# Feeding strategies of a small mammal (Phyllotis xanthopygus, Rodentia Cricetidae) at diverse altitudes in the Central Andes, Argentina

Paola L. Sassi, M. Fernanda Cuevas, Josefina Menéndez & María A. Dacar

Published online: 30 Jun 2016.

Submit your article to this journal ⬈

View related articles ⬈

View Crossmark data ⬈

Taylor & Francis
Taylor & Francis Group

# Feeding strategies of a small mammal (*Phyllotis xanthopygus*, Rodentia Cricetidae) at diverse altitudes in the Central Andes, Argentina

Paola L. Sassi[1,2,*], M. Fernanda Cuevas[1], Josefina Menéndez[2]
and María A. Dacar[1]

[1]*Grupo de Investigaciones de la Biodiversidad, Instituto Argentino de Investigaciones de Zonas Áridas, CCT, Mendoza, CONICET, Argentina*
[2]*Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Cuyo, Mendoza, Argentina*

Knowledge of feeding habits not only contributes information related to the resources that individuals need to survive and breed, but also leads to insights about the interactions between a species and its environment. The optimal foraging theory explains diet selection by several attributes of the trophic scenario such as availability, diversity, quality and predictability of food. Other models propose that digestive tract mass increases under high metabolic demands by cold, affecting food choice and intake. Thus, diet selection emerges as a behavioural trait shaped by intrinsic and extrinsic factors. The goal of our study was to determine variation in the trophic scenario among sites at different elevations, as well as variation in phenotypic traits relevant to the nutritional and energy balance in *Phyllotis xanthopygus*. This small rodent is widely distributed along the Andes Mountains. We assessed diet selection and digestive tract size in individuals collected at three elevations across its distribution range. Results on dietary proportion of specific trophic categories (green parts, fruits and arthropods) showed that *P. xanthopygus* alternates between omnivory and granivory/frugivory. Richness, diversity and quality of the available resources evidenced a relatively low-quality trophic scenario at high altitude. Nevertheless, the diets built in by animals from diverse altitudes lacked differentiation in quality or diversity. *P. xanthopygus* seems to behaviourally compensate environmental variation to cope with nutritional requirements, by changing diet composition and proportion of items included. The resultant uniform diet quality is consistent with the absence of variation in the gastrointestinal tract size. Considering the spatial variability and seasonality of the region, a behavioural response is probably the most convenient strategy to overcome short-term environmental heterogeneity. In a plastic species such as *P. xanthopygus*, behaviour is a fundamental aspect to take into account by predictive models in the forecasts of climate change effects on biological diversity.

*Corresponding author: Paola L. Sassi, Av. Ruiz Leal s/n, Parque General San Martín, CC 507 (5500), Mendoza, Argentina (E-mail: psassi@mendoza-conicet.gob.ar).

## INTRODUCTION

The foraging habit of a species is a phenotypic characteristic that can be assessed from different perspectives. The classical view of the optimal foraging theory explains diet selection by attributes of the trophic scenario: availability of food in the habitat, its diversity, quality and predictability, among other ultimate or external causes (MacArthur & Pianka 1966; Schoener 1971; Stephens & Krebs 1986; Pianka 1994). On the other hand, proximate causes like chemical identity, detoxification pathways, morphology of the gastrointestinal tract and specific metabolic demands have been also pointed out to account for diet selection (Karasov 1986; Sabat et al. 1993; Lepczyk et al. 2000; Rubenstein & Wikelski 2003; Simpson et al. 2004). Feeding choices are recognised to be jointly determined by both the ecological context and the processing machinery of animals (Bozinovic & Martínez del Río 1996). The resultant foraging habit is a species-specific trait, but within certain limits and depending on the taxonomic group, it can be quite flexible. Regarding dietary habits, there is general agreement that a specialist consumes more than 50% of its diet in the form of one particular item (Giannoni et al. 2005; Silva 2005). It is also a criterion used to arbitrarily assign the terms granivore, insectivore and herbivore to animals whose diets include more than 50% seeds, insects or plants, respectively, whereas omnivore refers to those species in which no particular category prevails (in the diet; Meserve et al. 1988; Kerley & Whitford 1994). At the intraspecific level, dietary plasticity has been reported by numerous studies, and highlighted as a keystone to the relationship among animals and their habitat (Sabat et al. 1998, 1999; Sabat & Bozinovic 2000). Trophic interactions established between animals and their environment are influenced by different factors, being susceptible to change with temporal and spatial heterogeneity. By means of diverse behavioural and physiological strategies, animals cope with environmental variation to maintain their homeostasis and performance (Bradshaw 2003). Among them, flexible responses, occurring on short time scales, make a major contribution to the adaptability of animals (Pigliucci 2001). In this sense, the range of behavioural plasticity is reported to increase with environmental variability (Komers 1997).

Animals can be modelled as systems processing energy and matter by means of acquisition (foraging, digestion and absorption) and expenditure (thermoregulation, growth, reproduction; Weiner 1992) events. Bottlenecks can operate on any stage of this process: the availability of resources, the digestive capacity of organs and/or the expenditure rate (Hayes & O'Connor 1999; Noren & Mangel 2004; Pryor & Bjorndal 2005). The interplay between diet and energetics has been approached several times from alternative perspectives. For instance, the food–habit hypothesis (McNab 1986), posits that food quality, availability and predictability directly affect basal metabolism. Its predictions have been partially supported by evidence, but the role of other traits like enzymatic plasticity or maximum thermogenic capacity has been suggested to shape this interaction (Cruz-Neto & Bozinovic 2004). On the other hand, recent investigations show that the level of energy expenditure estimated through basal metabolic rate is determined by ambient temperature, precipitation and foraging habits of the species (Naya et al. 2013a). Particularly for endotherms, the obligatory heat model (Naya et al. 2013b) proposes that digestive tract mass increases in order to generate enough

metabolic heat to offset the gap between ambient and body temperature. Furthermore, studies on phenotypic flexibility in digestive response have shown that acclimation to cold environments results in an increase of food intake and hypertrophy of food-processing organs (Hammond & Wunder 1995; Naya et al. 2005). The economic principle of Sibly (1981) predicts that moderate demands of energy imply changes in food processing while high demands of energy require additional changes in the mass of digestive organs. Therefore, in colder climates a herbivore would have a relatively larger gut, which allows it to increase the proportion of comparatively low-quality items (green plant parts) in the diet. Similarly, low-quality diets and high energy demands are connected to the increase of intestines and caecum at seasonal as well as geographical scales (Bozinovic et al. 1990; Hammond & Wunder 1991; Sassi et al. 2007).

