ORNITOLOGIA NEOTROPICAL 14: 173–194, 2003

THE FEEDING ECOLOGY AND DIGESTIVE TRACT MORPHOMETRY OF TWO SYMPATRIC TINAMOUS OF THE HIGH PLATEAU OF THE BOLIVIAN ANDES: THE ORNATE TINAMOU (*NOTHOPROCTA ORNATA*) AND THE DARWIN'S NOTHURA (*NOTHURA DARWINII*)

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Resumen. – Ecología alimentaria y morfometría del tracto digestivo de dos tinamúes simpátricos del altiplano de los Andes bolivianos: el Tinamú Pisacca (*Nothoprocta ornata*) y el Tinamú de Darwin (*Nothura darwinii*). – Estudiamos la amplitud de nicho trófico y el grado de solapamiento en la dieta invernal de dos especies simpátricas de tinamúes del altiplano boliviano, el Tinamú Pisacca (*Nothoprocta ornata*) y el Tinamú de Darwin (*Nothura darwinii*), analizando los contenidos de buches y mollejas de animales coleccionados por cazadores deportivos. También determinamos el grado de solapamiento en el uso invernal de los hábitats de forrajeo, y las diferencias en proporción de cada componente del tracto digestivo que puede implicar diferencias en la asimilación de los alimentos. Ambas especies consumen un amplio espectro de alimentos, preferentemente semillas y frutos monoseminados. El Tinamú de Darwin tiene una amplitud de nicho alimenticio mayor que el Tinamú Pisacca, pero el consumo de alimento es independiente de la especie y del sexo, lo cual es confirmado por un alto grado de solapamiento interespecífico. En cuanto al consumo en peso, hemos determinado diferencia interespecífica significativa solamente para un item (*Trifolium* spp). Existe un alto grado de solapamiento en el uso de hábitats de forrajeo, y no existe ninguna diferencia interespecífica en la proporción relativa de los componentes del tracto digestivo. Nuestros resultados indican que las poblaciones del Tinamú Pisacca y del Tinamú de Darwin en el altiplano boliviano muestran un bajo nivel de especialización trófica en su dieta invernal. Queda por responder si el generalismo y oportunismo son estrategias adaptativas de los tinamúes para explotar su nicho alimenticio o si son el reflejo de una restricción filogenética debida a sus particulares características craneocinéticas.

Abstract. – We studied the trophic niche breadth and the degree of overlap in the winter diets of two sympatric species of tinamous in the Bolivian Andes, the Ornate Tinamou (*Nothoprocta ornata*) and the Darwin's Nothura (*Nothura darwinii*), by analyzing crop and gizzard contents of birds collected by sport hunters. We also measured the overlap in the winter use of foraging habitats, and the proportion of differences between digestive tract components that could imply distinct assimilation of food resources. The Ornate Tinamou and the Darwin's Nothura consume a wide variety of food items, especially seeds and monoseminated fruits. The former has a greater niche breadth than the latter, but consumption of food items is species and sex independent, which is confirmed by high interspecific diet overlap. There was a significant interspecific difference in the amount of food consumed for only one item (*Trifolium* spp). There was high overlap in the use of foraging habitats, and no interspecific difference in the relative proportion of the components of the digestive tract. Our results indicate that the populations of the Ornate Tinamou and the Darwin's Nothura in the Bolivian highlands show low degree of trophic specialization in their winter diet. However, it is not clear whether generalism and opportunism are adaptive strategies that allow the tinamous to exploit their alimentary niche, or rather indications of phylogenetic restrictions related to the cranial kinesis of tinamous. *Accepted 27 August 2002.*

Key words: Bolivian Andes, Darwin's Nothura, feeding ecology, intestinal morphometry, *Nothoprocta ornata*, *Nothura darwinii*, Ornate Tinamou.

INTRODUCTION

Tinamous (Aves: Tinamiformes) are poorly known Neotropical birds, and few ecological studies have been carried out on the Ornate Tinamou (*Nothoprocta ornata ornata*) and the Darwin's Nothura (*Nothura darwinii agassizii*), two sympatric species which inhabit agrosystems in the Bolivian Andes (Pearson & Pearson 1955, Bump & Bump 1969, Mosa 1997, 2000; Garitano-Zavala 2000). This study examines trophic degree of generalism and opportunism, diet overlap and use of foraging habitat in these two species. These ecological parameters were chosen because they are indications of trophic niche specialization. This study deals with diet breadth specialization or relative polyphagy, and relative plasticity (Sherry 1990).

Differentiation in the relative proportion of the components of the digestive tract may indicate a corresponding differentiation in the assimilation of food resources. The few studies on the morphology and morphometry of the digestive tract in other tinamous species (Chikilián & Bee de Speroni 1989, 1996; Morato & Bohórquez 1994) have shown that the digestive tracts do not have particular morphological adaptations at the macroscopic level. Chikilián & Bee de Speroni (1996) reported a relative intra- and inter-specific homogeneity in the organization of the tract, with slight variations in morphometry and mucous surface. Therefore, this study also aims to determine whether the Ornate Tinamou and the Darwin's Nothura differ in some morphological components of their digestive tracts.

