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Does food abundance determine the diet of the Puna Rhea (*Rhea tarapacensis*) in the Austral Puna desert in Argentina?

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ABSTRACT

The Puna Rhea (*Rhea tarapacensis*) is a large, flightless herbivorous bird found in the Andes Mountains of four countries, namely Argentina, Chile, Bolivia and Peru. Despite its ample distribution range, little is known about the ecological requirements of the species. In this work, the diet and food selection behaviour of the Puna Rhea in the Argentine Puna desert were analysed. From 2011 to 2014, throughout the dry and wet periods of each year, fresh faeces were collected and vegetation cover was simultaneously recorded. Diet composition was determined by microhistological analysis of the faeces and diet selectivity was established statistically by the Bonferroni method. The diet of the Puna Rhea was completely herbivorous and mostly folivorous, consisting of 51% of the plant species in the study area. This species was highly selective, consuming scarce shrub and herbaceous species and rejecting grasses or graminoids. The strongly selective foraging strategy presented by the Puna Rhea was therefore unrelated to the abundance of particular species but probably influenced by factors such as nutritional value, mainly in terms of fibre content and plant secondary compounds, and predation risk. Consequently, conservation efforts aimed at the Puna Rhea should be focused on maintaining the availability of the few preferred plant species and reducing possible competition with other generalist herbivores.

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Diet; threatened species; Puna in Argentina; *Rhea tarapacensis*; selective foraging; nutritional content

Introduction

Diet selection by herbivorous vertebrates is strongly determined by abundance and distribution of trophic resources, which is clearly evident in arid environments characterised by scarce and heterogeneously distributed vegetation (Owen-Smith *et al.* 2015). This vegetation pattern occurs in numerous seasonal deserts, where vegetation is highly dependent on the scarce precipitations concentrated within a short period of the year (Whitford 2002). Therefore, herbivores face severe fluctuations in food abundance (Benítez *et al.* 2006) that may lead to important changes in their foraging behaviour, depending on each individual's nutritional requirements (Molokwu *et al.* 2011). When availability of selected food decreases drastically below a given threshold, the energetic cost of the search exceeds the benefit of consumption (Crawley 1983). Thus, during unfavourable periods, herbivores commonly opt to broaden their trophic niche (Mosca Torres and Puig 2010).

Generalist herbivores are faced with a variety of foods that differ in their nutritional value and in the costs involved in their search, intake and post-ingestive processing (Dearing *et al.* 2000). In particular, the diet of herbivorous birds is constrained by fibre content and plant secondary compounds, both of which impose restrictions on nutrient extraction from the cells (Lopez-Calleja and Bozinovic 2000). As a consequence, food items with high fibre content have low digestibility and are less selected than low-fibre items (Hume *et al.* 1993). Furthermore, in nutrient-poor environments such as deserts, plants develop secondary metabolites (e.g. terpenes and/or phenols) that act as anti-herbivore constitutive defences (Endara and Coley 2010), which are energetically costly for herbivores to detoxify (Sorensen *et al.* 2005). For this reason, individuals tend to minimise the consumption of species with large amounts of secondary compounds (Freeland and Janzen 1974). Another nutritional challenge that herbivores must overcome is related to the low concentration of essential nutrients in plant tissues (e.g. nitrogen), which varies greatly among plant species and parts of a single plant (Crawley 1983). Some herbivores therefore prioritise nutritional benefits that can be obtained from the ingested food (Weckerly

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1994). Under this hypothesis, herbivores are more selective particularly during periods of lower food availability, because only a minor fraction of food is palatable or maintains good nutritional quality (Weckerly and Kennedy 1992).

The Puna Rhea (*Rhea tarapacensis*) is a large, flightless herbivorous bird (Cajal 1988) associated with arid environments of central-western and north-western Argentina, northern Chile, south-western Bolivia and southern Peru (BirdLife International 2015). In Argentina, it is found mainly in the Puna desert, which is characterised by the absence of permanent rivers and lakes, and by the strong seasonality in rainfall (Cabrera 1976; BirdLife International 2015). At present, this ratite is illegally hunted by local people for its meat, eggs, feathers and skin, as well as for other sub-products used for food, medicinal and ritual purposes (Hernández *et al.* 2015). Consequently, this species has been categorised as 'Nearly threatened' by the IUCN (2015) and included in Appendix I of CITES (2015). However, little is known about the ecological requirements of the Puna Rhea, particularly relating to its diet (Cajal 1988; Lleellish *et al.* 2007; Echaccaya Álvarez 2013).

