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Posted Date: 23 May 2025

doi: 10.20944/preprints202505.1863.v1

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Article

Trophic Relationships Between *Thinocorus orbignyanus* (Charadriiformes: Thinocoridae), *Lepus europaeus* (Lagomorpha: Leporidae), and *Equus ferus caballus* (Perissodactyla: Equidae) in High Mountain Grasslands During the Summer Season

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Abstract: Depending on the importance of hydromorphic vegetation formations of high mountain areas were established relations between the attributes of these grasslands and botanical composition of the diet of grey-breasted seedsnipe (*Thinocorus orbignyanus*), brown hares (*Lepus europaeus*), and horses (*Equus ferus caballus*). Hares showed greater dietary diversity (J) than horses and grey-breasted seedsnipes, factor that was correlated in all three cases, negatively with vegetation diversity patch. Same response amplitude was found when analyzing food web. The dietary diversity for all species showed no relation to the dry matter productivity vegetable patches. While correlation the abundance of two species of Cyperaceae in the meadow with the presence of the same in the diet of herbivores, we found a negative relationship between the abundance of *Carex* sp and grey-breasted seedsnipe diet, and a positive relationship between the *Eleocharis pseudoalbibracteata* species abundance and frequency in the diet of hares and horses. About the group of species content of graminoids in the diet, it was determined an overlap of 30% dietary animal species assessed, depending on that, it could identify the existence of interspecific competition between herbivores, this would be conditioned by the response of individuals to the environment.

Keywords: Cyperaceae; dietary diversity; hydromorphic grassland

1. Introduction

The high-Andean grasslands of Chile are distributed from Atacama to the Araucania region in high-altitude areas of the Andes Mountains. These ecosystems are considered natural or altered systems, whose forage production can be utilized from mid-spring to summer [1]. The use of these high-altitude wetlands for seasonal livestock grazing involves the coexistence of domestic, introduced, and wild herbivorous vertebrates. Competitive interactions among these species are expected to intensify during these periods when food resources are scarce [2]. However, in Chile, there are few studies on this type of interaction and its intensity in these environments. Among the wild herbivores using these ecosystems are guanacos (*Lama guanicoe*), hares (*Lepus europaeus*), Andean geese (*Chloephaga melanoptera*), and grey-breasted seedsnipes (*Thinocorus orbignyanus*). The latter three species primarily utilize hydromorphic grasslands (wet grasslands), as do domestic livestock—mainly horses (*Equus ferus caballus*)—which occupy these areas during the summer months [3].

Given this, it is evident that forage resources are shared by both resident and occasional herbivores, a situation where a high trophic niche overlap among studied herbivores has been

identified [4,5]. This phenomenon depends on the type and abundance of forage resources, which, in high mountain environments, vary according to soil moisture availability. This is influenced by three combined factors: topographic conditions, wind exposure, and winter snow cover. These gradients determine the formation of a mosaic of plant communities [6]. The ability of herbivores to modify dietary components based on the temporal abundance of plant species in a patch distinguishes animal species that are efficient in resource use [7]. Thus, the goal is to establish relationships between diet and foraging area attributes as a first step toward understanding interactions in these environments [8]. These findings could facilitate inferences about niche overlaps or differentiation in at least one dimension of the trophic niche [9], enabling the coexistence of species competing for the same resource in a non-random manner, primarily based on nutritional aspects [10,11].

2. Materials and Methods

2.1. Study Area

The study was conducted at eight high-altitude wetland sites in the southern Andes of Cuncumén, Salamanca, in the Coquimbo Region of Chile (31°52'–32°02' S; 70°19'–70°26' W; 3,025–3,729 meters above sea level) (Figure 1).