METHODS

Specimen collection. All specimens were obtained from sport hunters (helped by pointer dogs) between 1995 and 1998. Specimens were collected between the end of May and the end of October, i.e., during the dry season (southern winter) of the Bolivian highlands. Birds were obtained between 10:45 and 17:25, most captures occurring from 13:00 to 16:30. The collection sites ranged from 16º12 'S to 17º04 'S (Fig. 1). Although these latitudes differ by almost 1°, we assumed that this parameter does not affect results because of the random distribution of collections.

Breath and overlap of feeding niches. The contents of 40 crops and gizzards (ten crops and gizzards per sex of the two species) were analyzed quantitatively to characterize winter diets. Ten individuals per sex was considered enough to characterize the diet of a species at a particular time of year (Rosenberg & Cooper 1990). In diet studies based on gastric contents, it is desirable to control the following factors: origin of the animals, habitat heterogeneity, time of day, weather on collection day and foraging activity (Rosenberg & Cooper 1990). We did not record these factors because of our dependence on the hunters.

Crops and gizzards were emptied and the contents were preserved separately in Petri capsules with 70% ethanol to separate and identify all the food items by means of a stereomicroscope. Quantitative analysis was car-

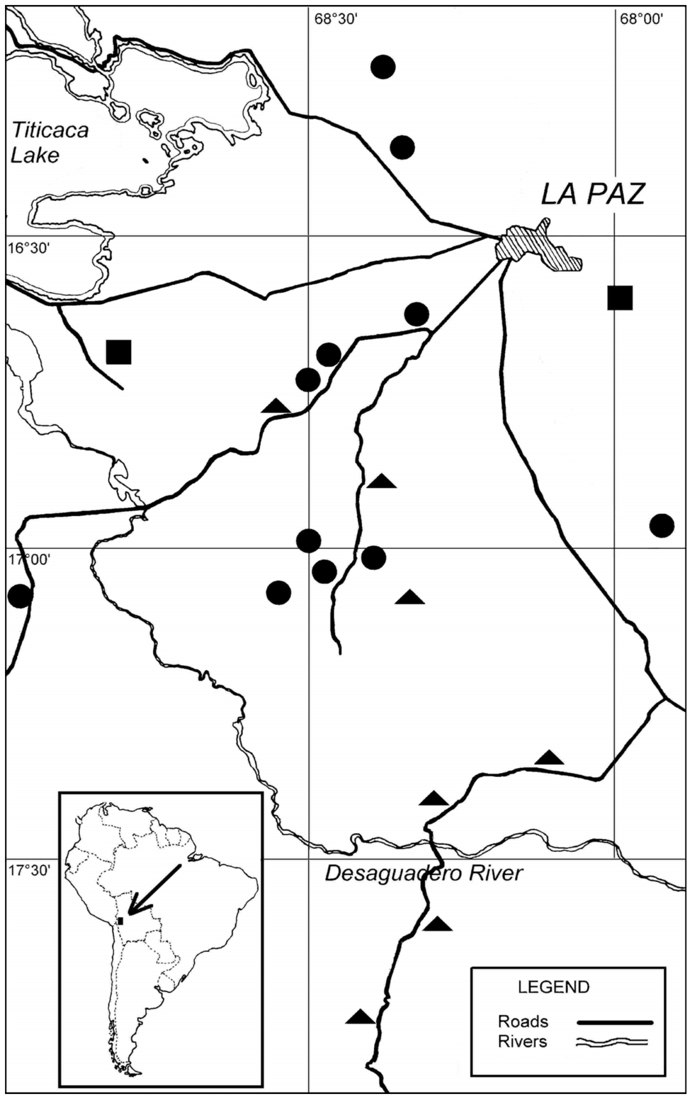

FIG. 1. Study sites in the northern Bolivian highlands. Circles: localities for habitat, diet and morphometric studies; triangles: localities for habitat and morphometric studies; squares: localities for morphometric study only.

ried out only on crop contents because they provide less biased results, since gizzard contents were already digested; therefore they were used only to complete the qualitative reports. Each item type was oven-dried at 40ºC to constant dry weight, taking advantage of the rapid dehydration allowed by ethanol. The dry weight of each item was measured with an accuracy of 0.0001 g in an electronic semi-microbalance (Sartorius® Research R160P). Arthropods and fragments were weighed as a whole. In the category of

