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RESEARCH ARTICLE

Selective consumption of rodents by the Variable hawk *Geranoaetus polyosoma* (Accipitriformes: Accipitridae) in the Atacama Desert, northern Chile

Andrés Muñoz-Pedreros[1], Heraldo V. Norambuena[2,3], Claudia Gil[2], Jaime Rau[2,4]

[1]*Núcleo de Investigación en Estudios Ambientales NEA, Facultad de Recursos Naturales, Departamento de Ciencias Ambientales, Universidad Católica de Temuco. Casilla 15-D, Temuco, Chile.*
[2]*Programa de Conservación de Aves Rapaces, Centro de Estudios Agrarios y Ambientales. Casilla 164, Valdivia, Chile.*
[3]*Departamento de Zoología, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción. Casilla 160-C, Chile.*
[4]*Laboratorio de Ecología, Departamento de Ciencias Biológicas & Biodiversidad, Universidad de Los Lagos. Casilla 933, Osorno, Chile.*
Corresponding autor: Heraldo V. Norambuena (buteonis@gmail.com)

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ABSTRACT. *Geranoaetus polyosoma* (Quoy & Gaimard, 1824) is a diurnal raptor widely distributed in South America. Although the trophic ecology of this bird has been more studied in the southern extreme of its range, little information is available on its dietary response to prey supply in desert environments. In the present study, we report on the trophic ecology of *G. polyosoma* in a sub-urban desert zone in northern Chile, with the following objectives: (1) to quantitatively describe its diet and (2) to determine its dietary selectivity in response to prey supply in the study area. The diet of *G. polyosoma* consisted mainly of rodents (97.2%). A greater preference ($p < 0.05$) was observed for the following large prey items (> 19.5 g): two native rodent species, *Phyllotis xanthopygus* (Waterhouse, 1837) and *Eligmodontia puerulus* (Philippi, 1896); and two introduced rodent species: *Rattus rattus* (Linnaeus, 1769) and *R. norvegicus* (Berkenhout, 1769).

KEY WORDS. Diet, predation, Red-backed hawk, trophic ecology.

INTRODUCTION

The diurnal raptor Variable hawk, *Geranoaetus polyosoma* (Quoy & Gaimard, 1824), is widely distributed in South America, from the central Andes of Colombia to Patagonia and Tierra del Fuego, including the Falkland Islands (Thiollay 1994, Ferguson-Lees and Christie 2001). The common subspecies in mainland Chile is *Geranoaetus polyosoma polyosoma*, present in many environments (e.g. arid and sub-humid zones, low-lying land, mountain shrubland, temperate forests, meadow shrubland and agroecosystems), from sea level to 4500 m in elevation; it also frequents sub-urban zones, entering through mountain chains (Pavez 2004).

In Chile and Argentina, the diet of the Variable hawk has been studied for only a few eco-regions (sensu Dinerstein et al. 1995). Consequently, information on the trophic ecology of this raptor bird is scarce, especially in arid environments (Ponce et al. 2018). The information available in the literature documents a diet based mainly on rodents, birds, reptiles, amphibians and invertebrates (Schlatter et al. 1980, Jiménez 1995, Figueroa et al. 2003, Baladrón et al. 2006, Travaini et al. 2012, Baladron 2014, Valladares et al. 2015, Ponce et al. 2018). Its dietary selectivity is subjected to geographical variations; for example, it is a generalist in Argentinean Patagonia (Monserrat et al. 2005), and a specialist on the south-east coast of the Province of Buenos Aires (Baladrón et al. 2006). Its trophic ecology has been insufficiently studied in the central and northern part of its range (Travaini et al. 2012, Ponce et al. 2018), and its dietary response to prey supply is unknown.