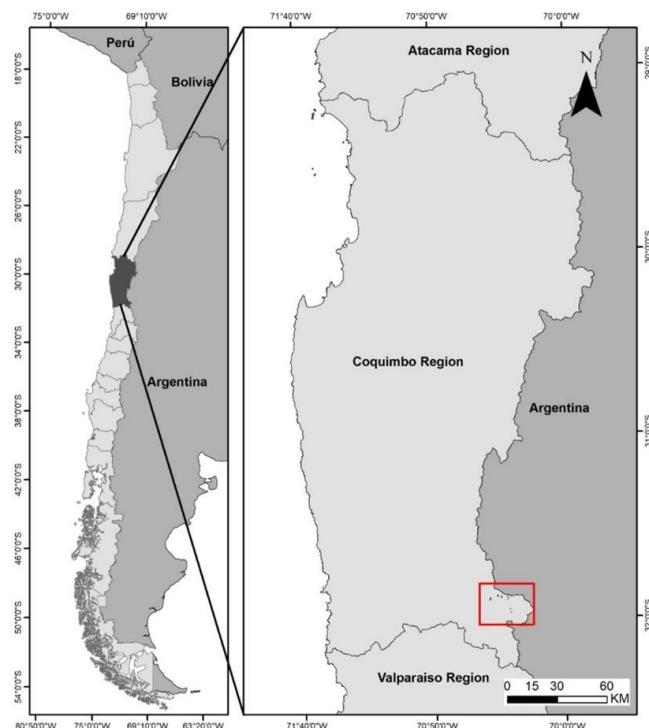


Figure 1. Location of the area where the study was carried out.

Evaluations of the botanical composition of hydromorphic grasslands were carried out in March of 2011 and 2012. The climate in the area corresponds to the Steppe Province with a very Cold Dry Summer or Mountain Summer Ecoregion, which, according to Köeppen [12], is classified as BSsk' climatic type. The hydric azonally distributed grasslands ("high-altitude wet grasslands"), which develop on hydromorphic soils, are the main source of high-quality forage for herbivores. These grasslands are dominated by graminoid species (families Cyperaceae and Juncaceae), notably *Eleocharis pseudoalbibracteata* S. González & Guagl. and *Carex gayana* E. Desv. These species are considered key components of this type of grassland [2]. The bromatological analysis of both species is presented in Table 1:

Table 1. Bromatological analysis of the plant species *Carex gayana* and *Eleocharis pseudoalbibracteata*, which provide details the content of neutral detergent fiber (NDF, %), acid detergent fiber (ADF, %), crude protein (CP, %), dry matter digestibility (DMD, %), and metabolizable energy concentration (ME, MJ kg⁻¹).

Plant species	NDF (%)	ADF (%)	CP (%)	DMD (%)	ME (MJ kg ⁻¹)
<i>C. gayana</i>	55.89	26.52	8.89	68.24	10.03
<i>E. pseudoalbibracteata</i>	50.48	30.70	8.63	64.98	9.47

Source: Animal Nutrition Laboratory. Agronomic Sciences Faculty. University of Chile.

2.2. Dry Matter Production in the Grassland

At each site in the plain and associated with each transect, dry matter (DM) production was estimated, which was measured by harvesting 31 exclusion plots of 3x3 m and 7.29 m² of usable area. At the beginning of the growing season, the remaining DM from the previous season was removed from each of the plots and at the end of the season, the phytomass accumulated during the growing season was harvested at ground level, which was subsequently dried in a forced air oven at 60°C for 48 hours, in order to express the forage production of the plot in terms of DM (kg ha⁻¹).

2.3. Evenness of Plant Species in the Grassland

To estimate the evenness of plant species in the wet grasslands, their botanical composition was determined by evaluating 31 20 m transects, arranged in eight sectors representative of this type of grassland. In each transect, the modified Point Quadrat method was used [13,14], which allows determining the relative participation of the different plant species in the community. With this information and in each evaluated line, the Shannon-Wiener diversity index was calculated [15]:

$$H = - \sum_{i=1}^n p_i \cdot \log_2(p_i) \quad (1)$$

This index was expressed as relative diversity or evenness (J_p) [16], according to the following equations:

$$J_p = \frac{H}{H_{max}} \quad (2)$$

$$H_{max} = \log_2(n) \quad (3)$$

In the previous equations, p_i is the proportion of i species in the grassland, and n is the number of species in it. H_{max} represents the value H would have if all species found in the grassland had the same frequency.