Elevation gradients entail special interest for ecological studies because climate sharply changes across relatively short distances. Therefore, the species whose distribution ranges are narrow along the altitudinal cline are strongly associated to local climate conditions (Theurillat & Guisan 2001). Quantifying the responses of organisms to environmental variations allows the revelation of mechanisms that relate physiology and behaviour with ecology and their evolutionary implications (Bozinovic et al. 2007). Our model species is *Phyllotis xanthopygus*, a small rodent widely distributed along the Andes Mountains in southwest Argentina towards southern Peru, encompassing high environmental heterogeneity (Steppan et al. 2007). In the Central Andes of Argentina, the species has been found at altitudes between 1500 and 3300 m (Novillo & Ojeda 2014). This altitudinal range covers a broad temperature and rainfall gradient across a steep slope, implying strong environmental variations. Climate estimates indicate that *P. xanthopygus* endures markedly different conditions at diverse altitudes, with a pronounced decrease in annual mean ambient temperature and an increase in relative humidity towards higher elevations (Sassi & Novillo 2015). It has been described as a herbivore, but high variation in diet is reported among subspecies as well as across altitudes (Kramer et al. 1999).

In this context, the goal of our study was to determine the variation in the trophic scenario (richness, diversity, abundance, and quality of trophic resources) among sites located along an elevation cline, as well as the variation in phenotypic traits relevant to the nutrients and energy balance (i.e. foraging habits and digestive tract size) in a species distributed across that cline. We expected that availability and quality of food items would be lower at comparatively higher altitude sites, and hypothesised that *P. xanthopygus* would show adjustments to cope with its maintenance requirements. According to the theoretical framework, we predicted that along the elevation gradient individuals collected at higher altitudes would present comparatively less diverse and lower-quality diets and larger digestive organs than animals collected at low-altitude locations.

## MATERIALS AND METHODS

*Study site*

The study was carried out at El Manzano Histórico Reserve (Mendoza Province, Argentina) between December 2012 and February 2014. We established sampling sites along an altitudinal transect at 1700 (33°35′35.8″S, 69°24′15.6″W), 2300 (33°36′48.4″S, 69°28′42.7″W) and 3100 (33°36′37.9″S, 69°32′14.5″W) m above sea level (asl). Sites were 3 to 4 km apart, encompassing gradual changes in the landscape. Since the access to the top site (3100 m asl) is blocked by snow during

winter and spring (between May and October) we decided to conduct the study during the summer. The focus of our study was to perform an altitudinal comparison, so we left aside seasonal variation. According to Méndez (2011), these sites belong to different phytogeographic provinces, where the sites at 1700 and 2300 m asl correspond to the Andean province while the one at 3100 m asl is within the High Andean region. With regard to temperature, there are marked differences in annual mean temperature among elevations: $14.91 \pm 6.83$ °C (1700 m asl), $11.15 \pm 5.65$ °C (2300 m asl), and $7.40 \pm 5.6$ °C (3100 m asl) (Sassi & Novillo 2015).

*Sampling and data collection*

In order to compare resource availability and quality among the elevations we assessed plant cover, richness and diversity. We set five strip transects per year at each sampling site, giving a total of 10 transects per site. Each transect consisted of 20 quadrats, the size of which was determined using the minimal area method (Matteucci & Colma 1982). Quadrat sizes were as follows: 1 m$^2$ (at 1700 m asl), 1.5 m$^2$ (at 2300 m asl), 2 m$^2$ (at 3100 m asl). Transects were at least 10 m apart. Samples were taken on 10 quadrats leaving 1 m$^2$ in between. At each quadrat, we assessed total percent cover and percent cover per plant species. Additionally, we collected samples from the most representative plant species in the diet (more than 10% of occurrence) which were dried in the laboratory for proximal chemical analysis (Bjorndal & Bolten 1993). The analysis included nitrogen and crude fibre determination (AOAC 1980). To estimate resource quality per site, we calculated nitrogen and fibre indexes per transect as [A]/g $i$ * Pi, where [A]/g is the concentration of nitrogen or fibre per gram of a trophic item $i$ and P is the mean proportion of the item $i$ (i.e. plant species) in each transect. Chemical analysis of 21 plant species is summarised in Table A1 (Appendix).

In order to characterise the variation of the species' diet among altitudes, we sampled fresh faeces of captured *P. xanthopygus*, using Sherman live traps at the three sampling sites (Sassi & Novillo 2015). Collected samples were taken to the laboratory for analysis. Ten grams from each faecal sample were analysed using a microhistological technique proposed by Dacar and Giannoni (2001) that allows identification of histological features of leaf epidermis, seed coats, fruits and arthropod body parts. On each slide, 50 randomly chosen microscope fields were observed at 40×. The presence of a food item was recorded and its relative frequency of occurrence was determined by dividing the number of microscope fields in which that item occurred by the total number of microscope fields observed (Holechek & Gross 1982). Only plant items were identified to species level when possible. Similarity in the composition of stomach and faecal contents is usually high, particularly when frequency values of food items are used in the analysis (Homolka & Heroldová 1992).

In the first year of sampling, we found significant amounts of arthropods in the diet; therefore, in the second year we considered it important to record their abundance at each site. For this purpose, we set five pitfall traps per site – consisting of jars (325 cm$^3$) half filled with water and a few drops of detergent to reduce surface tension – for a period of 3 days in February 2014 (guidelines by Woodcock 2008). Finally, we counted the total number of arthropods in each pitfall trap (Appendix, Table A2). All invertebrates were sorted to morphospecies following Oliver and Beattie (1993) – that is, using external morphology only and without the use of keys. To estimate the nutritional quality of arthropods we averaged nitrogen and crude fibre values taken from the literature (Ramos-Elorduy 1997; Ramsay & Houston 2003; Melo et al. 2011; Van Huis et al. 2013). To estimate diet quality, we calculated nitrogen and fibre indexes per individual diet as [A]/g $i$ * Pi, where [A]/g is the concentration of nitrogen or fibre per gram of a consumed item $i$ and P is the mean proportion of the item $i$ (i.e. arthropod/plant species) in each diet sample.