The Atacama Desert is one of the largest hyperarid deserts in the world. Desertification of the region began 14,000 years ago during the aridification of the world's climate. Sedimentological data from the Middle Miocene to the Upper Pliocene successions in the modern Atacama Desert indicate that a semi-arid climate persisted from 8 to 3 kyr, punctuated by a more arid phase around 6 kyr. Hyperaridity therefore began only in the Late Pliocene (Hartley and Chong 2002). Climatic conditions in this desert are extreme and primary production is low, limiting the supply of prey for top predators like birds of prey (Polis 1991, Megías et al. 2011, Carevic et al. 2013). Under these conditions, subsidiary sources are important for maintaining predator populations

(Megías et al. 2011, Kristan et al. 2004). Urban areas can offer a greater variety of food, independent of the natural supply in the area (Kristan et al. 2004), and this new supply and consumption may be important for human health if these allochthonous prey are health pests like rodents of the genera *Rattus* and *Mus* (Bordes et al. 2015).

In this study we report the trophic ecology of *G. polyosoma* in a sub-urban area of an oasis in the Atacama Desert, Chile, describing its diet quantitatively and determining its dietary selectivity in response to the supply of prey and the consumption of allochthonous prey species.

MATERIAL AND METHODS

Ojo Opache (22°29'S; 69°01'W) is a suburban oasis located by the Loa River, 5 km south-west of Calama (Fig. 1). It lies in the central valley of the Antofagasta Region of Chile. The Atacama Desert covers most of the Region, with a prevailing desert climate varying between coastal desert, normal desert and high-altitude marginal desert (Köppen 1948). The climate of the region is very arid, with scarce precipitation and almost no rivers. The desert climate is absolute, with relief formations and high soil salinity. The river Loa is the only important watercourse in the area. The vegetation belongs to the flash-flood desert type of the Andean desert sub-region (Gajardo 1994).

We collected 201 pellets from a *G. polyosoma* nesting site in a ravine in Ojo Opache during August 2002. Considering the meal-to-pellet interval reported by Houston and Duke (2007), we estimate that 201 pellets correspond to pellets accumulated under nest during 41-55 days for two hawks. Pellets were measured with a caliper, accuracy 0.1 mm, and dry weight was obtained in a digital scale, accuracy 0.01 gr. Prey items were identified to species level in micro-mammals, and family and genus level in birds and insects when the species could not be identified. We used as identification guides Reise's key (1973) and the insect guides of Peña (1986) and Arias (2000), as well as reference material from zoological collections. The contribution of each prey species to the biomass consumed was estimated following Marti (1987): $B_i = 100[(Sp_i N_i)/\Sigma(Sp_i N_i)]$, where Sp_i is the weight of species i, Ni is the number of individuals of species i consumed and Bi is the percentage of the total biomass contributed by species i. Mass values of mammals were obtained from the databases of the Chilean National History Museum and from the values documented by Muñoz-Pedreros (1992), Jaksic (2001) and Muñoz-Pedreros and Gil (2009). Mass values of birds were obtained from the literature (Morgado et al. 1987, Egli 1996). To estimate the diversity and abundance of rodents at the same area we used Sherman traps with an effort of 1,077 trap/nights.

The following trophic analysis were used to characterize diet: (a) diversity of prey consumed through the Shannon-Wie-