2.3. Evenness of the Diet

In each wet grassland site, fresh feces samples were collected from horses (*Equus ferus caballus*), hares (*Lepus europaeus*), and grey-breasted seedsnipes (*Thinocorus orbignyianus*). The samples (between 15 to 20 samples per herbivore) consisted of a set of 10 to 15 fresh fecal sub-samples from each animal species, obtained through a “cross-country” traversal of the wet grassland site. After collecting the samples, these were dehydrated in a forced-air oven at 60°C for 48 hours and stored in airtight jars until further processing. The botanical composition of the diet was determined through micro-histological analysis of feces [17–19]. This method is based on the microscopic identification of plant epidermal fragments that have characteristics allowing for the differentiation of plant species [20,21].

The results of the microscopic reading were expressed as the relative frequency for each plant species, which is considered a good estimator of dry weight in mixtures of known composition [22]. Subsequently, this frequency was converted into density using the tables of Fracker and Brischle [17,23]. The identified plant species were grouped into five categories: annual grasses (Poaceae), perennial grasses, graminoids (Cyperaceae and Juncaceae), dicotyledonous herbs, and shrub species.

With the botanical composition of each herbivore’s diet established, its relative evenness (J_d) was determined using the same equations employed to calculate the evenness of the grassland (Eqs. 1, 2, and 3). The J_d index ranges between 0 (very low dietary evenness) and 1 (all species in the diet have

the same abundance). Generally, when J_d values are below 0.3, it indicates highly specialized diets, while values above 0.6 suggest a generalist diet [24,25]

Finally, to determine the trophic niche overlap among the three herbivores studied, in terms of the relative contribution of graminoid species in the diet, Pianka's Index (O) [26] was calculated using the following equation:

$$O = \frac{\sum p_i \cdot q_i}{\sqrt{\sum p_i^2 \cdot \sum q_i^2}} \quad (4)$$

where p_i corresponds to the frequency of species i in the diet of herbivore A, and q_i corresponds to the frequency of the same species i in the diet of herbivore B. Like the evenness index, this variable ranges from 0 to 1. Values equal to or greater than 0.7 indicate a high dietary overlap.

2.4. Statistical Analysis

As this study was observational, an "a priori" experimental design was not carried out. Nevertheless, an analysis of variance (ANOVA) was carried out on the dietary evenness results (J_d) and trophic niche range (B_{est}), with a totally randomized design, with its correspondent assumptions taking into account the herbivore species as the only source for variation [27]. The differences among herbivores were determined through the Tukey test with a 5% level of significance. The association among the assessed variables were determined through the estimation of the Pearson correlation with a 5% level of significance and a regression analysis. All of the statistical analysis was done using the STATGRAPHICS Centurion XVI® software (Statgraphics Technologies, Inc., Virginia, VA, USA).

3. Results

3.1. Evenness of the Diet

The relative evenness index (J_d), which accounts for the similarity in the proportions of plant species that make up the diet, observed a significant effect attributed to the type of herbivore ($p = 0.0006$), with the diets of hares and horses being the most diverse, with values of 0.759 ± 0.028 and 0.750 ± 0.026 , respectively. The above values were statistically similar to each other, differing significantly from that found in the partridge diet in which J_d obtained a significantly lower value (0.593 ± 0.032) (Figure 2).