The aim of this study was to describe the diet and food selection by the Puna Rhea relative to the abundance of food in the Austral Puna desert. This environment has marked seasonal precipitations and it is therefore expected that as plant cover decreases during the dry period the foraging behaviour of the Puna Rhea will become less selective and more species will be incorporated into its diet.

Methods

Study area

The study was conducted in the Don Carmelo Multiple Use Private Reserve (400 km^2) located in the Andean Precordillera, San Juan, Argentina (30° 56′ 52″ S, 69° 05′ 02″ W; 3100 m a.s.l.). The dominant environment corresponds to the Puna desert subregion (Cabrera 1976) and in sectors below 3000 m a.s.l. the vegetation is representative of the Monte ecoregion (Márquez 1999). The climate is cold and dry (mean annual temperature: 10°C), with a wide daily thermal amplitude and annual precipitation below 100 mm, concentrated in summer (October to February) (Martínez Carretero 1995). This reserve harbours a well-managed Puna Rhea population (0.75 ind/km^2), where suitable habitat is not fragmented and disturbances such as mining, agriculture or mass tourism are banned (Marinero *et al.* 2014).

Table 1. Sampling dates during the dry and wet periods of each year from 2011 to 2014 and number of faeces of the Puna Rhea collected in the Don Carmelo Multiple Use Private Reserve

Year	Season	Month	Period	Number of faeces
1st	Autumn	April 2011	1st dry	46
	Winter	September 2011 (first week)		
	Spring	November 2011	1st wet	39
	Summer	December 2011 (last week)/ March 2012 (first week)		
2nd	Autumn	April 2012	2nd dry	38
	Winter	August 2012		
	Spring	November 2012	2nd wet	36
	Summer	February 2013		
3rd	Autumn	April 2014	3rd dry	41
	Winter	July 2014		
	Spring	October 2014	3rd wet	36
	Summer	December 2014		
Total faeces				236

Data were collected periodically over 3 years from 2011 to 2014. Given that the study area is a seasonal arid environment, we considered it appropriate to group the data into dry (March to September) and wet (October to February) periods for each year (Table 1).

Food abundance

Plant cover was considered a suitable estimator of food abundance as it is a direct indicator of vegetal biomass (Bonham 2013). On each sampling date, plant cover was recorded by walking the 20 transects established between transects used to determine the diet of the Puna Rhea (see below). Each transect was 100 m in length and was combined with 10 1 m^2 quadrats. In each quadrat, the percentage cover of each plant species was estimated visually as the projection of leaf area on the ground. Total plant cover was also determined (100% − % of bare ground). The relative frequency of each plant species was calculated by dividing the projection for each species by the total plant cover of all available species, expressing the result as a percentage.

Puna Rhea diet

On each sampling date, droppings of the Puna Rhea were collected by walking along 20 transects 500 m in length which were distributed randomly at intervals of at least 400 m. The droppings were initially examined to separate plant (leaves, seeds and fruits) from animal (invertebrates and vertebrates) material. However, no animal material was found in the faeces. The plant material was analysed using the microhistological technique (Holecheck *et al.* 1982). For this purpose, and with the aim of homogenising particle size, each dropping was ground using an electric mill, cleared with sodium hypochlorite and filtered through two sieves (0.249 and 0.149 mm). For each dropping, four microscope slides were prepared following the glycerine mounting technique (Castellaro *et al.* 2007; Zarlavsky 2014), and 50 microscope fields on each slide were examined systematically under a microscope at ×400. Each field had at least one identifiable epidermal fragment consisting of three or more diagnostic structures of the same species. These histological characteristics were compared with reference slides, which were prepared with plants collected from the study area following the same procedure used for the faeces. Wherever possible the plant material was identified to species level. Finally, the relative frequency of occurrence (RFO) for each species was calculated by dividing the number of microscopic fields where it occurred by the sum of frequencies of all identified species (Holecheck and Gross 1982), and then multiplying the result by 100.