From the captured individuals, we randomly chose five adults from each site and took them to the laboratory, where they were sexed and weighed to the nearest 0.1 g. Then, they were sacrificed following guidelines for animal care and use of the American Society of Mammalogists (ACUC 1998). Digestive tracts were removed and divided into four portions:

stomach, small intestine, caecum and colon. For each organ, we removed digestive contents and measured wet mass on an analytical balance to ± 0.1 mg.

*Statistical analysis*

To compare total vegetation cover among the sites we performed an analysis of variance (ANOVA), with plant cover as response variable and site as fixed factor, followed by a Tukey test for post-hoc comparisons. Data on plant cover was transformed to arcsine square root in order to meet the parametric analysis' requirements (normality and homoscedasticity; Zar 2010). To detect significant differences in the supply richness and diversity among the different elevation sampling sites, we calculated species richness and the Shannon–Wiener index (H') at each transect per site and then applied pairwise comparisons using a Wilcoxon for independent sample test (Zar 2010). To analyse the overlap of trophic resource availability among sites we used the proportional similarity (PS) index (Feinsinger et al. 1981). This index ranges from 0 to 1, the highest value indicating maximum similarity in the proportion of trophic resources between two sites. To evaluate the variation of nutritional quality supply, we performed an ANOVA using nitrogen and fibre indexes per transect as response variables and site as fixed factor.

As for the arthropods, we estimated differences in abundance among the sites using a non-parametric analysis (Kruskal–Wallis and post-hoc test), as the data did not fulfil the normal distribution assumption. The data for ant abundance was analysed separately from the data for the rest of the groups since the former are social insects and the presence of a colony could skew results (Turner & Foster 2009).

In order to determine variation in the foraging strategy, we calculated richness and the Shannon–Wiener diversity index using the frequency of food items in the diet. To define the prevailing tendency of the dietary habits at different elevations, we clustered food items in three categories based on nutritional quality: green parts, fruits and arthropods. To detect significant differences among the sites, we applied pairwise comparisons using a Wilcoxon for independent sample test (Zar 2010).

To compare diet niche breath among sites, we again calculated the PS index using the frequency distribution of items in the diet and the frequency distribution of resources at the sites. In this way, we determined the overlap between each individual's diet and its supply at each sampling site. Then we performed an ANOVA analysis with PS value as response variable and altitude as categorical predictor, to test for significant differences among sites.

To analyse diet selection (i.e. the degree to which a species is more likely to take one kind of food item rather than another) we only used plant matter. Plant species were clustered into six categories according to life form: herbs, grasses, cacti, ferns, sub-shrubs (shrubs less than 1 m tall) and shrubs. Food category selection was estimated by applying Manly's index of selectivity (Manly et al. 2002):

$$\alpha_i = (Pu_i/Pa_i) \times 1\Sigma(Pu_i/Pa_i)$$

where $Pu_i$ is the observed proportion of category i in each individual's diet and $Pa_i$ is the available proportion of category i in the environment. If $\alpha_i$ is greater than 1/k, k being the number of food categories, then category i is selected. If $\alpha_i$ is less than 1/k, then the category i is avoided. To test the reliability of Manly's index, we resampled the faeces 100 times by bootstrapping. We then calculated the average values and the 95% confidence intervals (CI) of Manly's index. The 95% CI that include the value 1/k indicate a use that is proportional to the availability.

We assessed variation of diet nutritional quality among altitudes, using ANOVAs to compare sites for nitrogen and fibre indexes per diet sample. In this case, nitrogen index values had to be transformed to arcsine square root in order to meet the normal distribution assumption of the parametric analysis (Zar 2010).

Finally, to evaluate differences in gut size among animals from the three elevations, we performed a MANOVA analysis with site as fixed factor and stomach, small intestine, caecum,

colon and total gastrointestinal tract weights as response variables. In order to standardise the data, each variable was divided by the individual's total body weight.

## RESULTS

Total vegetation cover did not differ significantly among the sites ($F_{(2,29)} = 0.63$; $P = 0.54$), being 50.4% for the 3100 m site, 54.45% for the 2300 m site and 52% for the 1700 m site. Plant richness and diversity were higher at 2300 m asl compared to the other two elevations, this difference being statistically significant with respect to the site at 3100 m asl only (Table 1). The overlap among plant communities is proportional to the distance among sites, being in general not higher than 15% (i.e. between 1700 and 2300 m asl = 0.15, between 2300 and 3100 m asl = 0.11) and even lower between the extremes of the cline at 1700 and 3100 m asl (PS = 0.03). Regarding the nutritional quality of plants in the supply, the nitrogen gradient was 1700 ≈ 2300 > 3100, while the crude fibre gradient was 3100 ≈ 2300 > 1700 (Table 1). These results suggest a comparatively higher quality trophic scenario at low elevation since the available plants at 1700 m elevation had on average less fibre and more nitrogen than plants at 3100 m asl. Finally, we found that both ants and the rest of the arthropods were significantly more abundant at the 3100 m asl site than at 1700 m asl. The 2300 m site showed no differences from the 1700 m one for the rest of the arthropods, while the value for ants was intermediate between the sites (Table 1).

We collected a total of 18 faeces samples at 1700 m, 14 at 2300 m and 12 at 3100 m elevation sites (one sample per captured individual). Species richness and diversity in the diets did not vary among the elevations, probably because foraging behaviour did (Table 2). In fact, the diet of *P. xanthopygus* changed across sites, as suggested by the varying proportions of different food categories in terms of their nutritional quality. For instance, at 1700 m asl green parts were more frequent than fruits and arthropods, the latter category being significantly less frequent than the others. At 2300 m asl, the greatest proportion corresponded to fruits followed by green parts and arthropods in significantly lower proportions. At 3100 m asl fruits followed by green parts were consumed in significantly greater proportion than arthropods. In general, *P. xanthopygus* includes

Table 1.

Richness, diversity, arthropods abundances and nutritional quality (mean ± SE) in food supply variables present at three elevation sites in El Manzano Histórico Reserve, Argentina. Different letters indicate significant differences among sites.

| Variables | Elevation sites (m above sea level) | | |
|---|---|---|---|
| | 1700 | 2300 | 3100 |
| Richness (no. species) | 12.8 ± 1.47[ab] | 13 ± 0.88[a] | 9.7 ± 0.62[b] |
| Shannon–Wiener index (H') | 1.62 ± 0.14[ab] | 1.9 ± 0.13[a] | 1.35 ± 0.06[b] |
| Nitrogen index (%) | 0.88 ± 0.05[b] | 0.81 ± 0.05[b] | 0.63 ± 0.05[a] |
| Crude fiber (%) | 11.57 ± 1.31[a] | 20.63 ± 1.31[b] | 20.99 ± 1.31[b] |
| Ants (no. individuals) | 19.4 ± 3.36[a] | 50.0 ± 14.6[ab] | 862.2 ± 113.42[b] |
| Rest of arthropods (no. individuals) | 5.6 ± 0.93[a] | 4.8 ± 1.40[a] | 22.2 ± 3.20[b] |

Table 2.