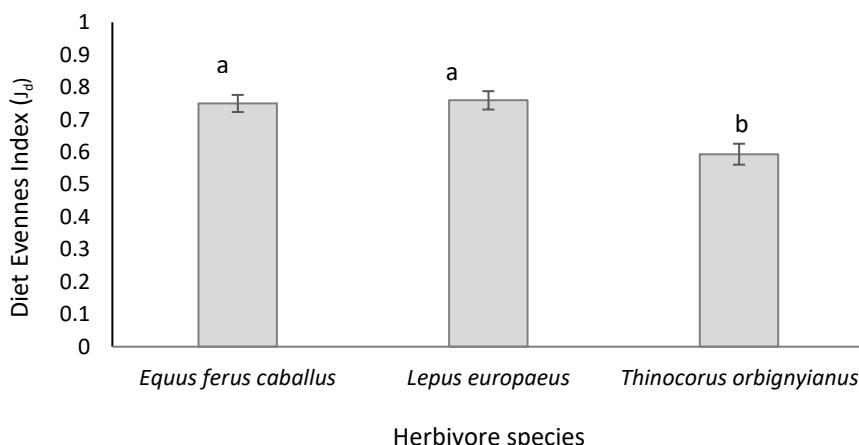


Figure 2. Relative evenness indices (J_d) for *Thinocorus orbignyanus*, *Lepus europaeus* and *Equus ferus caballus*, in high mountain hydromorphic grasslands. The bar around the mean value indicates \pm one standard error. Different letters above the bars indicate significant difference at Tukey's test at 5%.

3.2. Diet Evenness and Its Relationship with Grassland Patch Evenness and Dry Matter Production

The evenness of the partridge diet was negatively correlated with the evenness of the patch used as a food resource ($r = -0.708$; $p = 0.022$), while in the case of hares this correlation was lower and of

lesser significance ($r = -0.528$; $p = 0.064$). In the case of equines this correlation was even lower, lacking statistical significance ($r = -0.212$; $p = 0.449$) (Figure 3).

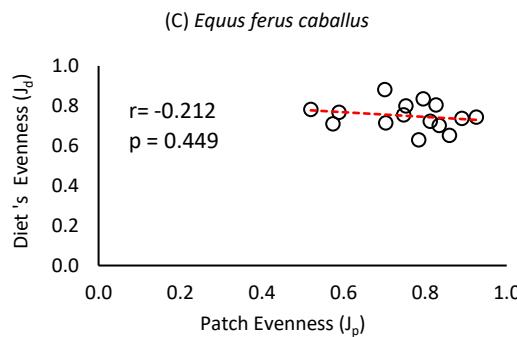


Figure 3. Relationship between diet evenness index (J_d) and grassland patch evenness (J_p) for (A) *Thinocorus orbignyianus*, (B) *Lepus europaeus* and (C) *Equus ferus caballus*, in high mountain hydromorphic grasslands.

No linear correlation was found between the evenness of the diet of equines and hares with the dry matter production of the patch, however, in the case of the dietary evenness of partridge, it observed a quadratic trend, which turned out to be significant ($p = 0.05$) and with an R^2 of 0.713 (Figure 4).

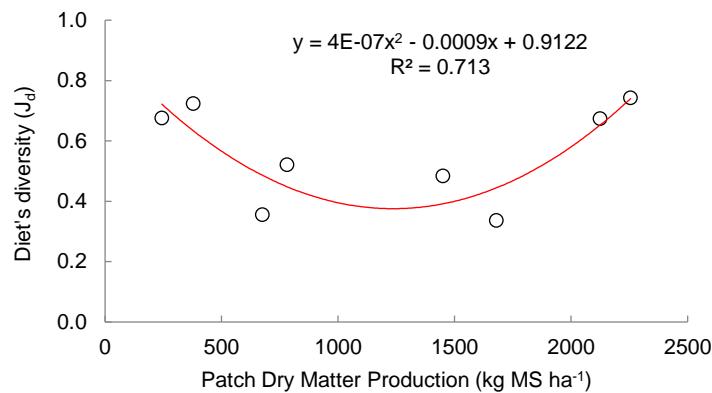


Figure 4. Relationship between the diet evenness index of *Thinocorus orbignyianus* (J_d) and the dry matter production of the grassland patch (kg DM ha^{-1}) in high mountain hydromorphic grasslands.