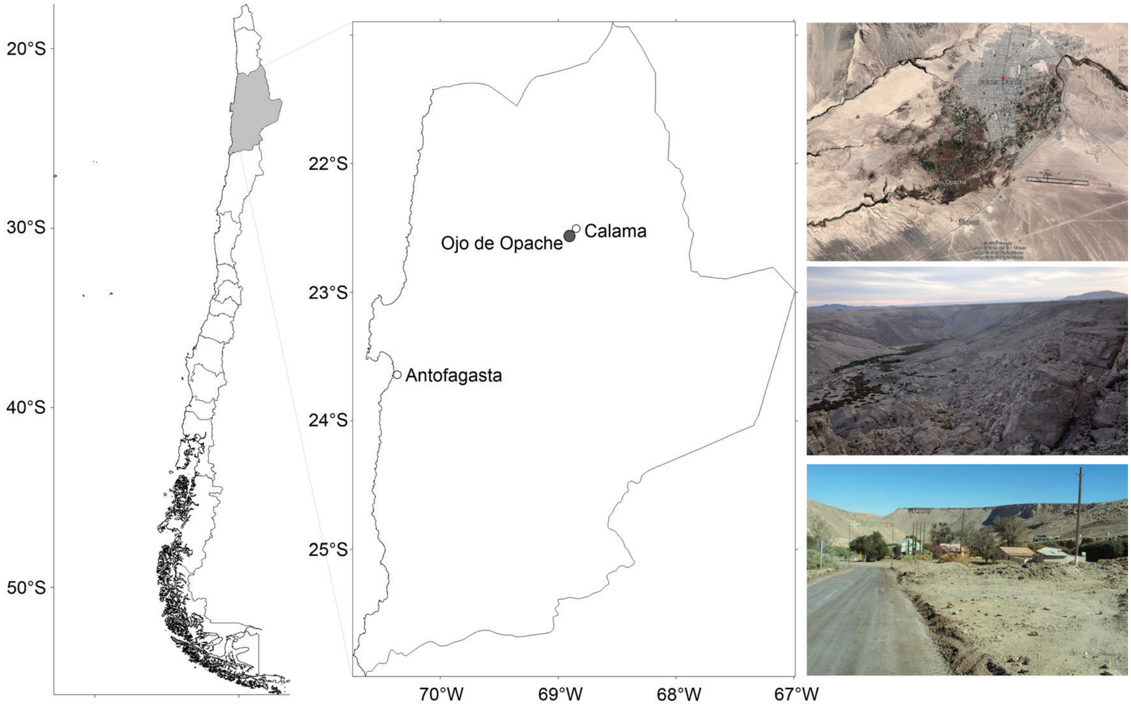

Figure 1. Map showing the location of Ojo Apache at Antofagasta region, Chile; and the type of habitat present in the area. Satellite view of the Ojo Apache (top left); broad view of the valley, showing the topography and main phytophysiognomy (in the centre); and detailed view of the local vegetation (bottom left).

ner index, being influenced by two main components: richness and equity. The formula for this index is: $H' = -\sum (p_i \times \log_2 p_i)$, where p_i is the proportion of the total number of individuals of the species in the sample. Its value ranges from zero, when there is only one species represented, to the maximum (H'max) which corresponds to $\log_2 S$. (b) Pielou's evenness index (J) was also calculated according to the equation: J= H'/H'max. The values of this index fluctuate between 0 (minimum heterogeneity) and 1 (maximum heterogeneity, i.e. the species are equally abundant) (Magurran 1998). (c) Simpson's reciprocal measure (Simpson 1949) or Levin's (1968) index: $B = 1 \Big/ \sum_{i=1}^{n} p_i^2$, where p_i is the relative occurrence of prey taxon $_i$ in the diet of a given species. This formula was used for the smaller taxonomic categories of prey. The trophic niche breadth values range from 1 (when only one category of prey is consumed) to n (when all categories of prey are consumed in equal amounts). (d) The dietary selectivity was calculated for more than 2 kinds of prey in the diet (Jaksic 1979) using: $\chi^2 = \sum (f_o - f_e)^2 \big/ f_e$ where f_o observed frequency of prey items found in the pellets and f_e expected frequency of prey items obtained in the field. The supply of prey in the study area was obtained from a synchronic study of mammals in the Ojo Opache area, using a grid of 215 Sherman traps baited with crushed oats. The frequency and relative abundance data of the micromammals captured in Ojo Opache were used to calculate the dietary selectivity. The information was processed using Biodiversity Professional software, version 2 (McAleece et al. 1998).

RESULTS

Morphometry of pellets and diet composition. The 201 compact, measurable pellets were subjected to morphometric analysis. Mean values recorded were length 26.6 mm (SD ± 7.94), breadth 19.5 mm (SD ± 5.68) and height 16.1 mm (SD ± 5.23). The number of prey remains recorded was 290, (1.44 per pellet), of which 287 were vertebrates and only three were invertebrates (Table 1).

Rodents made up most of the diet (97.2%) of *G. polyosoma*, while marsupials (0.7%) and birds represented only a marginal contribution (1.0%). The most frequent prey species, in descending order, were *Mus musculus* Linnaeus, 1758, *Eligmodontia puerulus* (Philippi, 1896), *Phyllotis xanthopygus* (Waterhouse, 1837) and *Rattus rattus* (Linnaeus, 1769). The rodents which contributed most to the diet by biomass, in descending order, were: *R. rattus*, *Rattus* sp., *P. xanthopygus*, *Rattus norvegicus* (Berkenhout, 1769) and *M. musculus*. Exotic rodent species (*Rattus* spp. and *M. musculus*) together contributed more than half the biomass (57.7%) of the diet of *G. polyosoma* in the Ojo Opache (Table 1). The equity was high (H' = 0.82, Hmax = 0.954, J = 0.86), meaning that the prey frequency tends towards heterogeneity.

