and an anonymous reviewer for their comments. This study was supported by National Agency for Science and Technology Promotion (ANPCyT) PICT No. 2046 directed by Luis A. Borrero, and for National Research Council of Argentina (CONICET), PIP No. 0083 directed by G. Lorena L'Heureux.

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