3.3. Presence of Indicator Plant Species in the Diet

The grassland “indicator” plant species, the graminoids *C. gayana* and *E. pseudoalbibracteata*, contributed to the botanical composition of the grasslands with percentages that varied between 48 and 59%, depending on the grassland site. These two species together were present in the diet of the grey-breasted seedsnipe, hares and horses in a percentage of 44.6 ± 7.4 ; 35.8 ± 6.5 and $43.8 \pm 6.0\%$, respectively, figures that were not statistically different from each other ($p = 0.579$). Given the importance of these species in the diet of the herbivores studied, the percentage contribution of the two “indicator” species in the diet was correlated with the percentage contribution of the same in each grassland patch. In the case of the grey-breasted seedsnipe, the result was negative, ($r = -0.758$; $p = 0.011$). Thus, as the percentage presence of this plant species in the plain increases, its content in the diet decreases, a relationship to which an exponential decline model could be adjusted (Figure 5).

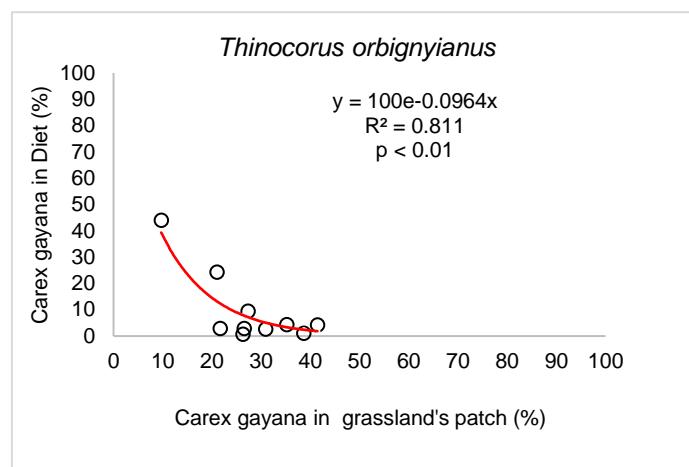


Figure 5. Relationship between abundance of *Carex gayana* in the diet of *Thinocorus orbignyanus* (%) and the abundance of *C. gayana* in the grassland patch (%), in high mountain hydromorphic grasslands.

For both hares and horses, this correlation was low and lacking statistical significance (Figure 6).

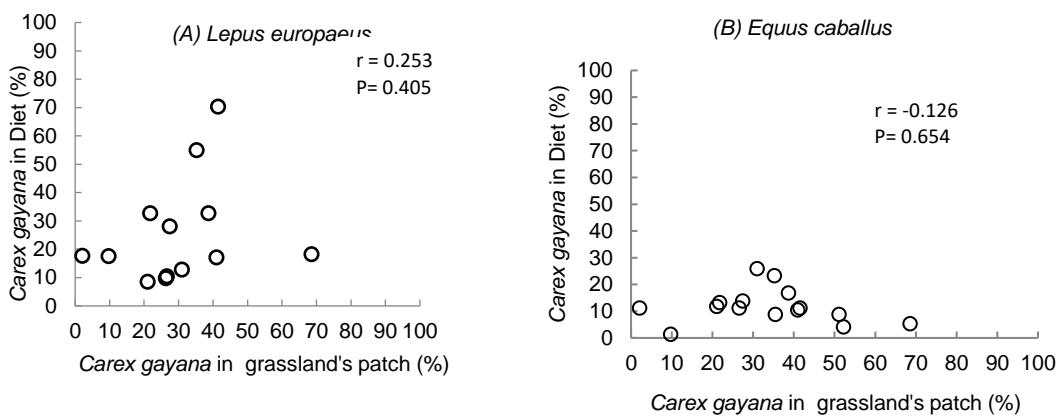


Figure 6. Relationship between abundance of *Carex gayana* in the diet (%) and abundance of *C. gayana* in the grassland patch (%), for *Lepus europaeus* and *Equus ferus caballus*, in high mountain hydromorphic grasslands.

When relating the content of *E. pseudoalbibracteata* present in the diet of the grey-breasted seedsnipe with the content of this graminoid in the wet grassland, a linear correlation coefficient of 0.624 ($p = 0.072$) was determined, which could indicate a tendency to an increase in the consumption of this plant species as its presence in the diet of this bird increases, this relationship being rather of the exponential type (Figure 7A). A linear response was found in the case of hares and equines, where the correlation coefficients were 0.578 ($p = 0.039$) and 0.737 ($p = 0.003$), respectively (Figure 7B and 7C).