Data analysis

Plant abundance and diet composition were compared among periods using the Kruskall–Wallis ANOVA test when data were non-normal, and via mixed models when they were heteroscedastic. In the latter case, the variance was modelled using the varIdent function (Pinheiro *et al.* 2016), considering the plant cover or the species proportion in the diet as dependent variables, whereas the periods were treated as fixed effects, and the sampling years represented the random effect. Lastly, Fisher´s least significant difference (LSD) comparison was carried out a posteriori, taking the differences as significant when $P \leq 0.05$. The statistical analyses were performed with Infostat software (Di Rienzo *et al.* 2016). Only plant species with relative frequencies of use or availability above 5% were considered for comparisons. Data are expressed as mean ± standard error. Diet selectivity was determined via Bonferroni's simultaneous confidence intervals (Neu *et al.* 1974; Martella *et al.* 1996), which were classified as being selectively consumed (S), neutrally consumed (N) or rejected (R), depending on whether the expected proportion was located below, within, or above the confidence intervals of the observed dietary frequency. Only those plant species found at least once in the diet were included in this test.

Results

Food abundance

Total plant abundance did not vary during the study among the dry and wet periods ($F_{5,\ 0.18} = 75.25$, $P = 0.970$) (Table 2). Of the 39 plants constituting the food availability throughout the study, only eight species had an abundance >5% during some periods, but without a predictable pattern. Two of these eight species showed higher plant cover during consecutive dry and wet periods: the shrub *Lycium* spp. ($F_{5,\ 6.25} = 220.65$, $P < 0.001$) and the graminoid *Oxychloë* sp. ($H = 4.95$, $P = 0.010$). Another species, the grass *Bouteloua barbata* had higher abundance during consecutive three periods ($F_{5,\ 11.27} = 105.17$, $P < 0.001$). The remaining plant species had higher cover during only one sampling date (dry or wet): *Artemisia mendozana* (3rd wet;$F_{5,\ 9.60} = 423$, $P < 0.001$); *Baccharis polyfolia* (1st wet; $F_{5,\ 3.84} = 15.33$, $P < 0.001$); *Sphaeralcea philippiana* (2nd wet; $F_{4,\ 7.19} = 28.61$, $P < 0.001$); *Stipa* spp. (2nd dry; $F_{5,\ 4.69} = 211.41$, $P = 0.003$); and *Nastanthus glomeratus* (1st wet; $H = 6.69$, $P = 0.001$) (Table 2).

Puna Rhea diet

The Puna Rhea diet consisted of 98.75% leaf matter, with very low proportions of fruit tissues of *Lycium* spp. (<0.25%) and flowers of *Chuquiraga ruscifolia* (<0.75%). Other components, such as insect remains, were completely absent in the faeces. A total of 20 plant species were observed in the diet, representing 51% of those recorded in the study area. Only nine of these species had a relative frequency >5% in the diet. Proportions of consumption within species varied throughout the study: three species were highly consumed during most of the study (three or four of the six periods): the shrubs *C. ruscifolia* ($H = 26$; $P < 0.001$) and *Lycium* spp. ($H = 20.08$; $P < 0.001$); and the herbaceous plant *Gomprhena pumila* ($H = 41.70$; $P < 0.001$). Others showed higher proportion in the diet during consecutive dry and wet periods, namely *Junellia seriphioides* (1st dry and wet; $H = 29.18$; $P < 0.001$), or periods of different years as in the case of the herbaceous plant *Hoffmannseggia doellii* (2nd dry and 3rd wet; $F_{5,\ 4.07} = 20.64$, $P = 0.003$). Furthermore, some trophic resources were consumed in larger proportions only during wet periods, such as the shrub *Tetraglochin alatum* (2nd and 3rd wet; $H = 35.20$; $P < 0.001$) and *Acantholippia seriphioides* (1st wet; $H = 9.20$; $P < 0.001$), whereas *Adesmia* sp. was consumed more in one dry period (3rd dry; $H = 7.80$; $P < 0.001$). Lastly, the grass *Stipa* spp. was consumed in lower proportions throughout the study ($H = 2.83$, $P = 0.520$) and almost under half the species were not consumed at all (*A. mendozana*, *A. trifurcata*, *Larrea cuneifolia*, *L. divaricata*, *L. nitida*,*Trycicla spinosa*, *Calceolaria luxurians*, *Taraxacum officinale*, *Deyeuxia* spp., *Carex* sp., *Eleocharis* sp., *Juncus* spp. and *Oxychloë* sp.) (Table 2).