Richness, diversity index, nutritional quality and similarity proportion index (mean ± SE) in the diet of *Phyllotis xanthopygus* in El Manzano Histórico Reserve, Argentina. Different letters indicate significant differences among sites.

| Variables | Elevation sites (m above sea level) | | |
| --- | --- | --- | --- |
| | 1700 | 2300 | 3100 |
| Richness (no. species) | 6.5 ± 0.35[a] | 6.43 ± 0.51[a] | 6.17 ± 0.67[a] |
| Shannon-Wiener index (H') | 0.59 ± 0.03[a] | 0.61 ± 0.03[a] | 0.55 ± 0.06[a] |
| Nitrogen index (%) | 6.7 ± 0.41[a] | 6.04 ± 0.43[a] | 6.65 ± 0.49[a] |
| Crude fiber (%) | 18.6 ± 1.32[a] | 23.49 ± 1.41[a] | 20.77 ± 1.59[a] |
| Proportional similarity index | 0.03 ± 0.005[a] | 0.12 ± 0.011[b] | 0.27 ± 0.048[c] |

similar amounts of green parts across the altitudinal transect with a lower proportion in the intermediate site, where fruits were eaten in a remarkably greater proportion. Conversely, arthropods were significantly more frequent in the diet of individuals stemming from 1700 and 3100 m asl than at the intermediate altitude (Fig. 1).
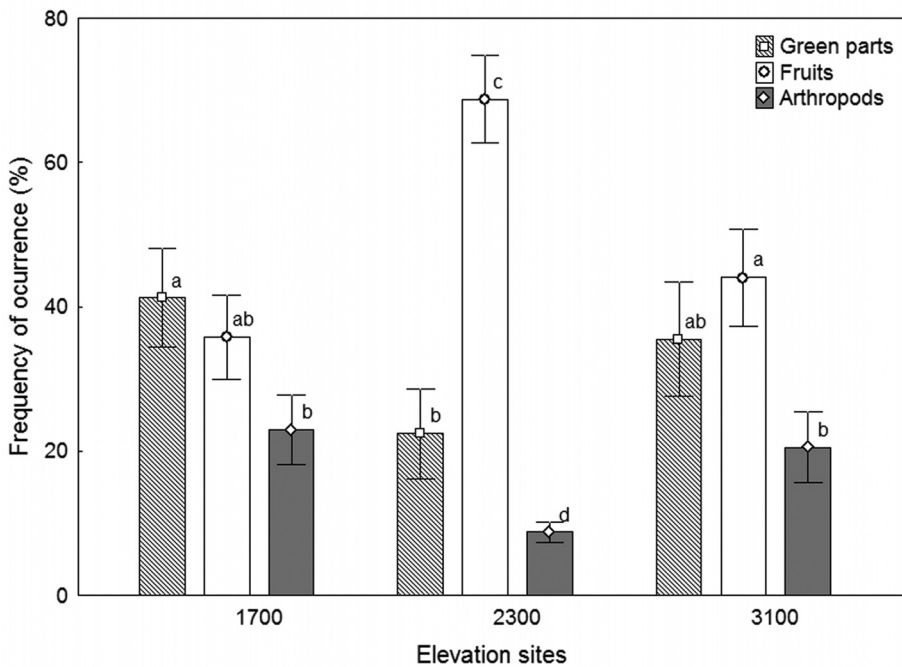


Fig. 1. — Altitudinal variation (mean ± SE) in the consumption of the different food categories found in *Phyllotis xanthopygus*' diet in El Manzano Histórico Reserve, Argentina. Different letters indicate significant differences within each site and among the three elevation sites.

Regarding the plant species included in the diet, the PS index between diet and food supply showed that the overlap is, in general, low, although it significantly varied among the sites food choice being more similar to food availability at high-altitude sites compared to low-altitude sites (Table 2). Regarding diet composition similarity (PS) among sites, it was around 50% between 1700 m and 2300 m, as well as 2300 m and 3100 m (0.563 and 0.495, respectively), whereas between 1700 m and 3100 m this index was slightly higher than 40% (0.434).

Results of the trophic selection analysis via Manly's index showed that at the 1700 m elevation site *P. xanthopygus* avoided grasses and ferns, and used the rest of the categories proportionally to their availability. At 2300 m asl the species avoided grasses, while herbs, subshrubs and shrubs were consumed in proportion to their availability. At 3100 m asl ferns were the only food category selected. Grasses and sub-shrubs were avoided, while herbs, shrubs and cacti were eaten proportionally to their availability (Fig. 2).

Dietary nitrogen and fibre indexes compared among individuals from each site revealed that the quality of diet did not show among-site variation (Table 2), unlike the nutritional quality variation found in the food supply and reported above (Table 1).

Finally, we found that individuals from different altitudes showed no significant differences in the weight of the total gastrointestinal tract or its sections (Wilks$_{(8,18)}$ = 0.48; $P$ = 0.49). Standardised means and standard errors for stomach, small intestine, caecum, colon and total gastrointestinal tract are detailed in Table 3.

## DISCUSSION

In order to maintain their energy and nutritional balance, animals cope with variations in the trophic scenario through behavioural and physiological adjustments that translate into their dietary choices (Sherry 1990; Chambers et al. 1995; Kyriazakis et al. 1999; Sassi et al. 2011). Furthermore, all this occurs under temperature and other climatic factors that impose diverse energy demands and restrictions to the foraging behaviour (Caraco et al. 1990; Murray & Smith 2012).

As expected from climate characteristics, the richness and diversity of the available trophic items are comparatively lower at higher sites. Similarly, the nutritional quality of the trophic scenario was lower in the high-altitude site compared to the low-altitude site. Nevertheless, despite facing a varying environment, diversity and quality of diets do not differ among sites: *P. xanthopygus* seems to compensate for among-site variation through diet selection. We suggest that the species' nutritional requirements are met behaviourally by changing diet composition, and especially the proportion of items included.