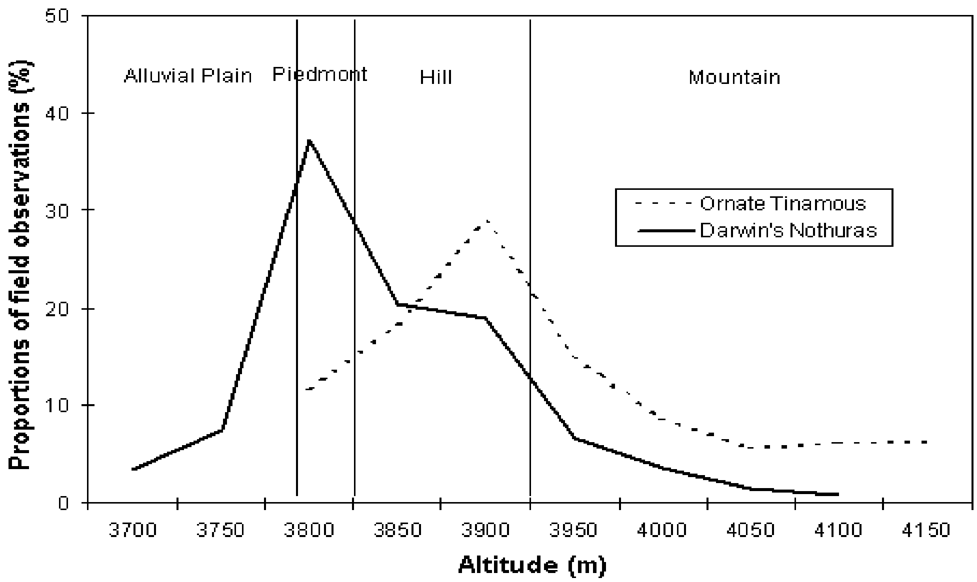

FIG. 2. Direct and indirect field observations of the altitudinal distribution of Ornate Tinamous and Darwin's Nothuras in the northern Bolivian highlands.

"others" we included all vegetable items that weighed less than 0.005 g. Thus, the total dry weight of the content of each crop included the dry weights of all the food items, the mineral material, and the unidentified vegetable material, plus detritus ingested with the food.

Feeding niche breadth is expressed by the richness of food items consumed, and by Levins' (1968) index of dietary diversity, using the relative biomass of each item. The frequency of each food item was determined as the number of given items per crop and gizzard divided by the total number of birds of each sex and species. We also considered food items that, owing to their scarcity, could not be quantified in dry weight. The feeding niche overlap was evaluated using Pianka's (1973) index over the relative frequency of each food item. The dependence or independence of the consumption of food items was determined for each species and sex within each taxon by a chi-square test in contingency tables, considering $P < 0.05$ to be significant. This test was preferred over the statistical *G* (Log-likelihood ratio) because some cells presented an absolute value of the difference between the expected and observed frequencies that was greater than the expected frequency (Williams 1976). When any of the expected frequencies of an item was smaller than five, a value that can affect the results of the test by rejecting the null hypothesis with a probability greater than α (Zar 1999), this item was not analyzed because no criterion of combination of cells reflected the true rate of consumption of each food item. Therefore the test was carried out only with the most frequent food items.

Dry weight proportion was obtained for each item in relation to the total weight of each crop content. To determine the interspecific difference of consumption, the dry weight proportions of items that presented a frequency of at least two repetitions per tinamous species were compared with the Kolmogorov-Smirnov statistic with Lilliefors significance level at 0.05. These comparisons were not carried out between sexes because of the low number of repetitions. All statistical analyses were done with SPSS 10.01 for Windows (SPSS 1999).

Overlap in feeding habitat use. The secretive habits of tinamous do not allow direct observations of their feeding behavior. The degree of interspecific overlap in the use of foraging habitats can be quantified by the frequency of Ornate Tinamous and Darwin's Nothuras in distinct habitat types, assuming that feeding is their main winter activity during the day.

Quantification was carried out according to both direct observations and indirect signals. Observations were recognition of a) young or adult individuals taking off with "explosive flight", or when observed feeding or running, b) vocalizations, and c) excrements, tracks, feathers and feeding remains, which were taken only when identification of the species was not doubtful.

Habitats were assigned to four altitude categories, corresponding to physiographic units, as follow: alluvial plain area (between local basal level to 3820 m a.s.l.), piedmont area (between 3820 to 3850 m a.s.l.), hill area (between 3850 to 3950 m a.s.l.), and mountain area (between 3950 to 4200 m a.s.l.). This classification was previously used by Garitano-Zavala (1995) to characterize tinamous habitats. In each unit, habitats were classified as: rocky areas, dense shrubs, open shrubs, bush areas, fallow and cultivated fields. Not all these habitats are present in all the physiographic units; therefore, the habitat factor was considered at 21 levels only. To determine the relative preference regarding altitude, altitude ranges were considered every 50 m (Fig. 2).

Observations were carried out in all the hunting excursions during the non-reproductive season (southern winters of 1996 at 1998), in a total of 18 localities (Fig. 1). The observational effort in each physiographic unit and habitat was homogenized by counting the observation hours in each of the habitat types in any one locality. In each of the 21 habitats, a total of 32 hours were devoted to observation. The hunting excursions in the final year of this study (1998) allowed us to complete the number of hours in those habitats in which this number had not been reached in preceding years. In this study, we assumed that the high number of observation hours in each habitat reduced the effect of locality, latitude, hour and date.