Table 2. Proportion (mean ± standard error) of food abundance in the environment and consumed by the Puna Rhea during the dry and wet periods of each year from 2011 to 2014. The rows show significant differences between periods for availability (upper case letters) and diet (lower case letters) ($P < 0.05$). Only those plant species with values >5% in diet and/or availability during one or more periods are included; 0 indicates absence of the plant species in the environment or in faeces

	Availability						Diet					
	1°		2°		3°		1°		2°		3°	
Species	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Shrubs												
Acantholippia seriphioides	0	0.19 (0.14)	0.44 (0.34)	0.53 (0.53)	0.79 (0.79)	0.35 (0.23)	0	5.73^{a} (2.04)	3.79^{ab} (1.28)	0	1.33^{b} (0.95)	2.59^{ab} (1.63)
Adesmia sp.	0.05 (0.04)	0.42 (0.40)	0	0.12 (0.12)	0.57 (0.57)	0	0	0	8.2^{b} (3.09)	0	16.4^{a} (5.67)	0
Artemisia mendozana	15.54^{C} (2.32)	26.70^{AB} (2.58)	17.49^{BC} (2.25)	16.81^{BC} (2.6)	20.86^{BC} (3.08)	47.71^{A} (2.89)	0	0	0	0	0	0
Baccharis polifolia	2.72^{B} (1.06)	6.39^{A} (1.50)	0.9^{B} (0.6)	1.61^{B} (0.85)	0.40^{B} (0.34)	0.95^{B} (0.59)	0	0	0	0	0	0
Chuquiraga ruscifolia	0.87 (0.64)	0.05 (0.05)	0.69 (0.48)	1.77 (1.17)	1.12 (0.80)	0.03 (0.44)	13.57^{ab} (2.02)	10.63^{ab} (1.63)	23.91^{a} (3.57)	23.85^{a} (3.9)	20.46^{a} (6.48)	0.72^{b} (0.4)
Junellia seriphioides	1.30 (0.76)	1.06 (0.44)	0.36 (0.17)	0	0.35 (0.31)	0.81 (0.43)	15.94^{a} (2.67)	15.78^{a} (3.09)	3.42^{b} (1.25)	5.86^{b} (1.05)	5.49^{b} (2.03)	5.29^{b} (4.2)
Lycium spp.	11.36^{B} (2.04)	8.21^{AB} (1.51)	10.6^{AB} (0.81)	7.49^{B} (1.35)	20.37^{A} (2.80)	17.39^{A} (2.03)	29.69^{a} (2.54)	23.16^{a} (1.97)	17.17^{b} (2.09)	23.83^{a} (3.38)	15.73^{b} (3.18)	27.02^{a} (4.55)
Tetraglochin alatum	3.59 (1.05)	1.31 (0.54)	2.19 (0.86)	1.06 (1.06)	0.78 (0.44)	0	11.72^{bc} (2.45)	12.7^{c} (1.59)	12.45^{c} (2.82)	24.48^{a} (4.91)	16.35^{bc} (5.41)	46.42^{a} (5.71)
Forbs												
Gomphrena pumila	0.30 (0.21)	1.69 (0.72)	1.12 (0.55)	4.89 (1)	0	0.62 (0.37)	11.2^{a} (1.59)	12.65^{a} (2.54)	0.41^{b} (3.65)	7.93^{b} (1.8)	0.99^{a} (0.75)	6.53^{a} (1.71)
Hoffmannseggia doellii	0.07 (0.07)	0.02 (0.02)	0.84 (0.43)	0.66 (0.34)	0.14 (0.07)	0.84 (0.37)	2.1^{b} (0.64)	0.83^{b} (1.49)	6.31^{a} (1.94)	1.01^{b} (2.01)	3.03^{b} (2.4)	6.63^{a} (3.24)
Nastanthus glomeratus	5.09^{AB} (1.37)	5.34^{A} (1.34)	2.08^{BC} (0.96)	1.57^{BC} (0.74)	0.17^{C} (0.09)	1.03^{BC} (0.41)	0	0	0	0	0	0
Sphaeralcea philippiana	0.11^{C} (0.08)	0.66^{BC} (0.23)	0.26^{BC} (0.19)	6.69^{A} (1.84)	0	1.85^{B} (0.61)	1.24 (0.46)	1.44 (0.49)	4.75 (1.53)	3.08 (1.41)	4.51 (2.34)	0.26 (0.26)
Grasses												
Bouteloua barbata	3.78^{B} (1.17)	1.95^{B} (0.59)	12.57^{A} (2.07)	10.13^{A} (1.64)	11.19^{A} (2.03)	3.53^{B} (0.60)	1.71 (1.11)	4.37 (1.38)	0.46 (0.27)	0.57 (0.34)	0.28 (0.28)	0.29 (0.29)
Stipa spp.	11.78^{AB} (1.95)	5.68^{B} (1.14)	16.7^{A} (2.21)	10.36^{AB} (1.86)	9.49^{AB} (1.88)	8.51^{B} (1.24)	2.45 (0.58)	1.8 (1.67)	5.19 (1.76)	4.21 (1.25)	5.34 (3.26)	2.07 (0.7)
Graminoids												
Oxychloë sp.	15.09^{A} (2.46)	14.48^{A} (2.33)	8.68^{AB} (1.99)	8.05^{AB} (1.98)	11.20^{AB} (3.08)	3.77^{B} (1.08)	0	0	0	0	0	0
Plant cover*	34.83	38.30	35.42	30.80	29.14	19.8						