Trophic niche breadth and diet selectivity. During field sampling, 84 specimens collected were from four species (Table 2). The χ^2 test indicated that, for this location, *G. polyosoma* did not consume all the vertebrate prey species in the same propor-

Table 1. Description of the diet of *Geranoaetus polyosoma* in Ojo Opache, central valley of the Antofagasta Region, Chile. (N) Number of individual, (%F) percentage frequency, (%B) percentage biomass, (B) Levins' Index, (Bsta) Standardised Levins' Index, (H') Shannon-Wiener Index.

Prey item	Mass (g)	N	%F	%B
Thylamys pallidior	31.2	2	0.7	0.4
Subtotal Marsupials		2	0.7	0.4
Phyllotis xanthopygus	57.3	36	12.4	12.1
Mus musculus	15.9	76	26.2	7.1
Eligmodontia puerulus	19.5	46	15.9	5.3
Rattus rattus	158	31	10.7	28.8
Rattus norvegicus	93.3	17	5.9	9.3
Rattus sp.	125.7	17	5.9	12.5
Indeterminate rodents	68.8	59	20.3	23.8
Subtotal Rodents		282	97.2	98.9
Total Mammals		284	97.9	99.3
Indeterminate birds	41	3.0	1.0	0.7
Total Birds		3	1.0	0.7
Total vertebrates		287	98.9	99.9
Cratomelus armatus	0.5	1	0.3	0.0
Orthoptera indeterminate	0.5	1	0.3	0.0
Scarabaeidae indeterminate	0.5	1	0.3	0.0
Total invertebrates		3	1.0	0.0
Total preys/g		290	100	100
Pellets (N)		201		
B		5.91		
Bsta s/invertebrates		0.53		
Bsta c/invertebrates		0.45		
H'		0.82		
Hmax		0.95		
J'		0.86		

Table 2. Frequency and relative abundance of micromammals in Ojo Opache and χ^2 values for vertebrate prey consumed by *G. polyosoma* ($\chi^2 = 15.507$, $p = 0.05$). In bold statistical significance $p < 0.05$.

Species	Frequency	Relative abundance	χ^2
Abrothrix olivaceus	4	4.8	0
Phyllotis magister	18	21.7	0
Mus musculus	59	71.1	3.8
Rattus rattus	2	2.4	**27.1**
Thylamys pallidior	0	0	2.0
Phyllotis xanthopygus	0	0	**36.0**
Eligmodontia puerulus	0	0	**46.0**
Rattus norvegicus	0	0	**17.0**
Rattus sp.	0	0	**17.0**
Total	83	100	

tion as their presence in the area ($\chi^2 = 15.507$, $p = 0.05$); significant selectivity was detected in favor of *R. rattus*, *P. xanthopygus*, *E. puerulus*, *R. norvegicus* and *Rattus* sp. (Table 2). No statistically significant differences were detected for the consumption of *M. musculus* and the marsupial *Thylamys pallidior* Thomas, 1902 (Table 2). The trophic niche breadth value for *G. polyosoma* in Ojo Opache was 5.913 (maximum 10).