The degree of overlap in habitat use was determined using the overlap index of Pianka (1973), considering the 10 altitude ranges, each of 50 meters, and the 21 habitat types in the four physiographic units.

Morphometric differences in the gastrointestinal tract. To remove the effect of individual size (which also implies the elimination of the sex factor) on the morphometric parameters of the gastrointestinal tract, external measurements of 69 Ornate Tinamous (27 males and 42 females) and 36 Darwin's Nothuras (23 males and 13 females) were obtained. The birds were obtained from sport hunters (helped by pointer dogs) in 20 localities (Fig. 1). It was not possible to control hunting date and locality, nor the number of specimens. The maximum latitudinal variation among localities was 1°34', greater than in the diet study, and birds were obtained between 3850 and 4200 m a.s.l. All birds were obtained during the southern winter, between May and October, except for three individuals killed in summer. Here we assumed that locality, altitude, and the date of hunting did not exert a significant influence on morphological variation.

Ten external morphometric variables were considered: body weight (measured immediately after death, with a manual Pesola with 0.1 g accuracy), flat and stretched wing length, bill length from the inflection point of the bill with the skull, head diameter at the level of the posterior orbital border, bill height at the level of the divergence point of the ramphothecal basal pieces, tarsus length, tarsus width, medium toe length, medium toe width and claw length. All measurements were obtained for all the individuals, except those affected by fractures or other injuries caused by the shot-gut bullets, impact with the ground, or the teeth of dogs. All measurements were performed with an accuracy of 0.1 mm, except for the flat and stretched wing length (0.1 cm, with ruler). Body length, which is a widely used variable in ornithological studies, is a soft measurement in the case of tinamous and has little reliability because the hair-like tail feathers do not have a defined edge. The skins of the individuals studied are deposited in the Colección Boliviana de Fauna of La Paz City (Bolivia).

The measurements of external morphometry were used to select the variable that could be used to correct the measurements of morphologic variation of the digestive tract between sexes and species. The effect of species size is evident, and it was therefore unnecessary to carry out statistical tests for this parameter. On average, the Ornate Tinamou doubles the weight (513.86 ± 69.27 g, n = 70) of the Darwin's Nothura (233.73 ± 32.41 g, n = 37) (values are means ± SD).

Determination of significant differences in the external morphometric variables between the sexes of each species was carried out by means of a t-test, at $P < 0.05$. Although the Ornate Tinamou and the Darwin's Nothura are phylogenetically related, it was not necessary to carry out corrections with phylogenetically independent contrasts (PICs) to eliminate the effect of differential phylogenetic relationships between taxa, because we studied only two species (Felsenstein 1985).

The morphometric variables of the gastrointestinal tract were obtained from 14 male and 16 female Ornate Tinamous, and 16 male and 20 female Darwin's Nothuras, all adults. Viscera were extracted on the first or second day after death and conserved in 70% ethanol. The following measurements were taken: total length of esophagus (including the cervical and thoracic portions), length of proventriculus from the beginning of their broadening until the gastric isthmus, maximum diameter of proventriculus, length, height and width of gizzard, sum of the maximum width of the caudodorsal and cranioventral gizzard walls in sagittal plane, intestine length from the beginning of duodenum to the intersection with the ceca, the sum of the length of both ceca, and the rectum plus cloaca length from the intersection with ceca until the cloacal opening. Proventriculus and gizzard measurements were obtained to 0.1 mm accuracy, while the others were made with a ruler with 0.1 cm accuracy; esophageal and intestinal diameters were not measured because they are highly modified by the contents of the gastrointestinal tract. In some individuals, we did not take measurements of the digestive tract components because they had been destroyed by the shot-gun bullets or the teeth of dogs. Results are expressed as means ± SD.

To determine the differences in the relative proportion of each digestive tract component between the two tinamous species, the effect of individual size was eliminated by means a linear regression index among the transformed $\log_{10}$ of total bird weight (g) and the transformed $\log_{10}$ value of each gastrointestinal variable (mm). The residuals (deviations) of the allometric regressions were retained to determine the morphometric differences between species with an analysis of variance (ANOVA) at $P < 0.05$. The use of the residuals of the allometric regressions implies the correction of each measurement for the effect of individual size.

RESULTS

Diet. A total of 81 food items were found in the two tinamous species, among which vegetable material prevailed with 69 species of seeds and monoseminated fruits, five leave types, four flower types or parts of them, and one tuber. Moreover, mouse excrements and whole animal material (contained in a single article) were present; the latter was composed almost entirely of insects in immature or imaginal phases, and occasionally spiders, chilopoda and acari. Animal material had a low mean proportion in weight in the crops: 1.4 ± 2.6% (n = 6) for Ornate Tinamou, and 2.5 ± 3.7% (n = 13) for Darwin's Nothura (Table 1). This observation allowed us to group material of animal origin into a single article.

Most of vegetable items were identified at genus level only, and some may account for more than one species that cannot be discriminated by the characteristics of the seeds, i.e., the genera *Trifolium*, *Relbunium* and *Azorella*. We were unable to identify 17 articles to genus level.