* Mean (± standard error) obtained by dividing total plant cover by the number of samples per period ($n = 400$ squares).

Species not included (<5%): *Azorella trifurcata, Ephedra chilensis, Fabiana peckii, Larrea cuneifolia, L. divaricata, L. nitida, Senecio gilliesianus, Trycicla spinosa, Astragalus arequipensis, Calceolaria luxurians, Descurainia* sp., *Erodium cicutarium, Taraxacum officinale, Bromus unioloides, Deyeuxia* spp., *Hordeum pubiflorum, Panicum urvilleanum, Poa annua, Scleropogon brevifolium, Carex* sp., *Eleocharis* sp., *Juncus* spp., *Maihueniopsis glomerata, Pterocactus reticulatus.*

Diet selection

Selectivity was not correlated with the total vegetal cover in the environment and selection of trophic resources was not correlated with the abundance of the different plant species. With the exception of the shrub *Lycium* spp. (2nd wet), the most abundant species were not selected (Tables 1 and 2). Throughout the entire study period only three shrub species, which generally had continuous availability but abundance <5%, were consumed in higher quantities than expected: *J. seriphioides*, *T. alatum* and *C. ruscifolia*. Others were selectively eaten in specific periods, such as the shrub *Acantholippia seriphioides* (1st wet), or in more than one period as the forb *H. doellii* (2nd and 3rd dry; and 3rd wet). There were also some trophic resources that were selectively eaten during one period but in others were consumed in similar proportion to their availability (i.e. neutrally consumed), such as *Adesmia* sp., *G. pumila* and *S. philippiana*. Both grasses *Stipa* spp. and *B. barbata* were rejected in most periods (Table 3).

Discussion

To our knowledge this is the first paper describing the foraging strategy of the Puna Rhea. The diet of this ratite was completely herbivorous and mostly folivorous, possibly owing to the limited change in plant availability among periods and the perennial nature of the food consumed. The lack of other components in the diet, such as insects, which are commonly consumed by rheas as a source of proteins and vitamins (Martella *et al.* 1996; Paoletti and Puig 2007), could be attributed to the low availability of this resource in

Table 3. Selected plant species (S) rejected (R) or foraged neutrally (N) by the Puna Rhea during the dry and wet periods of each year from 2011 to 2014. Bonferroni simultaneous confidence intervals are indicated as LL (lower limit) and UL (upper limit). Acronyms: expected proportion (EP); observed proportion (OP). Plant species: *Acantholippia seriphioides* (AS), *Adesmia* sp. (AD), *Chuquiraga ruscifolia* (CR), *Junellia seriphioides* (JS), *Lycium* spp. (LY), *Tetraglochin alatum* (TA), *Gomphrena pumila* (GP), *Hoffmannseggia doellii* (HD), *Sphaeralcea philippiana* (SP), *Bouteloua barbata* (BB), *Stipa* spp. (ST)