The adjustments in the foraging strategy are evidenced by the various indexes used. Among them, the PS index reveals a relatively low similarity in the frequency of available trophic items among sites (i.e. 10%), while the similarity among the proportion of items included by *P. xanthopygus* in the diets was relatively high among sites (i.e. 50%). The PS index also suggests that the overlap between diet and supply is comparatively higher at high elevation, where the supply diversity is less than at lower elevations. This is in agreement with theoretical expectations from the optimal foraging theory: the greater the variability of resources, the greater the specialisation of the foraging strategy (MacArthur & Pianka 1966; Schoener 1971; Feinsinger et al. 1981). Most interpretations posit that in an environment with a relatively poor food supply, it would be too costly for a consumer to bypass certain alimentary items because mean
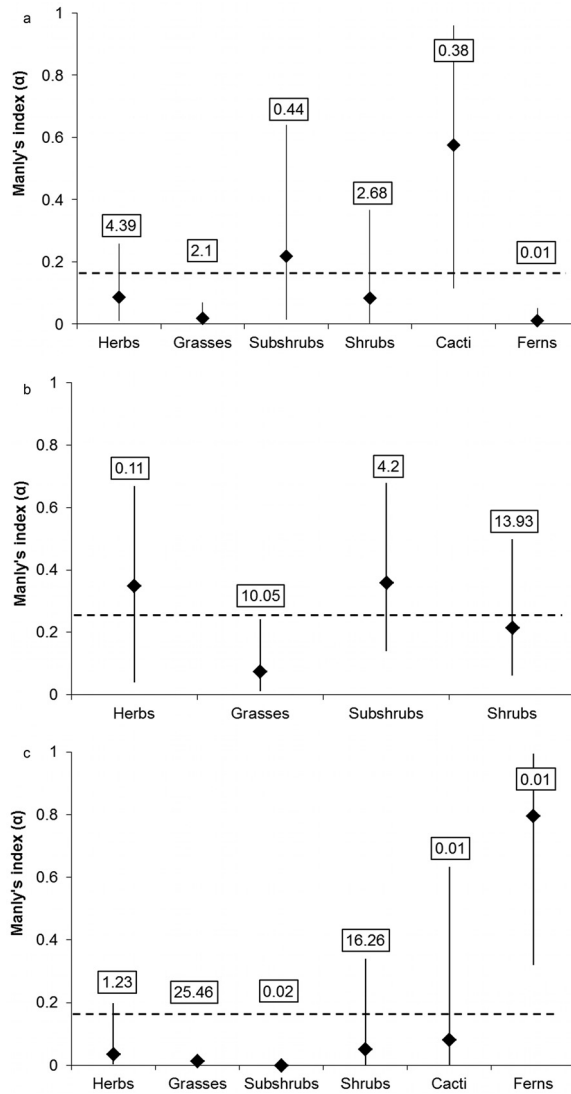
Fig. 2. — Manly's selectivity index (± 95% CI) for food categories at the three elevation sites: (A) 1700, (B) 2300 and (C) 3100 m above sea level. Dotted line indicates 1/k for a proportional use to the availability. Values within the squares indicate the available proportions of each food category.

search time per item is long and expectation of encounter is low. Therefore, a broad niche maximises return per unit expenditure, promoting generalisation. On the other hand, in a food-rich environment, search time is comparatively low, implying that less preferred food items can be bypassed because prospects of finding more suitable items are high. Thus, rich food supplies are expected to lead to narrow dietary breadths (Wiens 1989).

Table 3.

Standardised weight (g) of stomach, small intestine, caecum, colon and total digestive tract (mean ± SE) compared among animals from the three elevation sites in El Manzano Histórico Reserve, Argentina.

| Elevation (m asl) | Stomach | Small intestine | Cecum | Colon | Total gut |
|---|---|---|---|---|---|
| 1700 | 0.063 ± 0.0074 | 0.043 ± 0.0051 | 0.05 ± 0.0089 | 0.032 ± 0.0049 | 0.19 ± 0.0084 |
| 2300 | 0.051 ± 0.0079 | 0.043 ± 0.0048 | 0.05 ± 0.006 | 0.028 ± 0.0033 | 0.17 ± 0.0167 |
| 3100 | 0.04 ± 0.008 | 0.028 ± 0.0057 | 0.035 ± 0.0074 | 0.024 ± 0.0032 | 0.13 ± 0.022 |

asl: above sea level.

Considering food selection through Manly's index using only vegetation life forms, results indicated that ferns were the only food category positively selected by *P. xanthopygus* at 3100 m asl. The rest of the categories were avoided or eaten proportionally to their availability depending on each site. Particularly at 3100 m asl, the supply trophic quality, diversity and richness were lower than in the other sites. Nitrogen and fibre content of ferns show it is a highly nutritious food item (Borges et al. 2013). So, *P. xanthopygus* facing the extreme climate conditions found at high altitudes selectively incorporates high-quality food items, such as ferns.

Foraging habits of the Muridae family in the region have been previously reported to show great variation among localities (Silva 2005). Particularly for *P. xanthopygus*, dietary proportion of specific trophic categories changes noticeably among several studies. According to the 50% criteria, the species has been categorised as a herbivore (90% plant green parts, Silva 2005; López Cortés et al. 2007), omnivore (at 1700 and 3100 m asl, this study and Pizzimenti & De Salle 1980), granivore/frugivore (2300 m asl, this study and Bozinovic & Rosenmann 1988) and insectivore (54% arthropods, Pizzimenti & De Salle 1980). Thus, the question arises: what governs this versatility?

It has been pointed out many times that food selection is not only a matter of energy needs to fuel metabolic processes (Bozinovic & Martínez del Río 1996). Foraging decisions are also guided by the requirement for water, essential amino acids, vitamins and minerals, among other things. Therefore, under its physiological conditions, an animal's food choice is moulded by the fulfilment of its nutritional needs. The resultant foraging pattern depends on the interplay between energy and nutrient requirements and the distribution of alimentary items in the environment. For instance, the availability of arthropods follows the pattern 1700 < 2300 < 3100, although their incorporation in the diet occurred mostly at 1700 and 3100 m asl. Thus, the behavioural mechanism should be different between sites, since the proportion of arthropods in the diets is similar irrespective of their availability. We propose that the variability in the proportion of green parts, fruits and arthropods consumed is indicative of a flexible foraging strategy and active behaviour of diet selection possibly shaped not only by the nature of alimentary options in the environment but also by the nutritional requirements of the species (Chambers et al. 1995; Simpson et al. 2004). Indicative of this is the lack of differences in the quality of the diets built in by animals from different altitudes, despite the quality variation reported for the extant trophic scenario. A uniform diet quality throughout the sites along the gradient is also consistent with the absence of variation in the gastrointestinal tract among animals from different elevations.