Plant material comprised species of annual herbs belonging to 18 angiosperm families. The most diverse families were, in diminishing order, Poaceae, Asteraceae and Fabaceae. Of the 79 vegetable items, 75 were weeds from cultivated and fallow fields, and four were from cultivated species (Table 1).

The food of animal origin was composed of a great diversity of arthropod species, particularly insects which were not separated taxonomically to avoid lowering the relative frequencies and weights in crops. The orders found were, in diminishing order, Coleoptera (juveniles and adults, mainly Curculionidae and Carabidae), Hymenoptera (juveniles and adults, mainly Formicidae), Hemiptera (nymphs and adults), Homoptera (adults), Lepidoptera (caterpillars) and Diptera (adults and juveniles).

Feeding niche breath and overlap. Of the 81 food items identified, 60 were present in Ornate Tinamous and 67 in Darwin's Nothuras; thus the latter showed a slightly wider diet. The indexes of niche breadth confirmed greater niche breadth in Darwin's Nothuras (6.65 vs. 3.06 for Ornate Tinamous).

Only 46 food items were consumed by both species. However, the 35 articles eaten by only one tinamou species were rather casual because the majority appeared only once, and the others never more than three times (Table 1). In contrast, only few items were detected frequently. In Ornate Tinamous, only six food items were present in half or more of the crops of both sexes (*Trifolium*, arthropodes, *Erodium cicutarium*, *Hordeum vulgare*, *Bromus* and *Tagetes* sp. 1). In Darwin's Nothuras, 10 items were eaten more frequently (*Trifolium*, arthropodes, *Erodium cicutarium*, mouse excrements, *Tarassa tenella*, *Relbunium*, *Agrostis* sp. 1, *Festuca*, *E. cicutarium* and *Paspalum pygmaeum*).

The chi-square test on all food items demonstrates consumption independence between the two tinamous ($\chi^2_{80} = 84.50$, $P = 0.34$). However, this analysis contains 77% of cells with expected frequencies less than five, and although the null hypothesis was accepted, the same analysis was carried out with the 17 most frequent food items (to avoid the contingency table showing cells with expected frequencies less than five). The analysis demonstrates the lack of a significant difference in the consumption frequency of the most frequent food items ($\chi^2_{16} = 15.16$, $P = 0.51$).

With respect to the consumption of the food items that differentiated the sexes, 100% of male and female Darwin's Nothuras consumed *Trifolium* and insects while, in Ornate Tinamous, 100% of females vs 60% males consumed this seed. *Trifolium* is the food item most frequently consumed by the tinamous of the Bolivian highlands. No statis-tically signif-

TABLE 1. Occurrence, occurrence percentage, weight means and weight percentages of each food item present in the winter diet of Ornate Tinamous and Darwin's Nothuras from the Bolivian highlands. Sex discrimination is presented only for item occurrence.

	Ornate Tinamou					Darwin's Nothura				
	Item occurrence			Item weitht		Item occurrence			Item weight	
	Occurrence/Occurrence %			Weight (g)	%	Occurrence/Occurrence %			Weight (g)	%
Food items	Male	Female	Total	Mean ± SD (n)	Mean ± SD (n)	Male	Female	Total	Mean ± SD (n)	Mean ± SD (n)
SEED & FRUITS										
Cyperaceae										
Cyperaceae sp. 1	0/0	0/0	0/0	0	0	0/0	1/0.8	1/0.4	< 0.005[a]	Nc[a]
Ciperaceae sp. 2	0/0	0/0	0/0	0	0	1/0.6	1/0.8	2/0.7	< 0.005	Nc
Eleocharis	0/0	0/0	0/0	0	0	0/0	1/0.8	1/0.4	0.03 (1)	2.0 (1)
Iridaceae										
Sisyrinchium	2/1.6	1/0.8	3/1.2	0.01 (1)	1.7 (1)	0/0	0/0	0/0	0	0
Gramineae										
Gramineae sp. 1	1/0.8	0/0	1/0.4	< 0.005	Nc	2/1.3	0/0	2/0.7	0.56 ± 0.77 (2)	34.0 ± 47.0 (2)
Gramineae sp. 2	1/0.8	0/0	1/0.4	< 0.005	Nc	1/0.6	1/0.8	2/0.7	< 0.005	Nc
Gramineae sp. 3	1/0.8	0/0	1/0.4	< 0.005	Nc	1/0.6	0/0	1/0.4	< 0.005	Nc
Agrostis sp. 1	1/0.8	3/2.5	4/1.6	< 0.005	Nc	7/4.5	3/2.5	10/3.6	< 0.005	Nc
Agrostis sp. 2	0/0	0/0	0/0	< 0.005	Nc	1/0.6	0/0	1/0.4	< 0.005	Nc
Bromus	6/4.8	5/4.1	11/4.5	1.14 ± 2.21 (8)	17.2 ± 24.1 (8)	5/3.2	1/0.8	6/2.2	0.28 (1)	16.6 (1)
Eragrostis	2/1.6	1/0.8	3/1.2	0.02 ± 0.01 (2)	4.5 ± 5.0 (2)	1/0.6	0/0	1/0.4	0.01 (1)	0.3 (1)
Festuca	4/3.2	4/3.3	8/3.3	0.08 ± 0.04 (2)	4.2 ± 4.0 (2)	5/3.2	5/4.1	10/3.6	0.23 ± 0.30 (7)	7.4 ± 8.5 (7)
Hordeum vulgare *	5/4.0	7/5.8	12/4.9	5.33 ± 4.27 (9)	68.9 ± 34.2 (9)	6/3.8	4/3.3	10/3.6	2.42 ± 3.07 (6)	42.0 ± 34.4 (6)
Nassella sp. 1	2/1.6	1/0.8	3/1.2	0.01 (1)	0.1 (1)	4/2.5	2/1.6	6/2.2	0.01 ± 0.01 (2)	0.5 ± 0.2 (2)
Nassella sp. 2	1/0.8	1/0.8	2/2.0	< 0.005	Nc	3/1.9	1/0.8	4/1.4	0.02 (1)	0.6 (1)
Nassella sp. 3	1/0.8	4/3.3	5/2.0	0.03 (1)	1.7 (1)	5/3.2	4/3.3	9/3.2	0.02 ± 0 (3)	1.1 ± 0.4 (3)
Paspalum pygmaeum	3/2.4	3/2.5	6/2.4	0.22 ± 0.15 (3)	5.4 ± 4.0 (3)	7/4.5	3/2.5	10/3.6	0.15 ± 0.20 (4)	22.7 ± 40.3 (4)
Piptochaetium	1/0.8	1/0.8	2/0.8	0.04 ± 0.02 (2)	8.3 ± 9.9 (2)	0/0	0/0	0/0	0	0
Sporobolus indicus	0/0	1/0.8	1/0.4	< 0.005	Nc	0/0	0/0	0/0	0	0
Stipa ichu	4/3.2	1/0.8	5/2.0	< 0.005	Nc	1/0.6	2/1.6	3/1.1	< 0.005	Nc