DISCUSSION

The general composition of the diet of *G. polyosoma* in the study area agrees with reports for different eco-regions (Schlatter et al. 1980, Fuentes et al. 1993, Jiménez 1995, Figueroa et al. 2003, Baladrón et al. 2006, 2014, Travaini et al. 2012, Ponce et al. 2018), in the sense that rodents are the most important prey item. However, our findings in the oasis of Ojo Opache, Calama, in the Atacama Desert, differ from those of Valladares et al. (2015), also an arid environment, who reported a high consumption of lizards (*Liolaemus* and *Callopistes*) (57.1%) and a low consumption of rodents (19.8%). The same finding is reported in Pampa del Tamarugal, where the lizard *Microlophus theresioides* (Donoso-Barros, 1966) was the most frequent species (45.3%) in the diet, followed by the native rodent *Phyllotis darwini* (Waterhouse, 1837) (40.4%, Ponce et al. 2018). The low consumption of invertebrates also differs from findings in another semi-arid environment (Las Chinchillas National Reserve) by Jiménez (1995), who documented a high consumption of insects (27.6%). The equity and trophic niche breadth are greater than in the Chilean matorral eco-region (e.g. La Dehesa, Metropolitan Region) ($H' = 0.82$ versus $H' = 0.6$; $B_{sta} = 0.532$ versus $B_{sta} = 0.187$). To summarize, in Ojo Opache *G. polyosoma* acts as a selective predator of rodents, preferring native rodents (*P. xanthopygus* and *E. puerulus*) and allochthonous species of *Rattus* and *Mus*, with a prey frequency tending towards equity. Considering that our data correspond to the winter period (June to August) the differences in relation to the other studies in the Atacama Desert (i.e. Ponce et al. 2018) may also be due to seasonality in the supply of prey or energy requirements of the species.

Geranoaetus polyosoma is considered a highly flexible generalist predator (Thiollay 1994), with a diet that has been shown to vary geographically and seasonally (Schlatter et al. 1980, Fuentes et al. 1993, Jiménez 1995, Figueroa et al. 2003, Baladrón et al. 2006, Travaini et al. 2012, Valladares et al. 2015) and is influenced by the type of habitat occupied (Monserrat et al. 2005, Baladrón et al. 2006, Travaini et al. 2012, Valladares et al. 2015). Although some works do not consider prey availability (e.g. Schlatter et al. 1980, Fuentes et al. 1993, Jiménez 1995, Figueroa et al. 2003), the marked geographical variation in the diet of this species suggests that it is basically an opportunistic predator (cf. Jaksic 1989), preying on the most locally abundant items and alternating prey species according to their distribution.

In extreme environments like deserts, where productivity and prey supply are low, any subsidiary contribution to the diet of a top predator like *G. polyosoma* may determine the presence or absence of that predator in the community. A functional response occurs when predators respond to changes in the availability of their prey by varying their diet; thus, the functional response of a predator measures its consumption rate as a function of prey availability (Monserrat et al. 2005). In theory, every functional response curve reaches saturation level with high prey densities. Three main types of functional response are recognized: linear, convex and sigmoid (Holling 1959); raptors that easily consume allochthonous prey tend to present a sigmoid response, and may even stabilize the populations of these alternative prey species (Korpimäki and Norrdahl 1989, Norrdahl and Korpimäki 2000, Salamolard et al. 2000, Monserrat et al. 2005).

Jaksic et al. (1992) found no significant functional response in birds of prey studied in Chile, but they did find a strong numerical response to fluctuations in small mammals. Other authors (e.g. Pavez et al. 1992, Hiraldo et al. 1995, Monserrat et al. 2005) have suggested the existence of a functional response in the black-chested buzzard-eagle, *Geranoaetus melanoleucus* (Vieillot, 1819), with respect to allochthonous prey; however they found no significant functional response in *G. polyosoma* in the Patagonia eco-region to an allochthonous prey, *Lepus europaeus* Pallas, 1778 (Monserrat et al. 2005). We documented a different situation for the Calama oasis in the Atacama Desert, where most of biomass consumed (> 55%) came from three allochthonous rodent species. Our study represents only a fraction of what the species' diet might be in the region (see Valladares et al. 2015, Ponce et al. 2018), since the sampling covered only 1-2 months (July-August) and suggest that a larger study should be carried out to verify whether the observed result corresponds to a seasonal variation, as observed in other studies (Figueroa et al. 2003, Baladrón et al. 2006, Travaini et al. 2012, Ponce et al. 2018). In future studies it will be important to explore the functional response of *G. polyosoma* to these three allochthonous rodents in view of the implications that it might have for the biological control of these species, which are also health and farm pests (see Ostfeld and Holt 2004, Muñoz-Pedreros et al. 2010, Bordes et al. 2015, Kosoy et al. 2015).

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