

## Scorpion diversity of the Central Andes in Argentina

**F. Fernández Campón, S. Lagos Silnik and L. A. Fedeli:** Laboratorio de Entomología, IADIZA - CONICET,  
CCT Mendoza, Av. Ruiz Leal s/n, Parque Gral. San Martín, Mendoza (5500), Argentina. E-mail:  
fcampón@mendoza-conicet.gov.ar

**Abstract.** Mountain habitats host a large number of endemic species, which are vulnerable to climate change. We studied scorpion communities of the Central Andes in Argentina at 17 sites located in Andean and extra-Andean areas between 900 and 3400 m elevation. Using pitfall traps, we collected 254 individuals from seven species, all from the Bothriuridae family. Although we expected a decrease in richness towards the high altitude sites, we did not find a clear pattern. In turn, the lowest site was the most diverse and rich; other sites had similar richness values regardless of altitude. High-altitude sites were characterized by the presence of *Orobothriurus* Maury 1975 species. *Orobothriurus alticola* (Pocock 1899) has been found exclusively on Andean sites located above 3200 m, and *O. grismadoi* Ojanguren-Affilastro et al. 2009 has only been found at extra-Andean sites on Cerro Nevado. Community composition showed an association with altitude, with some species exclusive to high altitude sites and others only found at lower sites. Because of the ecological importance of scorpions in arid environments, this study provides base information that may help design conservation actions for these habitats. In particular, the presence of high-altitude specialists like *Orobothriurus* species seems relevant, since they may be used as bioindicator species.

**Keywords:** Altitude, mountains, community, species richness

Approximately one fourth of the Earth's surface is covered with mountains. Mountain habitats support a third of the plant diversity (and probably a similar proportion of animal species) and supply half of the drinking water for human populations (Körner 2007). Given the particular conditions of climate and isolation prevailing in mountains, these habitats can be hotspots of diversity (Lomolino 2001; Prendini & Bird 2008) and usually host a large number of endemic species (Prendini & Bird 2008; Flores & Pizarro-Araya 2006; Roig-Juñent et al. 2008).

Altitude is a variable that is frequently related to changes in species richness and community composition (Brown 1995). However, altitude per se does not necessarily have an effect on species distribution. Environmental variables that change with altitude may have an effect on community composition. Mountain areas are characterized by a decrease in richness and abundance as altitude increases (e.g., Prendini & Bird 2008; Munyai & Foord 2012; Salas-Morales & Meave 2012), though the highest richness and abundance might not be found at the lowest but at intermediate altitudes (Lomolino 2001; Munyai & Foord 2012).

The Central Andes in Argentina comprise the arid part of the Andes range. Within this area of the Andes we can find different biomes associated with differences in altitude, soil and history, which in turn cause differences in species richness and biodiversity and high levels of endemism (Flores & Pizarro-Araya 2004; Augusto et al. 2006; Ochoa et al. 2011). This is particularly true for some groups adapted to arid conditions, such as insects (Tenebrionidae: Coleoptera), which are very rich and diverse in this part of the Andes (Flores & Pizarro-Araya 2004; Flores & Gómez 2005). These Andean habitats are also important water reservoirs; snowpacks accumulated in the mountains are the main source of rivers that water the lowlands (Masiokas et al. 2006). In addition, altitude makes these habitats very susceptible to global climate changes and intense exploitation of natural resources (e.g., mining). An increase in global temperature will cause high-altitude habitats to shrink

their area, with the possibility of local extinction of species adapted to these types of habitats. Despite its relevance for diversity conservation, there is little knowledge of the arthropod fauna of this area. Thus, a first step towards conservation of the area and its wildlife is to know the composition and distribution pattern of its communities.

Among arthropods, scorpions are important due to their abundance in arid regions. Recent studies suggest that, in certain arid areas of the world, scorpions are the major group of predators in terms of density, biomass and diversity (Polis 1990). Being generalist predators, they have a fundamental role in the structure of communities (Polis 1990).

Although scorpions have been reported to occur in high-altitude regions up to 4900 m (Ochoa et al. 2011), no community studies have been conducted for these habitats in South America. Added to the fact that high-altitude species are more at risk under a climate change scenario, this highlights the importance of such studies in high-altitude areas. The aim of our study was to describe the scorpion community in mountain habitats of the Central Andes and analyze its composition in relation to environmental variables associated with altitude.