TABLE 1. Continuation.

	Ornate Tinamou					Darwin's Nothura				
	Item occurrence			Item weitht		Item occurrence			Item weight	
	Occurrence/Occurrence %			Weight (g)	%	Occurrence/Occurrence %			Weight (g)	%
Food items	Male	Female	Total	Mean ± SD (n)	Mean ± SD (n)	Male	Female	Total	Mean ± SD (n)	Mean ± SD (n)
Amaranthaceae										
Amaranthus	3/2.4	3/2.5	6/2.4	0.03 ± 0.01 (2)	0.5 ± 0.2 (2)	2/1.3	1/0.8	3/1.1	0.01 ± 0.01 (2)	0.8 ± 0.8 (2)
Umbellifera										
Azorella	0/0	0/0	0/0	0	0	2/1.3	1/0.8	1/1.1	0.10 ± 0.08 (2)	3.6 ± 1.5 (2)
Daucus montanus	0/0	0/0	0/0	0	0	0/0	1/0.8	1/0.4	< 0.005	Nc
Compositae										
Compositae sp. 1	0/0	0/0	0/0	0	0	1/0.6	0/0	1/0.4	< 0.005	Nc
Baccharis sp. 1	0/0	0/0	0/0	0	0	1/0.6	0/0	1/0.4	< 0.005	Nc
Baccharis sp. 2	2/1.6	0/0	2/0.8	0.34 (1)	9.1 (1)	2/1.3	4/3.3	6/2.2	0.05 ± 0.02 (2)	0.9 ± 0.6 (2)
Bidens andicola	3/2.4	6/5.0	9/3.7	0.04 ± 0.03 (4)	0.5 ± 0.4 (4)	4/2.5	2/1.6	6/2.2	0.02 ± 0.01 (2)	1.2 ± 0.4 (2)
Bidens sp. 1	0/0	1/0.8	1/0.4	0.63 (1)	5.6 (1)	0/0	1/0.8	1/0.4	0.02 (1)	0.7 (1)
Chuquiraga	0/0	0/0	0/0	0	0	1/0.6	0/0	1 / 0.4	0.17 (1)	5.2 (1)
Cotula	0/0	0/0	0/0	0	0	2/1.3	1/0.8	3/1.1	< 0.005	Nc
Eupatorium	0/0	0/0	0/0	0	0	1/0.6	0/0	1/0.4	< 0.005	Nc
Heterosperma nana	3/2.4	2/1.7	5/2.0	0.14 ± 0.21 (4)	22.2 ± 3.0 (4)	2/1.3	0/0	2/0.7	0.13 (1)	4.2 (1)
Hymenoxys	0/0	0/0	0/0	0	0	0/0	1/0.8	1/0.4	< 0.005	Nc
Hypochoeris	2/1.6	0/0	2/0.8	0.01 (1)	0.1 (1)	1/0.6	2/1.6	3/1.1	0.06 (1)	1.9 (1)
Schkuhria multiflora	3/2.4	3/2.5	6/2.4	0.09 ± 0.07 (4)	3.0 ± 3.0 (4)	3/1.9	5/4.1	8/2.9	0.14 ± 0.18 (6)	3.9 ± 6.1 (6)
Sigesbeckia	0/0	0/0	0/0	0	0	1/0.6	0/0	1/0.4	0.02 (1)	0.7 (1)
Stevia	0/0	0/0	0/0	0	0	1/0.6	0/0	1/0.4	< 0.005	Nc
Tagetes sp. 1	6/4.8	5/4.1	11/4.5	0.21 ± 0.31 (6)	5.1 ± 9.1 (6)	2/1.3	3/2.5	5/1.8	0.26 ± 0.38 (5)	10.1 ± 18.6 (5)
Tagetes sp. 2	0/0	1/0.8	1/0.4	< 0.005	Nc	0/0	0/0	0/0	0	0
Cruciferae										
Cruciferae sp. 1	3/2.4	1/0.8	4/1.6	< 0.005	Nc	1/0.6	0/0	1/0.4	< 0.005	Nc
Lepidium	0/0	0/0	0/0	0	0	1/0.6	0/0	1/0.4	< 0.005	Nc