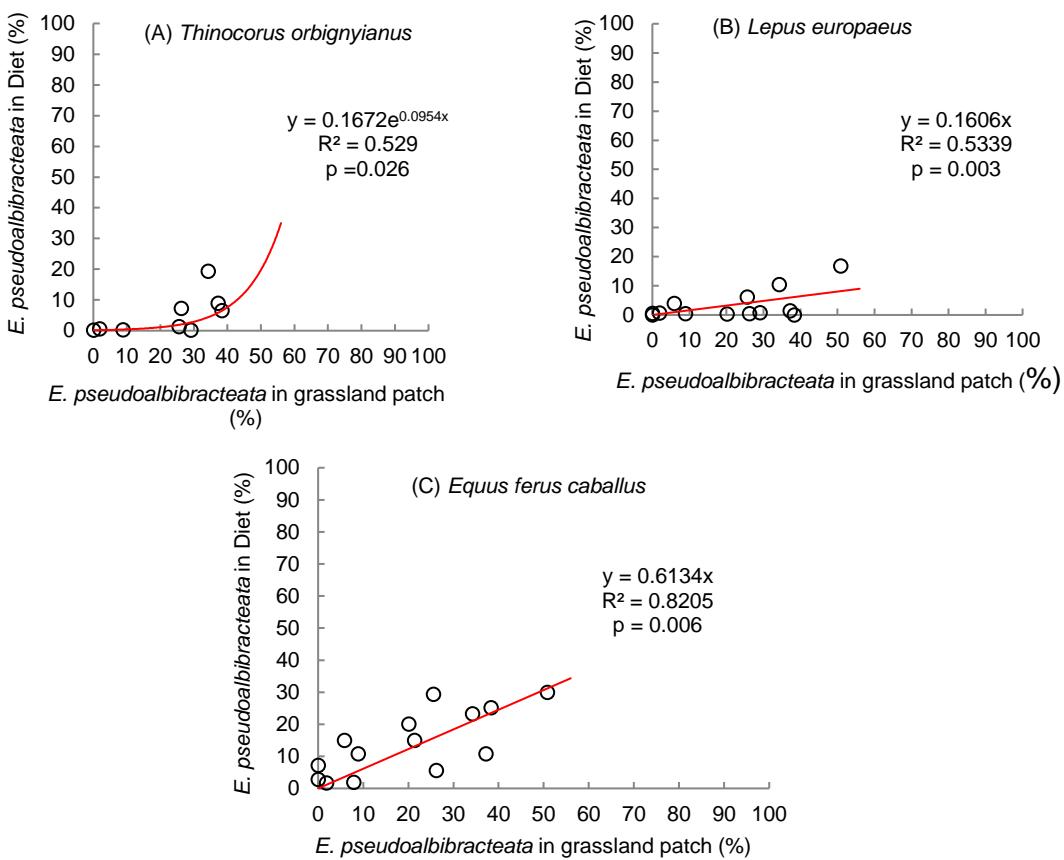


Figure 7. Relationship between the abundance of *Eleocharis pseudoalbibracteata* in the diet (%) and the abundance of *E. pseudoalbibracteata* in the grassland patch (%), for (A) *Thinocorus orbignyanus*, (B) *Lepus europaeus*, and (C) *Equus ferus caballus*, in high-altitude hydromorphic grasslands.

3.4. Dietary Overlap

Based on the relative importance of graminoids in the diet of the three herbivores, the dietary overlap for this item was determined using Pianka's index, with the results shown in Table 2. The magnitude of the overlap reached more than one-third for all analyzed species, tending to be higher between *Lepus europaeus* and *Thinocorus orbignyanus*.

Table 2. Pianka's dietary overlap index (0–1) for graminoid functional types among *Thinocorus orbignyanus*, *Lepus europaeus*, and *Equus ferus caballus* in high-altitude hydromorphic grasslands.