### METHODS

**Study area.**—The study was carried out at 17 sites within an area that includes Andean as well as extra-Andean sites (i.e., Cerro Nevado) (Table 1). Sites located at different altitudes contain different habitat types (Fig. 1, Table 1). The Monte is characterized by shrubby vegetation dominated by creosote bush (*Larrea divaricata* and *L. cuneifolia*). The pre-Puna or “cardonal” extends onto the hillsides and canyons and supports many of the species of the Monte plus some endemic grasses, cacti and legumes. The Puna lies above 2800 m elevation and is characterized by a dry shrubby steppe with small shrub species not exceeding 40–150 cm. High-altitude grasslands occur at 1900–2500 m and are dominated by species such as *Stipa tenuissima* that occupy large areas called

Table 1.—Location and description of the study sites. Altitude is an average of the four altitudes registered in each sampling period.

Site	Code	Altitude (m.a.s.l.)	Habitat type
Villavicencio (Road 52)	N1	1000	Monte
Villavicencio	N2	1700	Prepuna
Paramillos	N3	2850	Puna
Pampa Canota	N4	2800	Altitude grassland
Estancia Tambillos	N5	2400	Monte
Puntas de Vacas	N6	2400	2nd altoandino
Horcones	N7	2900	2nd altoandino
Las Cuevas	N8	3200	2nd altoandino
Alvarado (Northen slope)	S1	2300	2nd altoandino
Alvarado (Southern slope)	S2	2300	2nd altoandino
Pampa de los Avestruces	S3	3570	3rd altoandino
Reserva Laguna del Diamante	S4	3350	2nd altoandino
Laguna del Diamante	S5	3300	2nd altoandino
Cerro Nevado	Ne1	2350	Patagonian steppe
Cerro Nevado	Ne2	2600	2nd altoandino
Cerro Nevado	Ne3	2950	2nd altoandino
Cerro Nevado	Ne4	3100	3rd altoandino

“pampas”. Andean highlands (Altoandina region) are characterized by low-growing plants and large areas of bare soil. The vegetation layer is dominated by shrubs of the genus *Adesmia* (Cabrera 1971).

**Sampling design.**—We sampled scorpions for two consecutive years during the austral spring and summer (December 2004 and February 2005, January 2005 and February 2006), which is the time of the year when epigean arthropods are active at all sites. We set up two altitudinal transects running up the Andes range (north transect: sites N1–N8 and south transect: sites S1–S5; at 33° and 35° S latitude respectively). Sites along the transects were selected in order to have representatives of those habitat types found in mountain areas at these latitudes. In addition, a third extra-Andean transect was sampled from the base up to the summit of Cerro Nevado mountain (sites Ne1–Ne4; Fig. 1) to examine historical differences of the Andes range. Each transect followed an altitudinal gradient including different habitat types. At each site, we randomly set up eight 1×1 m quadrats with a pitfall trap at each corner and left them at the site for 10 days. For data analysis the four traps in each quadrat were pooled. Pitfall traps were plastic cups of 10 cm diameter filled with 100 ml of a 20% propylene glycol solution. Keeping the same sampling techniques in all sites (pitfall traps) enabled us to compare sites in terms of abundance.

Scorpions were identified using the keys to genera and species by Ojanguren-Affilastro (2005) and a reference collection provided by the same author. Collected specimens were preserved in 70% ethanol and, after identification, were deposited in the permanent Arachnology Collection at the Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA – CONICET, CAI).

**Statistical analyses.**—To explore the relationship between species and environmental variables, a Canonical Correspondence Analysis (CCA) was applied to data from sampling sites. Data on species density and environmental variables were transformed by applying  $\ln(x+1)$ . Explanatory variables included in the models were related to temperature and precipitation, and were obtained from WorldClim version 1.4 (Hijmans et al. 2005). The spatial resolution of the climatic

data is 30 s (approximately 1 km<sup>2</sup>). Thus, the values are the same for all quadrats within a locality at each sampling period. Variables related to productivity (NDVI) were obtained from NASA (NASA 2001, online at [http://lpdaac.usgs.gov/get\\_data](http://lpdaac.usgs.gov/get_data)). These variables are shown in Appendix 1. Prior to the CCA, Spearman correlation analysis was performed among environmental variables to test whether there was a high level of correlation between them. Variables showing a correlation  $P > 0.60$  were excluded from the analysis. CCA was performed using the analytical software MVSP version 3.1.