*P. xanthopygus*' phenotypic versatility has been reported previously at the species level as well as at the population level. Recent investigations across the geographical area approached in this study revealed a remarkable physiological and behavioural plasticity (Sassi & Novillo 2015; Sassi et al. 2015). Gastrointestinal tract size of several rodent species has been reported to vary along latitudinal clines in consistency with predictions of the obligatory heat model (Naya et al. 2012, 2013a). Particularly, this model proposes that herbivorous habits are more frequent in species living at higher latitudes. With a similar logic, in the present study we searched for a predominance of green plant parts over fruits and arthropods in the diet of high-altitude individuals of a single species. At our relatively small geographical scale and intraspecific analysis, the obligatory heat model does not explain the variation in foraging habits in *P. xanthopygus*. Our results did not fit its expectations, suggesting that a latitudinal pattern does not necessarily predict an altitudinal one.

Due to the seasonality of this temperate region (Sassi & Novillo 2015), the lack of access to high-altitude sites in winter prevents us from taking a complete picture of the *P. xanthopygus* diet. Therefore we recognise that our results allow for partial conclusions on the species' feeding strategy, which could also change throughout the year. Still, our summer data reveal significant variation in parameters that describe the food supply across sites, and a diverse selection of trophic items among animals at different sites. At such a geographical scale, we propose that behavioural flexibility is the strategy of this species to deal with the variation in availability and quality of the trophic scenario. This is mirrored in the morphological stability of the digestive system. Considering the spatial variability along the elevation transect, and the seasonality suggested by climate data, a behavioural response is probably the most convenient strategy to overcome short-term environmental heterogeneity. In addition to a demonstrated capacity of *P. xanthopygus* to display acclimation in other phenotypic traits, behaviour is still a first-line response to change. This is a fundamental aspect to take into account by predictive models in the forecasts of climate change effects on biological diversity.

## DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

## FUNDING

## REFERENCES

ACUC [Animal Care and Use Committee]. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. J Mammal. 79:1416–1431.

AOAC [Association of Official Analytical Chemists]. 1980. Official methods of analysis. 13th ed. Washington (DC): Association of Official Analytical Chemists.

Bjorndal KA, Bolten AB. 1993. Digestive efficiencies in herbivorous and omnivorous freshwater turtles on plant diets: do herbivores have a nutritional advantage? Physiol Zool. 66:384–395.

Borges JA, Camacaro O, Dominguez L, Graterol A. 2013. Composición bromatológica de *Pteridium aquilinum* subs. *arachnoideum* colectado en el municipio Bolívar, estado Yaracuy, Venezuela. Bromatological composition of *Pteridium aquilinum* subs. *arachnoideum* collected in the municipality Bolivar, Yaracuy, Venezuela. Revista de la Facultad de Agronomía LUZ. 30:431–440. Spanish, English.

Bozinovic F, Martínez del Río C. 1996. Animals eat what they should not: why do they reject our foraging models? Rev Chil Hist Nat. 69:15–20.

Bozinovic F, Muñoz JL, Cruz-Neto AP. 2007. Intraspecific variability in the basal metabolic rate: testing the food habits hypothesis. Physiol Biochem Zool. 80:452–460.

Bozinovic F, Novoa FF, Veloso C. 1990. Seasonal changes in energy expenditure and digestive tract of *Abrothrix andinus* in the Andes range. Physiol Zool. 63:1216–1231.

Bozinovic F, Rosenmann M. 1988. Comparative energetics of South American cricetid rodents. Comp Biochem Phisiol A. 91:195–202.

Bradshaw D. 2003. Vertebrate ecophysiology: an introduction to its principles and applications. Cambridge: Cambridge University Press.

Caraco T, Blanckenhorn WU, Gregory GM, Newman JA, Recer GM, Zwicker SM. 1990. Risk-sensitivity: ambient temperature affects foraging choice. Anim Behav. 39:338–345.

Chambers PG, Simpson SJ, Raubenheimer D. 1995. Behavioural mechanisms of nutrient balancing in *Locusta migratoria* nymphs. Anim Behav. 50:1513–1523.

Cruz-Neto AP, Bozinovic F. 2004. The relationship between diet quality and basal metabolic rate in endotherms: insights from intraspecific analysis. Physiol Biochem Zool. 77:877–889.

Cuevas MF, Ojeda RA, Dacar MA, Jaksic FM. 2013. Seasonal variation in feeding habits and diet selection by wild boars in a semi-arid environment of Argentina. Acta Theriol. 58:63–72.

Dacar MA, Giannoni SM. 2001. A simple method for preparing reference slides of seed. J Range Manage. 54:191–193.

Feinsinger P, Spears EE, Poole RW. 1981. A simple measure of niche breadth. Ecology. 62:27–32.

Giannoni SM, Borghi CE, Dacar M, Campos CM. 2005. Main food categories in diets of sigmodontine rodents in the Monte (Argentina). Mastozool Neotrop. 12:181–187.

Hammond KA, Wunder BA. 1991. The role of diet quality and energy need in the nutritional ecology of a small herbivore, *Microtus ochrogaster*. Physiol Zool. 64:541–567.

Hammond KA, Wunder BA. 1995. Effect of cold temperatures on the morphology of gastrointestinal tracts of two microtine rodents. J Mammal. 76:232–239.

Hayes JP, O'Connor CS. 1999. Natural selection on thermogenic capacity of high-altitude deer mice. Evolution. 53:1280–1287.

Holechek JL, Gross BD. 1982. Evaluation of different calculation procedures for microhistological analysis. J Range Manage. 35:721–723.

Homolka M, Heroldová M. 1992. Similarity of the results of stomach and faecal contents analyses in studies of the ungulate diet. Folia Zool. 41:193–208.

Karasov WH. 1986. Energetics, physiology and vertebrate ecology. Trends Ecol Evol. 1:101–104.

Kerley GIH, Whitford WG. 1994. Desert-dwelling small mammals as granivores: intercontinental variations. Aust J Zool. 42:543–555.