TABLE 1. Continuation.

	Ornate Tinamou					Darwin's Nothura				
	Item occurrence			Item weitht		Item occurrence			Item weight	
	Occurrence/Occurrence %			Weight (g)	%	Occurrence/Occurrence %			Weight (g)	%
Food items	Male	Female	Total	Mean ± SD (n)	Mean ± SD (n)	Male	Female	Total	Mean ± SD (n)	Mean ± SD (n)
Caryophyllaceae										
Paronychia	0/0	2/1.7	2/0.8	0.01 (1)	0.1 (1)	1/0.6	1/0.8	2/0.7	< 0.005	Nc
Chenopodiaceae										
Atriplex	2/1.6	1/0.8	3/1.2	< 0.005	Nc	6/3.8	1/0.8	7/2.5	0.29 ± 0.23 (3)	6.9 ± 6.4 (3)
Chenopodium quinoa *	0/0	1/0.8	1/0.4	0.01 (1)	0.1 (1)	1/0.6	1/0.8	2/0.7	1.16 ± 1.26 (2)	46.4 ± 60.6 (2)
Chenopodium sp. 1	1/0.8	0/0	1/0.4	< 0.005	Nc	1/0.6	1/0.8	2/0.7	< 0.005	Nc
Convolvulaceae										
Dichondra seriacea	1/0.8	0/0	1/0.4	0.51 (1)	81.0 (1)	0/0	1/0.8	1/0.4	< 0.005	Nc
Euphorbiaceae										
Chamaesyce	1/0.8	0/0	1/0.4	0.12 (1)	3.3 (1)	0/0	0/0	0/0	0	0
Leguminosae										
Adesmia	2/1.6	1/0.8	3/1.2	0.25 (1)	3.6 (1)	1/0.6	0/0	1/0.4	0.05 (1)	1.5 (1)
Astragalus	0/0	0/0	0/0	0	0	1/0.6	0/0	1/0.4	0.07 (1)	2.0 (1)
Lupinus	0/0	3/2.5	3/1.2	0.28 ± 0.36 (2)	2.6 ± 3.0 (2)	3/1.9	4/3.3	7/2.5	0.57 ± 0.78 (5)	46.3 ± 43.0 (5)
Medicago	0/0	0/0	0/0	0	0	1/0.6	0/0	1/0.4	0.01 (1)	0.4 (1)
Trifolium	6/4.8	10/8.3	16/6.5	0.43 ± 0.68 (12)	12.5 ± 20.0 (12)	10/6.4	10/8.2	20/7.2	1.08 ± 1.01 (14)	31.1 ± 27.2 (14)
Vicia faba *	1/0.8	0/0	1/0.4	0.38 (1)	19.0 (1)	0/0	0/0	0/0	0	0
Geraniaceae										
Erodium cicutarium	6/4.8	6/5.0	12/4.9	0.27 ± 0.47 (7)	18.4 ± 24.0 (7)	8/5.1	6/4.9	14/5.0	0.98 ± 1.35 (9)	18.3 ± 18.8 (9)
Malvaceae										
Tarassa tenella	7/5.6	2/1.7	9/3.7	0.32 ± 0.35 (7)	14.4 ± 17.7 (7)	9/5.7	3/2.5	12/4.3	0.36 ± 0.56 (6)	12.7 ± 18.7 (6)
Urocarpidium	1/0.8	0/0	1/0.4	< 0.005	Nc	1/0.6	1/0.8	2/0.7	0.04 ± 0.05 (2)	1.5 ± 1.3 (2)
Portulacaceae										
Portulaca	0/0	0/0	0/0	0	0	0/0	1/0.8	1/0.4	< 0.005	Nc
Rubiaceae										
Relbunium	4/3.2	3/2.5	7/2.8	< 0.005	Nc	5/3.2	7/5.7	12/4.3	0.01 (1)	0.2 (1)

TABLE 1. Continuation.