## RESULTS

We collected 254 individuals (north: 116; south: 103; extra-Andean: 35), all belonging to the Bothriuridae family. No scorpions were caught in pitfall traps at sites N3 and S5. Thus, these sites were excluded from the analyses. The most abundant genus (38%) was *Orobothriurus* Maury 1975, followed by *Brachistosternus* (Pocock 1893) (29%), then *Bothriurus* Peters 1861 (22%) with only one species (*B. burmeisteri* Kraepelin 1894), and *Timogenes* Simon 1880 (11%). At the specific level, the most abundant species were *Orobothriurus alticola* (Pocock 1899) (28%), most abundant at sites located above 3000 m elevation, and *Brachistosternus weissenberghi* (Thorell 1876) (27%) (Table 2). They were followed by *Bothriurus burmeisteri*, a species present on most of the sites (22%), *Orobothriurus grismadoi* Ojanguren-Affilastro et al. 2009 (10%), *Timogenes elegans* (Mello-Leitão 1931) (7%), and *T. haplochirius* Maury & Roig Alsina 1977 (4%) [the last two species were only found at the lower Monte site (N1)], and *Brachistosternus montanus* Roig Alsina 1977 (2%). Diversity and evenness were higher at N1 and N6 and were zero at sites with only one species present, such as N8 and S4 with *O. alticola*, and S1 with *Bothriurus burmeisteri* (Table 2).

In the CCA, the first two axes explained 69.36% of the cumulative variance, suggesting a good relationship between species distribution and the environmental variables considered. Figure 2 shows the distribution of the sites and species within the environmental space delimited by axes 1 and 2. Variables that significantly positively correlated with

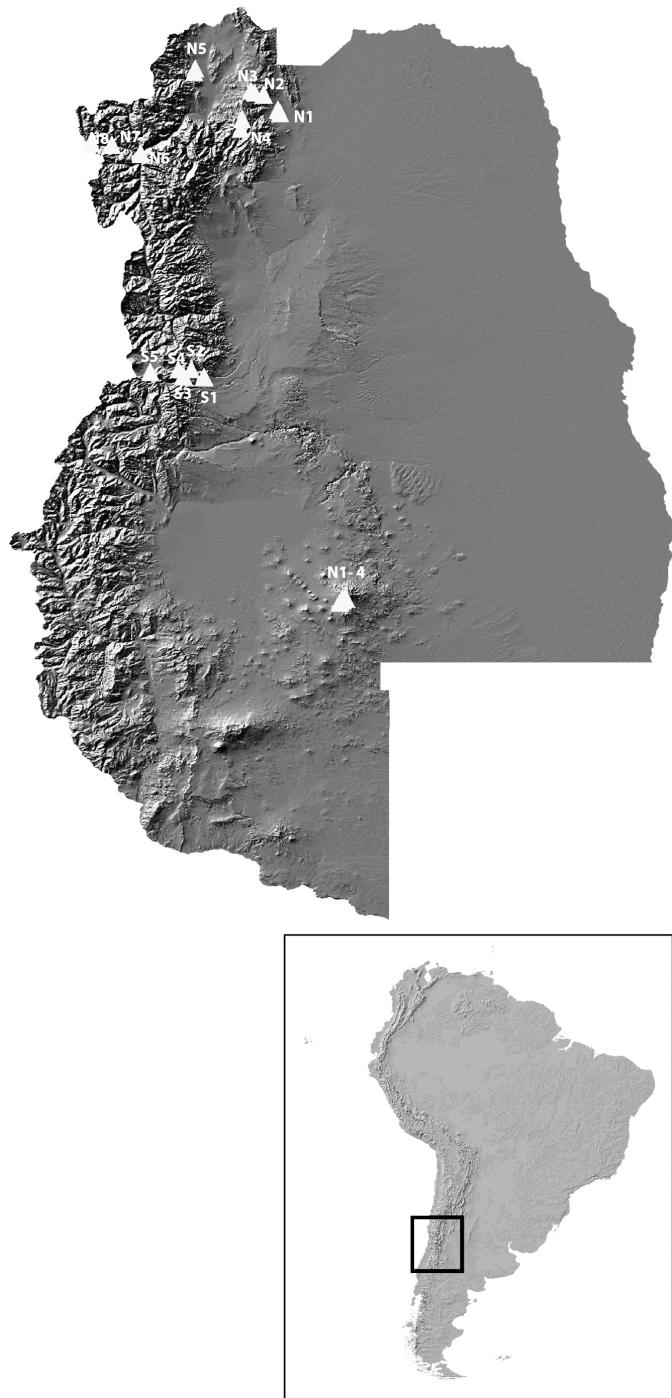


Figure 1.—Maps of Mendoza province (top) indicating the locations of the study sites within transects, and of South America (bottom) showing the location of Mendoza province.

environmental axis 1 ( $r > 0.50$ ) were isothermality and precipitation in the coldest quarter (snow) of the year, whereas seasonality in temperature and average annual productivity were negatively correlated with this axis. The variables that correlated positively with axis 2 were seasonality in temperature and precipitation in the warmest quarter (rain), whereas precipitation in the coldest quarter and isothermality showed a negative correlation with this axis.