Herbivore species	<i>Thinocorum orbignyanus</i>	<i>Lepus europaeus</i>	<i>Equus ferus caballus</i>
<i>Thinocorus orbignyanus</i>	---	0.397	0.328
<i>Lepus europaeus</i>	0.397	---	0.303
<i>Equus ferus caballus</i>	0.328	0.303	---

4. Discussion

It is complex to assess interspecific competition in vertebrates [28], given the difficulty of controlling all the factors that would be influencing such interactions. Currently, there are no studies that clearly demonstrate the trophic competition that might exist among these three species; however, the degree of similarity in the botanical composition of their diets could provide indications of the existence of this phenomenon [3,4,24]. The evenness (J_a) (homogeneity) of the diets of the three herbivores is considered medium to high, which could indicate that they are species with generalist feeding strategies [11], especially in the case of *Lepus europaeus* and *Equus caballus*. Studies conducted on rodents (*Dolichotis patagonum*) in Argentine Patagonia corroborate that such species would be

generalists in their food selection [29]. Meanwhile, for equines, it is well known that their grazing behavior allows for equitable selection of the plant species that make up their diet [30]. Castellaro et al. [3] reported a dietary evenness index of around 0.77 for horses in this same environment. *Thinocorus orbignyianus* exhibited the least diverse (most homogeneous) diet, tending to consume a greater proportion of a specific plant species at the expense of others. Korzun et al. [31] conducted a study on the anatomy of birds of the genus *Thinocorus*, describing the morphology of their skulls, which could offer an explanation for the dietary preferences these animals exhibit in qualitative terms. However, most of these birds exhibit marked dietary preferences, which have been better studied in granivorous and frugivorous types [32]. Orellana et al. (2021) [33] found J_d values ranging from 0.49 to 0.70 in the diets of wild geese (*Chloephaga melanoptera*) in high Andean environments, with graminoid species dominating their diets. The values obtained for dietary breadth indicate that hares and equines have a broader range in this attribute compared to the grey-breasted seedsnipe, a pattern similar to that found in the study by Rodríguez and Dacar [29] on *Dolichotis patagonum*. Horses showed dietary evenness similar to that of hares, but different from that observed in the grey-breasted seedsnipe, which could be due to lower ease in harvesting food based on bite size. While this allows them to select the grazing area, it limits their ability to separate one species from the others growing alongside it. Each herbivore species has anatomical adaptations that allow them to better select and obtain specific parts of the plant to consume, as well as physiological adaptations that enable them to process these plants effectively [34,35]. The narrower trophic niche breadth of *Thinocorus orbignyianus*, reflected in a lower relative evenness index, suggests greater specificity in the selection of forage resources [36], ending toward less generalist dietary habits [25], though not reaching the level of specialization. This behavior could be due to morphophysiological differences among herbivores [7,35], as the bird's oral apparatus would allow for more rigorous food selection.

As the evenness of plant communities in the hydromorphic grassland (J_p) increased, the dietary evenness in the grey-breasted seedsnipe and hares decreased. This observation could be explained by the evenness in species frequency within the wet grassland, which would increase the animals' ability to select specific plant species. The animals tend to focus on those plant species that provide the greatest nutritional benefit [36]. In the case of horses, this behavior was not observed, as their J_d was unaffected by the increase in plant species evenness in the grassland.

It was not possible to establish a relationship between dietary evenness and the availability of plant dry matter, suggesting that an increase in grassland productivity does not necessarily indicate greater species richness [18].