Komers PE. 1997. Behavioural plasticity in variable environments. Can J Zool. 75:161–169.

Kramer KM, Monjeau JA, Birney EC, Sikes RS. 1999. *Phyllotis xanthopygus*. Mammal Species. 617:1–7.

Kyriazakis I, Tolkamp BJ, Emmans G. 1999. Diet selection and animal state: an integrative framework. P Nutr Soc. 58:765–772.

Lepczyk CA, Murray KG, Winnett-Murray K, Bartell P, Geyer E, Work T. 2000. Seasonal fruit preferences for lipids and sugars by American robins. Auk. 117:709–717.

López Cortés F, Cortés A, Miranda E, Rau JR. 2007. Dietas de *Abrothrix andinus, Phyllotis xanthopygus* (Rodentia) y *Lepus europaeus* (Lagomorpha) en un ambiente altoandino de Chile [Diets of *Abrothrix andinus, Phyllotis xanthopygus* (Rodentia) and *Lepus europaeus* (Lagomorpha) in a high Andean environment, Chile]. Rev Chil Hist Nat. 80:3–12. Spanish.

MacArthur RH, Pianka ER. 1966. On optimal use of a patchy environment. Am Nat. 100:603–609.

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP. 2002. Resource selection by animals: statistical design and analysis for field studies. 2nd ed. Dordrecht: Kluwer Academic.

Matteucci SD, Colma A. 1982. Metodología para el estudio de la vegetación [Methodology for the study of vegetation]. Washington: Secretaría General de la Organización de los Estados Americanos (OEA). Programa Regional de Desarrollo Científico y Tecnológico. Serie Biología. Monografía No. 22. Spanish.

McNab BK. 1986. The influence of food habits on the energetics of eutherian mammals. Ecol Monogr. 56:1–19.

Melo V, García M, Sandoval H, Jiménez HD, Calvo C. 2011. Quality proteins from edible indigenous insect food of Latin America and Asia. Emir J Food Agric. 23:283–289.

Méndez E. 2011. La vegetación de los altos Andes: El flanco oriental del Cordón del Portillo (Tunuyán, Mendoza, Argentina) [The vegetation of the high Andes: The eastern flank of Cordón del Portillo (Tunuyán, Mendoza, Argentina)]. Bol Soc Argent Bot. 46:317–353. Spanish.

Meserve PL, Lang BK, Patterson BD. 1988. Trophic relationships of small mammals in a Chilean temperate rainforest. J Mammal. 69:721–730.

Murray IW, Smith FA. 2012. Estimating the influence of the thermal environment on activity patterns of the desert woodrat (*Neotoma lepida*) using temperature chronologies. Can J Zool. 90:1171–1180.

Naya DE, Bacigalupe LD, Bustamante DM, Bozinovic F. 2005. Dynamic digestive responses to increased energy demands in the leaf-eared mouse (*Phyllotis darwini*). J Comp Physiol B. 175:31–36.

Naya DE, Spangenberg L, Naya H, Bozinovic F. 2012. Latitudinal pattern in rodent metabolic flexibility. Am Nat. 179:172–179.

Naya DE, Spangenberg L, Naya H, Bozinovic F. 2013a. How does evolutionary variation in basal metabolic rates arise? A statistical assessment and a mechanistic model. Evolution. 67:1463–1476.

Naya DE, Spangenberg L, Naya H, Bozinovic F. 2013b. Thermal conductance and basal metabolic rate are part of a coordinated system for heat transfer regulation. Proc R Soc Lond B. 280:20131629.

Noren DP, Mangel M. 2004. Energy reserve allocation in fasting northern elephant seal pups: inter-relationships between body condition and fasting duration. Funct Ecol. 18:233–242.

Novillo A, Ojeda RA. 2014. Elevation patterns in rodent diversity in the dry Andes: disentangling the role of environmental factors. J Mammal. 95:99–107.

Oliver I, Beattie AJ. 1993. A possible method for the rapid assessment of biodiversity. Conserv Biol. 7:562–568.

Pianka ER. 1994. Comparative ecology of *Varanus* in the Great Victoria desert. Aust J Ecol. 19:395–408.

Pigliucci M. 2001. Phenotypic plasticity: beyond nature and nurture. Baltimore (MD): Johns Hopkins University Press.

Pizzimenti JJ, De Salle R. 1980. Dietary and morphometric variation in some Peruvian rodent communities: the effect of feeding strategy on evolution. Biol J Linn Soc. 13:263–285.

Pryor GS, Bjorndal KA. 2005. Symbiotic fermentation, digesta passage, and gastrointestinal morphology in bullfrog tadpoles (*Rana catesbeiana*). Physiol Biochem Zool. 78:201–215.

Ramos-Elorduy J. 1997. Insects: a sustainable source of food? Ecol Food Nutr. 36:247–276.

Ramsay SL, Houston DC. 2003. Aminoacid composition of some woodland arthropods and its implications for breeding tits and other passerines. Ibis. 145:227–232.

Rubenstein DR, Wikelski M. 2003. Seasonal changes in food quality: a proximate cue for reproductive timing in marine iguanas. Ecology. 84:3013–3023.

Sabat P, Bozinovic F. 2000. Digestive plasticity and the cost of acclimation to dietary chemistry in the omnivorous leaf-eared mouse *Phyllotis darwini*. J Comp Physiol B. 170:411–417.

Sabat P, Bozinovic F, Zambrano F. 1993. Insectivoría en *Marmosa elegans* (Marsupicarnívora): ¿una restricción fisiológica-evolutiva? [Insectivory in *Marmosa elegans* (Marsupicarnivora): a physiological-evolutionary restriction?]. Rev Chil Hist Nat. 66:87–92. Spanish.

Sabat P, Lagos JA, Bozinovic F. 1999. Test of the adaptive modulation hypothesis in rodents: dietary flexibility and enzyme plasticity. Comp Biochem Physiol A. 123:83–87.

Sabat P, Novoa F, Bozinovic F, Martínez del Río C. 1998. Dietary flexibility and intestinal plasticity in birds: a field and laboratory study. Physiol Biochem Zool. 71:226–236.

Sassi PL, Borghi CE, Bozinovic F. 2007. Spatial and seasonal plasticity in digestive morphology of cavies (*Microcavia australis*) inhabiting habitats with different plant qualities. J Mammal. 88:165–172.