In Fig. 2 we can identify four groups of species. Two of these groups include one of the two species of *Orobothriurus*. Both species of *Orobothriurus* are found at high altitudes (above 2300 m in Cerro Nevado and above 3200 m in the Andes). However, the sites where they were recorded appear in different parts of the environmental space. In fact, all sites on Cerro Nevado (Ne1–4) form a distinct group clustering around *O. grismadoi*. From Fig. 2 we can see that these sites are less thermally stable than those at the cordillera (S3 and S4) and receive less snow during the winter as well. The third group in the plot includes both *Timogenes* species. These are only found at site N1 (Table 2). This site is within the Monte desert biome and based on the environmental space of the plot in Fig. 2, it has high rainfall during the warmest quarter, it is thermally seasonal and has high minimum temperatures during the coldest month compared to the other sites. Finally, in the fourth group *Brachistosternus* and *Bothriurus* species were present at most locations. They appear in the center of the environmental space, probably indicating their widespread distribution at the study sites.

The plot of altitudinal range reinforces results from previous analyses (Fig. 3). It shows the presence of altitude specialists with a narrow altitudinal range at high altitude (both *Orobothriurus* species) and at low altitude (*Timogenes* species). In addition, there are some generalists such as *Bothriurus* sp. and *Brachistosternus weijenberghi* with a wide altitudinal range.

## DISCUSSION

Despite the importance of mountain areas due to their sensitivity to climate changes and their biodiversity value (e.g., endemisms), there are few studies on scorpion communities in these types of habitats (Prendini & Bird 2008). Without taking into account sites of very high scorpion richness and abundance, such as Baja California Peninsula, Mexico (Jiménez-Jiménez & Palacios-Cardiel 2010), and several sites in southern Africa (e.g., Prendini & Bird 2008), richness values found in our study are similar to those obtained for other arid regions of South America. Augusto et al. (2006) reported nine species (maximum richness of three at a site) in a study involving a latitudinal transect in Chile; Acosta (1995) found nine sympatric species in Chancani (Cordoba, Argentina); and Ochoa (2005) reported 24 species in his study area covering a mosaic of biomes in the Peruvian Andes, and a highest richness of six in some dry habitats (Lomas, Serranía esteparia, Queswa).

Comparing community composition of scorpions in our study with that of other studies in South America such as Ochoa's study (2005) of the Andes of Peru, we find certain differences in dominance of the genera found. Although Ochoa (2005) presents data on species occurrence and not on abundance, it is possible to make some comparisons. Within his study area, almost 80% of the species ( $n = 19$ ) belonged to the family Bothriuridae and among those, *Brachistosternus* was the most dominant genus with 10 species present in all habitats except in the Yungas (the only mesic habitat found in his study). Among them, three species of *Brachistosternus* occur in a narrow altitudinal belt at high altitude (above 2900 m). In our study, *Br. montanus* belongs to this group (Andean group in Ojanguren-Affilastro & Ramírez 2009) but

Table 2.—Species frequencies and ecological indices estimated for the study sites. *Bb*: *Bothriurus burmeisteri*; *Brw*: *Brachistosternus weijenberghi*; *Brm*: *Brachistosternus montanus*; *Te*: *Timogenes elegans*; *Th*: *Timogenes haplochirius*; *Oa*: *Orobothriurus alticola*; *Og*: *Orobothriurus grismadoi*. In parentheses we show the abundance of females plus juveniles and males. Females and juveniles are shown together because they could not be distinguished according to Ojanguren-Affilastro (2005).