	1st				2nd				3°			
	DRY		WET		DRY		WET		DRY		WET	
	EP	**OP (LL – UL)**	EP	OP (LL – UL)	EP	OP (LL – UL)	EP	OP (LL – UL)	EP	OP (LL – UL)	EP	OP (LL – UL)
Shrubs												
AS			0.006	0.057 (0.039 – 0.075)^{S}								
AD					0.007	0.082 (0.060 – 0.103)^{N}			0.012	0.164 (0.134 – 0.193)^{S}		
CR	0.024	0.135 (0.108 – 0.163)^{S}	0.001	0.109 (0.084 – 0.133)^{S}	0.011	0.272 (0.237 – 0.306)^{S}	0.027	0.239 (0.204 – 0.183)^{S}	0.023	0.204 (0.172 – 0.237)^{S}		
JS	0.016	0.159 (0.130 – 0.189)^{S}	0.035	0.157 (0.129 – 0.186)^{S}			0.000	0.059 (0.040 – 0.037)^{S}	0.007	0.054 (0.037 – 0.073)^{S}	0.027	0.068 (0.048 – 0.089)^{S}
LY	0.315	0.310 (0.273 – 0.347)^{N}	0.279	0.231 (0.199 – 0.264)^{N}	0.192	0.162 (0.133 – 0.190)^{N}	0.169	0.238 (0.204 – 0.324)^{S}	0.438	0.180 (0.150 – 0.212)^{R}	0.604	0.270 (0.235 – 0.306)^{R}
TA	0.010	0.117 (0.091 – 0.143)^{S}	0.043	0.100 (0.077 – 0.124)^{S}	0.037	0.105 (0.081 – 0.128)^{S}	0.001	0.245 (0.210 – 0.160)^{S}	0.016	0.133 (0.106 – 0.161)^{S}	0.000	0.458 (0.419 – 0.499)^{S}
Forbs												
GP	0.008	0.117 (0.0912 – 0.142)^{S}	0.000	0.126 (0.100 – 0.152)^{S}			0.110	0.079 (0.058 – 0.163)^{N}			0.009	0.062 (0.043 – 0.082)^{S}
HD					0.014	0.063 (0.044 – 0.082)^{S}			0.002	0.084 (0.062 – 0.107)^{S}	0.007	0.065 (0.046 – 0.085)^{S}
SP					0.048	0.004 (0.031 – 0.064)^{N}	0.118	0.031 (0.017 – 0.134)^{N}	0.000	0.056 (0.038 – 0.075)^{S}		
Grasses												
BB			0.078	0.043 (0.027 – 0.059)^{R}	0.212	0.005 (–0.001 – 0.010)^{R}	0.227	0.006 (0.000 – 0.227)^{N}	0.238	0.002 (–0.001 – 0.007)^{R}	0.076	0.002 (–0.001 – 0.007)^{R}
ST	0.024	0.327 (0.012 – 0.036)^{N}	0.195	0.018 (0.007 – 0.028)^{R}	0.312	0.052 (0.035 – 0.069)^{R}	0.232	0.042 (0.026 – 0.257)^{N}	0.202	0.053 (0.035 – 0.071)^{R}	0.201	0.019 (0.009 – 0.031)^{R}

Species not included (<5%): *Azorella trifurcata*, *Ephedra chilensis*, *Fabiana peckii*, *Larrea cuneifolia*, *L. divaricata*, *L. nitida*, *Senecio gilliesianus*, *Trycicla spinosa*, *Astragalus arequipensis*, *Calceolaria luxurians*, *Descurainia* sp., *Erodium cicutarium*, *Taraxacum officinale*, *Bromus unioloides*, *Deyeuxia* spp., *Hordeum pubiflorum*, *Panicum urvilleanum*, *Poa annua*, *Scleropogon brevifolium*, *Carex* sp., *Eleocharis* sp., *Juncus* spp., *Maihueniopsis glomerata*, *Pterocactus reticulatus*.

Andean environments above 3000 m a.s.l. (Marquet *et al.* 1998). Another component barely consumed by the Puna Rhea was *Lycium* spp. seeds that are used by the other species *R. pennata* as an energy supplement (Paoletti and Puig 2007). Instead, the Puna Rhea supplements its diet with the herbaceous *H. doellii* and *S. philippiana*, both considered excellent natural forage, and with higher protein levels than *Lycium* spp. (Ulibarri 1979; Cuevas *et al.* 2013).

The Puna Rhea consumed a large variety of the plant species recorded in the study area, a behaviour corresponding to a generalist foraging strategy (Recher 1990). From an evolutionary perspective, this is considered an adaptive strategy for herbivorous species that live in arid environments because it permits them to be flexible in their diet, consuming diverse types of vegetal species to cover their nutritional requirements (Puig *et al.* 1996). This generalist exploitation of various types of forage is facilitated in the rheas by their post-gastric digestion, in which their very long and relatively dilated caeca and their colon contain numerous aerobic and anaerobic bacteria, both serving as fermentation chambers that efficiently and rapidly reduce cellulose and hemicelluloses (Noble 1991; Sales 2006; Frei *et al.* 2015).