It is evident that, both spatially and temporally, the three evaluated herbivores utilize the same resource, as confirmed by the significant presence of graminoid species in their diets, with a minimum value of 30%. Abrams [37] suggests that interaction among herbivores can be demonstrated if at least some dimensions of their ecological niches overlap, necessitating an evaluation of resource dynamics in relation to each feeding strategy. One species identified as an "indicator" was *C. gayana*, whose frequency decreased in the diet of the grey-breasted seedsnipe as the abundance of this plant species increased in the patch. This pattern suggests that consumption of this resource may be modulated by anti-apostatic selection [38], wherein consumers avoid more abundant resources in favor of less common ones. Such behavior is rare in birds but has been documented in some wild marine species [39]. In contrast, no relationship was found between the frequency of *C. gayana* in the diets of the other two herbivores and its abundance in the grassland. Evaluating the dietary preferences of horses and hares, and how these change in response to resource availability is crucial due to the potential impact of species selection on the ecosystem [40]. Studies on the effects of introduced ungulates in New Zealand have concluded that herbivory can lead to a reduction in floristic evenness, attributable to the lack of defenses in certain plant species [41].

An increase in the abundance of *E. pseudoalbibracteata* corresponded with a higher presence of this species in the diets of all three evaluated herbivores, particularly in the grey-breasted seedsnipe and horses. This suggests that selection of this resource could be characterized as apostatic [42], where consumers prefer more common resources. The consumption of this species in relation to its

abundance may also explain its high frequency in the evaluated grasslands. Nutritionally, this plant species differs from *C. gayana*, especially in its cell wall content (NDF), which could be significant for these herbivores. This is particularly relevant for the grey-breasted seedsnipe, which generally may have a lower capacity to digest fibrous plant material compared to lagomorphs and equines [35].

Based on the provided data and the estimation of dietary overlap using Pianka's index, a potential competition between hares and equines can be inferred, with a trophic niche overlap associated with graminoid species of approximately 30%. This figure is lower than that reported for rabbits and cattle in the Argentine pampas, and lower than that determined between these same herbivores by Castellaro et al. [3] in this environment. The interaction between the grey-breasted seedsnipe and horses over the same resource is around 32%, while the overlap between hares and grey-breasted seedsnipes reaches nearly 40%. However, given the magnitude of these dietary overlaps, the potential trophic competition among the three studied herbivores would be considered medium to low [18].

5. Conclusions

According to our results, the trophic niche breadth suggests that the diets of the three studied herbivores are composed of a limited number of plant species, particularly in the case of the grey-breasted seedsnipe. However, these diets are relatively balanced, a trait more evident in equines and hares, which also exhibit more pronounced generalist feeding habits. Only in the case of the grey-breasted seedsnipe was an association observed between dietary evenness and the evenness of plant species in the grassland patch. This indicates that, for this bird, as the evenness in the frequency of plant species in the grassland increases, the likelihood of selecting specific plant species also increases, resulting in a decrease in the evenness of its diet. The availability of dry matter (DM) in the grassland does not influence the herbivores' ability to select more diverse diets. An exception may be the grey-breasted seedsnipe, for which a quadratic trend was observed—dietary evenness tends to be higher at very low or very high relative values of DM availability. Among the key species in the hydromorphic grassland, only *E. pseudoalbibracteata* was relevant as a modulator of diet composition in the three studied herbivores, showing a positive association: as its abundance in the pasture increases, its contribution to the herbivores' diet also increases, playing a significant nutritional role in maintaining physiological processes. In the case of *C. gayana*, its dietary contribution becomes important when its presence in the pasture is low, and this is only relevant for the grey-breasted seedsnipe. Based on the feeding strategy that results in low dietary overlap, a low probability of interspecific trophic competition among the studied herbivore species can be expected.

Author Contributions: Conceptualization, methodology, data analysis and manuscript draft by G.C., C.L.O., J.P.E. and C.N.E; execution of field experiments by G.C., C.L.O. and J.P.E. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Project "CS-1650 MLP-CEA—Characterization Study of the Wetlands of the South Cordillera of Cuncumén". Antofagasta Minerals Los Pelambres-CEA S.A.

Institutional Review Board Statement: Ethical review and approval for this study was waived, due to the stool samples used in the dietary analysis by microhistology, were collected from the ground surface, without requiring any manipulation of the animals.

Data Availability Statement: The data presented in this study is available on request from the corresponding author.

Conflicts of Interest: The authors declare no conflict of interest.

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