Site	<i>Bb</i>	<i>Brw</i>	<i>Brm</i>	<i>Te</i>	<i>Th</i>	<i>Oa</i>	<i>Og</i>	Total abundance	Relative abundance	Shannon's index	Evenness
N1	7 (1,6)	21 (16,5)	0	18 (4,14)	9 (9,0)	0	0	55	0.22	1.29	0.54
N2	4 (2,2)	3 (3,0)	0	0	0	0	0	7	0.03	0.68	0.28
N3	0	0	0	0	0	0	0	0	0.00	0.00	0.00
N4	1 (0,1)	1 (0,1)	0	0	0	0	0	2	0.01	0.69	0.29
N5	2 (1,1)	36 (30,6)	0	0	0	0	0	38	0.15	0.21	0.29
N6	1 (1,0)	4 (4,0)	2 (2,0)	0	0	0	0	7	0.03	0.96	0.04
N7	3 (2,1)	3 (3,0)	0	0	0	0	0	6	0.02	0.69	0.29
N8	0	0	0	0	0	1 (1, 0)	0	1	0.00	0.00	0.00
S1	13 (12,1)	0	0	0	0	0	0	13	0.05	0.00	0.00
S2	14 (4,10)	0	3 (0,3)	0	0	0	0	17	0.07	0.47	0.19
S3	1 (1,0)	2 (2,0)	0	0	0	17 (10,7)	0	20	0.08	0.52	0.22
S4	0	0	0	0	0	53 (4,49)	0	53	0.21	0.00	0.00
S5	0	0	0	0	0	0	0	0	0.00	0.00	0.00
Ne1	5 (1,4)	0	0	0	0	0	5 (3,2)	10	0.04	0.69	0.29
Ne2	1 (1,0)	0	0	0	0	0	1 (1,0)	2	0.01	0.33	0.14
Ne3	1 (0,1)	0	0	0	0	0	9 (2,7)	10	0.04	0.54	0.22
Ne4	3 (2,1)	0	0	0	0	0	10 (7,3)	13	0.05	0.69	0.29

we found it in very low abundances. It is the *Orobothriurus* species that seems to mostly occupy the highest altitudinal sites in our study. In Ochoa's study, *Orobothriurus* was the second most important genus with six species. *Orobothriurus* occurred at all sites with the highest richness (six). However, no more than one species of *Orobothriurus* occurred at any one particular site. In our study we also found only one species of *Orobothriurus* in the sites where the genus occurs, but they were only present at high altitude sites (Table 2). *Orobothriurus grismadoi* seems to be a habitat specialist found only in Altoandina vegetation of this mountain. The narrow distribution area of *O. grismadoi* (only in Cerro Nevado) is probably due to historical factors that isolated it from other mountain areas where related species of *Orobothriurus* occur (Ochoa et al. 2011). This makes *O. grismadoi* very vulnerable under a climate change scenario, with an increase in temperature leading to a potential shrinkage of suitable habitat. In fact, Cerro Nevado is known to have other endemic species of high-altitude arthropods (e.g., carabid beetles, Roig-Juñent et al. 2008), with closely related species found at high-altitude locations in the Andes range (Roig-Juñent et al. 2007).

Most species of the genus *Orobothriurus* are found primarily in high-altitude habitats (over 2000–2500 m, with a maximum recorded at 4190 m) from Central Peru to Argentina (Mattoni et al. 2012). With the exception of *O. alticola*, which is found in the Andes range, the remaining three species of *Orobothriurus* from Argentina (*O. compagnucci* Ochoa et al. 2011; *O. famatina* Acosta & Ochoa 2001; *O. calchaqui* Ochoa et al. 2011) exhibit a narrow distribution and have been recorded so far only at their type localities in extra-Andean mountains (Ochoa et al. 2011).

The second most important genus in abundance following *Orobothriurus* was *Brachistosternus*. This genus showed high abundances at lower sites, but specifically at those sites belonging to the Monte habitat. This happened at both the lower Monte (N1, 1000 m) as well as in the high-altitude

Monte (N5, 2400 m), suggesting that despite differences in environmental conditions between these two sites, certain characteristics of the Monte habitat are suitable for the species. All described species of *Brachistosternus* are known from arid and semi-arid regions in South America, from southern Patagonia to central Ecuador. Within the subgenus *Brachistosternus* there are two monophyletic groups: Andean and Plains groups (Ojanguren-Affilastro & Ramírez 2009). In our study, *Br. weijenberghi* (Plains group) was much more abundant than *Br. montanus*, which was found in very low abundances along both the northern and southern transects and in sympatry with *Bothriurus burmeisteri* (N6 and S2) and *Br. weijenberghi* (N6). Finally, the third most important genus was *Bothriurus*. Although this is one of the most diverse genera within Bothriuridae (Ojanguren-Affilastro 2005), it was only represented by a single species, *B. burmeisteri*. This species has a widespread distribution in Argentina from the central part of the country to the southern tip in Patagonia, and probably also in Tierra del Fuego, inhabiting the phytogeographic areas of Monte, Patagonia and Espinal (Ojanguren-Affilastro 2005).