Clearly, the shrub and herbaceous species represent important food resources for this species, as they were always selectively consumed irrespective of their availability. Possibly, this selection occurs because of their high nutritional value, given their high protein content and low fibre content compared to graminoids and monocot grasses from the Puna desert (Borgnia *et al.* 2010). This selective consumption by the Puna Rhea represents a foraging behaviour common to the other rhea species, namely the Greater Rhea (*Rhea americana*) and Lesser Rhea (*R. pennata*) (Martella *et al.* 1996; Paoletti and Puig 2007). However, both rheas from arid environments, the Puna Rhea and Lesser Rhea, show differences regarding their use of graminoids, which are found only in vegas (also called 'mallines' or 'bofedales'), because these habitats have availability of permanent water during most of the year (Squeo *et al.* 2006). Despite the presence of vegas in our study area, the selectivity exhibited by the Puna Rhea coincides with that observed in Lesser Rheas of northern Patagonia, where vegas are absent (Puig *et al.* 2013). On the contrary, it differs from the selectivity of those populations of southern Patagonia, where vegas exist and are used by these species, which incorporate a small amount of graminoids in their diet (Bonino *et al.* 1986; Bellis *et al.* 2006). Possibly, the avoidance of vegas by rheas in our study area is related to a higher predation risk by their main predator, the Puma (*Puma* *concolor*) (Cappa *et al.* 2014) and the difficulty of escape, given the rough topography that encloses the vegas in this region (Marinero *et al.* 2015).

According to our hypothesis, we expected the Puna Rhea to become less selective as plant cover decreases during the dry period. However, the Puna Rhea always exhibited a selective foraging behaviour despite the fact that the plant cover remained constant, probably facilitated by the continuous availability of selected food. It should be noted that the absence of seasonal changes in plant cover was also observed in other research conducted in the Puna (Paoletti and Puig 2007). Besides, in our study area, the abundance of vegetal species did not lead to selective foraging by the Puna Rhea, which always selectively consumed the less abundant shrubs *J. seriphioides*, *T. alatum* and *C. ruscifolia*. This selective foraging behaviour can be better understood under the toxin dilution hypothesis (Freeland and Janzen 1974), since the most abundant species such as *A. mendozana* (and other shrubs not consumed by the Puna Rhea) belong to genera and species containing phenolic resins, terpenes and alkaloids, among other compounds (Lima *et al.* 2008, 2015; Ríos *et al.* 2008). These chemical compounds induce a decrease in consumption of those foods that contain them because they inhibit digestive enzymes, and reduce the digestion and absorption of nutrients (Mangione *et al.* 2004), and when ingested in large quantities may cause weight loss, an imbalance in water and energy budgets, and even death (Freeland and Janzen 1974). Likewise, this selective consumption of species with low concentrations of secondary compounds (phenols) has been described in ostriches inhabiting arid regions of southern Africa (Milton *et al.* 1994).

The plant species selected by the Puna Rhea during the study can be characterised, in general, by their low relative protein content, compared to the two rejected species and the 13 species that were not consumed (see Benítez *et al.* 2006). However, there were different periods when this species selectively consumed both shrubs (*Adesmia* sp.) and herbaceous species (*G. pumila*, *H. doellii* and *S. philippiana*), which are characterised by their high protein content (Cuevas *et al.* 2013). In this sense the selection of food resources in terms of their nutritional value is a behaviour that the Puna Rhea shares with northern populations of the Lesser Rhea (Puig *et al.* 2013).

The highly selective behaviour of the Puna Rhea leads us to think that this species could be negatively affected by the diet overlap with other herbivores that inhabit the Puna, such as the Guanaco (*Lama guanicoe*), which consumes a large variety of shrubs and herbs (Puig *et al.* 2008).

In conclusion, the diet of the Puna Rhea was found to be determined by a selective foraging strategy that did not correspond to the level of abundance of the plant species. Hence, the incidence of other factors such as nutritional quality, mainly in terms of plant secondary compounds and fibre content, and habitat use, should be taken into account in future studies on the nutritional ecology of this species. In addition, based on these results, conservation efforts aimed at the Puna Rhea should be focused on maintaining the availability of the few preferred plant species and reducing possible competition with other generalist herbivores.

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