Sassi PL, Borghi CE, Dacar MA, Bozinovic F. 2011. Geographic and seasonal variability in feeding behaviour of a small herbivorous rodent. Acta Theriol. 56:35–43.

Sassi PL, Novillo A. 2015. Acclimating to thermal changes: intraspecific variation in a small mammal from the Andes Mountains. Mamm Biol - Z Saugetierkd. 80:81–86.

Sassi PL, Taraborelli P, Albanese S, Gutierrez A. 2015. Effect of temperature on activity patterns in a small Andean rodent: behavioral plasticity and intraspecific variation. Ethology. 121:840–849.

Schoener TW. 1971. Theory of feeding strategies. Annu Rev Ecol Syst. 2:369–404.

Sherry TW. 1990. When are birds dietarily specialized? Distinguishing ecological from evolutionary approaches. Stud Avian Biol. 13:337–352.

Sibly RM. 1981. Strategies in digestion and defecation. In: Townsend CR, Calow P, editors. Physiological ecology: an evolutionary approach to resource use. Oxford (UK): Blackwell Scientific Publications; p. 109–139.

Silva SI. 2005. Posiciones tróficas de pequeños mamíferos en Chile: una revisión [Thophic positions of small mammals in Chile: a review]. Rev Chil Hist Nat. 78:589–599. Spanish.

Simpson SJ, Sibly RM, Lee KP, Behmer ST, Raubenheimer D. 2004. Optimal foraging when regulating intake of multiple nutrients. Anim Behav. 68:1299–1311.

Stephens DW, Krebs JR. 1986. Foraging theory. Princeton (NJ): Princeton University Press.

Steppan SJ, Ramirez O, Banbury J, Huchon D, Pacheco V, Walker LI, Spotorno AE. 2007. A molecular reappraisal of the systematics of the leaf-eared mice *Phyllotis* and their relatives. In: Kelt DA, et al., editors. The quintessential naturalist: Honoring the life and legacy of Oliver Pearson. California: UC Publications in Zoology, University of California Press; p. 799–826.

Theurillat JP, Guisan A. 2001. Potential impact of climate change on vegetation in the European Alps: a review. Clim Change. 50:77–109.

Turner EC, Foster WA. 2009. The impact of forest conversion to oil palm on arthropod abundance and biomass in Sabah, Malaysia. J Trop Ecol. 25:23–30.

Van Huis A, Van Itterbeeck J, Klunder H, Mertens E, Halloran A, Muir G., Vantomme P. 2013. Edible insects: Future prospects for food and feed security. FAO Forestry paper 171. Rome: Food and Agriculture Organization of the United Nations.

Weiner J. 1992. Physiological limits of increased dietary cellulose on the anatomy, physiology and behaviour of captive water voles, *Arvicola terrestris* (L.) (Rodentia: Microtinae). Comp Biochem Phys. 94:615–621.

Wiens JA. 1989. The ecology of bird communities. Volume 1: Foundations and patterns. Cambridge: Cambridge University Press.

Woodcock BA. 2008. Pitfall trapping in ecological studies. In: Leather SR, editor. Insect sampling in forest ecosystems. Oxford: Blackwell Publishing; p. 37–56.

Zar JH. 2010. Biostatistical analysis. Upper Saddle River (NJ): Prentice Hall.

## APPENDIX

Table A1.

Nitrogen and fibre contents in plant species with more than 10% of occurrence in the diet of *Phyllotis xanthopygus*.

| Plant species | Nitrogen (%) | Fibre (%) |
| --- | --- | --- |
| *Adesmia trijuga* | 2.27 | 34.61 |
| *Astragalus arnottianus* (leaf) | 3.29 | 24.25 |
| *Astragalus arnottianus* (fruit) | 2.96 | 18.12 |
| *Baccharis* sp. | 1.07 | 35.84 |
| *Berberis empetrifolia* (leaf) | 1.71 | 43.54 |
| *Berberis empetrifolia* (fruit) | 1.03 | 20.05 |
| *Cerastium arvense* | 1.54 | 23.25 |
| *Chenopodium* sp. (leaf) | 1.21 | 33.34 |
| *Chenopodium* sp. (fruit)[1] | 2.13 | 23.94 |
| *Colettia spinossisima* | 1.52 | 42.76 |
| *Descurrainia argentina* | 2.31 | 19.33 |
| *Dichondra sericea* | 1.03 | 25.96 |
| *Ephedra chilensis* | 1.01 | 51.54 |
| *Ephedra frustillata* (leaf) | 0.78 | 52.26 |
| *Ephedra frustillata* (fruit) | 1.54 | 25.89 |
| *Glandularia parodii* | 1.48 | 25.43 |
| Ferns[2] | 2.57 | 21 |
| *Junellia juniperina* | 0.88 | 31.18 |
| *Lecanophora ameghinoi* | 2.12 | 23.78 |
| *Lycium chilense* | 1.91 | 24.25 |
| *Oxalis erythrorhiza* | 1.39 | 16.68 |
| *Philibertia gilliesii* | 1.75 | 27.71 |
| *Poa resinulosa* (leaf) | 0.45 | 49.50 |
| *Poa resinulosa* (fruit) | 1.62 | 37.10 |
| *Senecio filaginoides* | 0.72 | 39.86 |
| *Sisymbrium andinum* | 1.76 | 29.18 |

[1]Cuevas et al. 2013; [2]Borges et al. 2013.

Table A2.

Abundance and proportion (%) of arthropod groups from the total sample collected in pitfall traps per site.

| Morphospecies | 1700 | 2300 | 3100 |
| --- | --- | --- | --- |
| Ant (Hymenoptera) | 97 (77.6%) | 250 (91.2%) | 4311 (97.5%) |
| Fly (Diptera) | 12 (9.6%) | 5 (1.8%) | 2 (0.05%) |
| Mosquito (Diptera) | 2 (1.6%) | 2 (0.7%) | 2 (0.05%) |
| Spider (Araneae) | 2 (1.6%) | 6 (2.2%) | 6 (0.14%) |
| Grasshopper (Orthoptera) | 1 (0.8%) | 0 | 1 (0.02%) |
| Cockroach (Blattodea) | 2 (1.6%) | 0 | 0 |
| Woodlouse (Isopoda) | 0 | 1 (0.4%) | 0 |
| Moth (Lepidoptera) | 0 | 0 | 1 (0.02%) |
| Unidentified | 9 (7.2%) | 10 (3.7%) | 100 (2.26%) |