Based on the pattern of abundance of these genera, it seems that there is a change in dominance depending on altitude (and habitat type): while at high sites (Altoandina region) *Orobothriurus* dominates, *Brachistosternus* is the most dominant genus at lower sites, at least in the Monte habitat. This does not mirror the altitudinal range pattern of the species (Fig. 3). Although *Br. weijenberghi* has high abundances at lower sites, it also occurs in low abundance even at our highest site (S3). *Orobothriurus*, on the other hand, have a range restricted to high-altitude sites.

This is the first study on scorpion communities from the South American Andes inhabiting a vulnerable area under threat from climate change. Because of the ecological importance of scorpions in arid environments (Polis 1990), this study provides base information that will serve to monitor these habitats. In particular, the presence of high-altitude

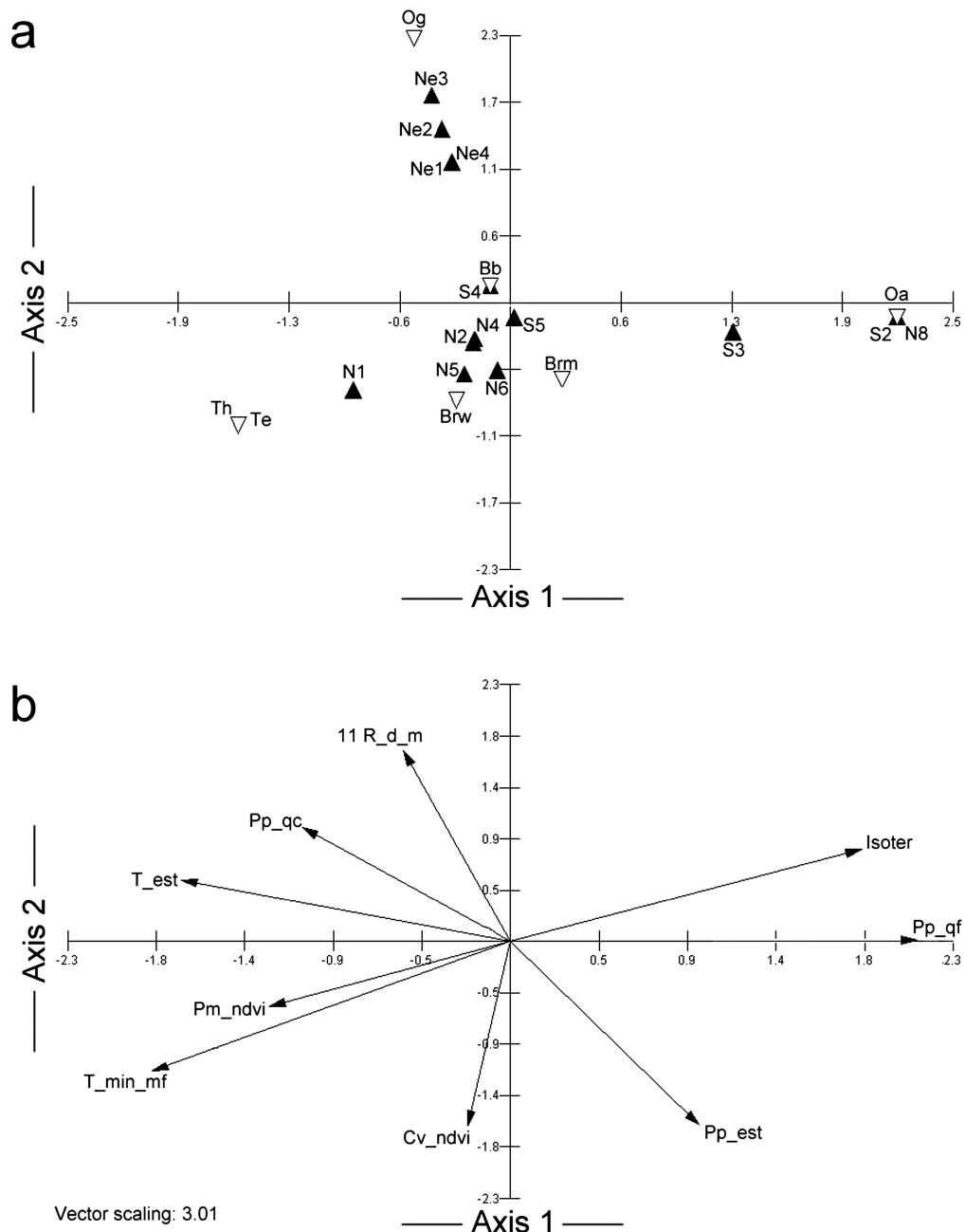


Figure 2.—CCA plot of species and sites (a) and environmental variables (b). Refer to Table 2 for species abbreviations and to Appendix 1 for abbreviations of environmental variables.

specialists, such as species of the genus *Orobothriurus*, seems to be relevant as they would be suitable for this purpose.

#### ACKNOWLEDGMENTS

We want to thank Dr. Andrés Ojanguren-Affilastro (MACN) for providing us with a reference collection and Dr. Rodolfo Carrara (IADIZA) for facilitating data on WorldClim variables for the study sites. This study was part of a larger project on arthropod diversity from mountain areas of central-west Argentina carried out by personnel from the Entomology Laboratory at IADIZA, CCT-Mendoza. Thus, work in the field and sample processing was a team effort. This study was

supported by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina, by a grant of the Agencia Nacional de Promoción Científica y Tecnológica (ANPCYT), Argentina (“Diversidad de artrópodos en ambientes montanos del centro-oeste argentino”, PICT 01-11.120).

#### LITERATURE CITED

- Acosta, L.E. 1995. The scorpions of the Argentinian western Chaco. I. Diversity and distributional patterns. Biogeographica 71:49–59.
- Augusto, P., C.I. Mattoni, J. Pizarro-Araya, J. Cepeda-Pizarro & F. López-Cortés. 2006. Comunidades de escorpiones (Arachnida:

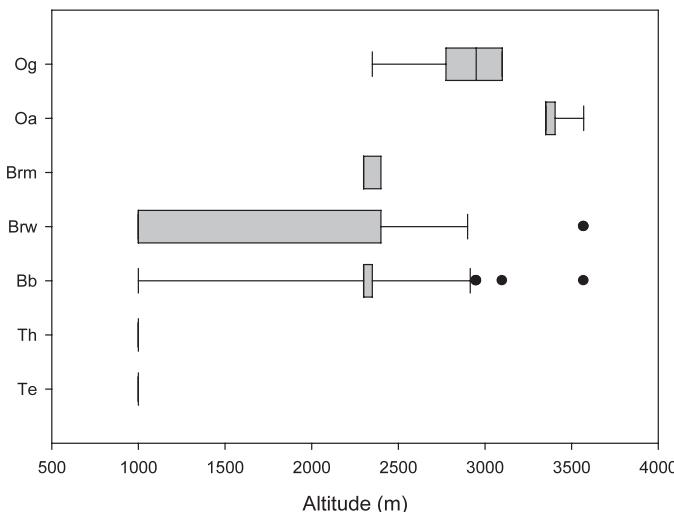


Figure 3.—Boxplot of the altitude range of the seven species of scorpions found in the study. The central line within the box represents the median abundance for the species, the box represents the inter-quartile range, and the lines are 1.5 times the interquartile range; black dots are outliers. Bb: *Bothriurus burmeisteri*; Brw: *Brachistosternus weissenberghi*; Brm: *Brachistosternus montanus*; Te: *Timogenes elegans*; Th: *Timogenes haplochirus*; Oa: *Orobothriurus alticola*; Og: *Orobothriurus grismadoi*.

- Scorpiones) del desierto costero transicional de Chile. Revista Chilena de Historia Natural 79:407–421.
- Brown, J.H. 1995. Macroecology. University of Chicago Press, Chicago, Illinois.
- Cabrera, Á.L. 1971. Fitogeografía de la República Argentina. Boletín de la Sociedad Argentina de Botánica 14:1–42.
- Flores, G.E. & R.S. Gómez. 2005. Taxonomía y biogeografía de cuatro especies de *Psectrascelis* (Coleoptera: Tenebrionidae) de la Precordillera y Cordillera de los Andes en Mendoza, Argentina. Revista de la Sociedad Entomológica Argentina 64:93–106.
- Flores, G.E. & J. Pizarro-Araya. 2004. *Caenocrypticoides triplehorni* new species, the first record of Caenocrypticini (Coleoptera: Tenebrionidae) in Argentina, with cladistic analysis of the genus. Annales Zoologici 54:721–728.
- Flores, G.E. & J. Pizarro-Araya. 2006. The Andes mountain range uplift as a vicariant event in the Pimeliinae (Coleoptera: Tenebrionidae) in southern South America. Cahiers Scientifiques (Muséum d'Histoire Naturelle, Lyon) 10:95–102.
- Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones & A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.
- Jiménez-Jiménez, M.L. & C. Palacios-Cardiell. 2010. Scorpions of desert oases in the southern Baja California Peninsula. Journal of Arid Environments 74:70–74.

- Körner, C. 2007. The use of altitude in ecological research. Trends in Ecology and Evolution 22:569–574.
- Lomolino, M.V. 2001. Elevation gradients of species-density: historical and prospective views. Global Ecology and Biogeography 10:3–13.
- Masiokas, M.H., R. Villalba, B.H. Luckman, C. Le Quesne & J.C. Aravena. 2006. Snowpack variations in the central Andes of Argentina and Chile, 1951–2005: Large-scale atmospheric influences and implications for water resources in the region. Journal of Climate 19:6334–6352.
- Mattoni, C.I., J.A. Ochoa, A.A. Ojanguren-Affilastro & L. Prendini. 2012. *Orobothriurus* (Scorpiones: Bothriuridae) phylogeny, Andean biogeography, and the relative importance of genitalic and somatic characters. Zoologica Scripta 41:160–176.
- Munyai, T.C. & S.H. Foord. 2012. Ants on a mountain: spatial, environmental and habitat associations along an altitudinal transect in a centre of endemism. Journal of Insect Conservation 16:677–695.
- NASA Land Processes Distributed Active Archive Center (LP DAAC). 2001. ASTER L1B. USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota.
- Ochoa, J.A. 2005. Patrones de distribución de escorpiones de la región andina en el sur peruano. Revista Peruana de Biología 12:49–68.
- Ochoa, J.A., A.A. Ojanguren-Affilastro, C.I. Mattoni & L. Prendini. 2011. Systematic revision of the Andean scorpion genus *Orobothriurus* Maury, 1976 (Bothriuridae), with discussion of the altitude record for scorpions. Bulletin of the American Museum of Natural History 359:1–90.
- Ojanguren-Affilastro, A.A. 2005. Estudio monográfico de los escorpiones de la República Argentina. Revista Ibérica de Aracnología 11:75–241.
- Ojanguren-Affilastro, A.A. & M.J. Ramírez. 2009. Phylogenetic analysis of the scorpion genus *Brachistosternus* (Arachnida, Scorpiones, Bothriuridae). Zoologica Scripta 38:183–198.
- Polis, G.A. 1990. Ecology. Pp. 247–293. In: The Biology of Scorpions. (G.A. Polis, ed.). Stanford University Press, Stanford, California.
- Prendini, L. & T.L. Bird. 2008. Scorpions of the Brandberg Massif, Namibia: Species richness inversely correlated with altitude. African Invertebrates 49:77–107.
- Roig-Juñent, S.A., R. Carrara, E. Ruiz-Manzanos, F. Agrain, P. Sackmann & M.F. Tognelli. 2007. Phylogenetic relationships and biogeographic considerations of four new species of *Cnemalobus* (Coleoptera: Carabidae) from Patagonia. Insect Systematics and Evolution 38:267–292.
- Roig-Juñent, S.A., F. Agrain, R. Carrara, E. Ruiz-Manzanos & M.F. Tognelli. 2008. Description and phylogenetic relationships of two new species of *Baripus* (Coleoptera: Carabidae: Broscini) and considerations regarding patterns of speciation. Annals of Carnegie Museum 77:211–227.
- Salas-Morales, S.H. & J.A. Meave. 2012. Elevational patterns in the vascular flora of a highly diverse region in southern Mexico. Plant Ecology 213:1209–1220.

*Manuscript received 25 April 2013, revised 31 March 2014.*

Appendix 1.—List of environmental variables included in the analysis after removal of correlated variables (see text for explanation).

Environmental variable	Abbreviation
Mean diurnal range of temperature (mean of all the weekly diurnal temperature ranges)	R_d_m
Isothermality (mean diurnal range (V1) divided by the annual temperature range * 100)	Isoter
Temperature seasonality (standard deviation of monthly mean temperature * 100)	Temp_est
Minimum temperature of coldest month	T_min_mf
Precipitation seasonality	Pp_est
Precipitation of warmest quarter	Pp_qc
Precipitation of coldest quarter	Pp_qf
Mean of productivity estimator	Pm_ndvi
Coefficient of variation of productivity estimator	Cv_ndvi