	Ornate Tinamou					Darwin's Nothura				
	Item occurrence			Item weitht		Item occurrence			Item weight	
	Occurrence/Occurrence %			Weight (g)	%	Occurrence/Occurrence %			Weight (g)	%
Food items	Male	Female	Total	Mean ± SD (n)	Mean ± SD (n)	Male	Female	Total	Mean ± SD (n)	Mean ± SD (n)
Indeterminates										
Indeterminate 1	1/0.8	1/0.8	2/0.8	< 0.005	Nc	3/1.9	1/0.8	4/1.4	< 0.005	Nc
Indeterminate 2	0/0	0/0	0/0	0	0	1/0.6	0/0	1/0.4	< 0.005	Nc
Indeterminate 3	1/0.8	2/1.7	3/1.2	0.04 (1)	0.4 (1)	1/0.6	0/0	1/0.4	< 0.005	Nc
Indeterminate 4	0/0	1/0.8	1/0.4	0.01 (1)	0.6 (1)	0/0	0/0	0/0	0	0
Indeterminate 5	0/0	2/1.7	2/0.8	< 0.005	Nc	0/0	1/0.8	1/0.4	< 0.005	Nc
Indeterminate 6	0/0	0/0	0/0	0	0	0/0	1/0.8	1/0.4	< 0.005	Nc
Indeterminate 7	1/0.8	1/0.8	2/0.8	0.31 (1)	72.2 (1)	0/0	0/0	0/0	0	0
Indeterminate 8	1/0.8	0/0	1/0.4	0.01 (1)	0.2 (1)	0/0	0/0	0/0	0	0
Indeterminate 9	0/0	1/0.8	1/0.4	0.05 (1)	7.0 (1)	0/0	0/0	0/0	0	0
Indeterminate 10	1/0.8	0/0	1/0.4	0.01 (1)	0.3 (1)	0/0	0/0	0/0	0	0
Indeterminate 11	0/0	2/1.7	2/0.8	< 0.005	Nc	1/0.6	2/1.6	3/1.1	0.04 ± 0.03 (2)	1.4 ± 1.6 (2)
OTHER VEG. PARTS										
Anthers of Gramineae	2/1.6	3/2.5	5/2.0	< 0.005	Nc	0/0	1/0.8	1/0.4	< 0.005	Nc
Leaves of *B. incarum*	1/0.8	0/0	1/0.4	< 0.005	Nc	0/0	0/0	0/0	0	0
Flowers of Compositae	2/1.6	1/0.8	3/1.2	< 0.005	Nc	1/0.6	2/1.6	3/1.1	< 0.005	Nc
Buds of Compositae	0/0	0/0	0/0	0	0	0/0	1/0.8	1/0.4	0.02 (1)	1.0 (1)
Flowers of Geraniaceae	0/0	1/0.8	1/0.4	0.02 (1)	0.2 (1)	0/0	0/0	0/0	0	0
Leaves of *Trifolium*	1/0.8	5/4.1	6/2.4	0.10 ± 0.14 (3)	0.9 ± 1.1 (3)	2/1.3	3/2.5	5/1.8	< 0.005	Nc
Leaves of *L. pinnata*	2/1.6	1/0.8	3/1.2	< 0.005	Nc	2/1.3	2/1.6	4/1.4	0.03 ± 0.04 (3)	1.0 ± 1.1 (3)
Leaves 1 Longs	5/4.0	2/1.7	7/2.8	0.31 ± 0.02 (2)	3.1 ± 2.4 (2)	3/1.9	1/0.8	4/1.4	< 0.005	Nc
Leaves 2 Succulents	2/1.6	0/0	2/0.8	1.28 ± 1.80 (2)	18.9 ± 26.3 (2)	0/0	0/0	0/0	0	0
TUBERS										
Solanaceae										
Solanum tuberosum *	5/4.0	3/2.5	8/3.3	0.69 ± 0.63 (7)	14.7 ± 17.0 (7)	0/0	2/1.6	2/0.7	0.65 (1)	12.2 (1)

TABLE 1. Continuation.

	Ornate Tinamou					Darwin's Nothura				
	Item occurrence			Item weight		Item occurrence			Item weight	
	Occurrence/Occurrence %			Weight (g)	%	Occurrence/Occurrence %			Weight (g)	%
Food items	Male	Female	Total	Mean ± SD (n)	Mean ± SD (n)	Male	Female	Total	Mean ± SD (n)	Mean ± SD (n)
MISCELLANEOUS										
Mouse feces	3/2.4	4/3.3	7/2.8	0.05 ± 0.05 (5)	1.5 ± 1.5 (5)	7/4.5	7/5.7	14/5.0	0.08 ± 0.10 (9)	2.4 ± 2.2 (9)
Arthropods	5/4.0	7/5.8	12/4.9	0.07 ± 0.10 (6)	1.4 ± 2.6 (6)	10/6.4	10/8.2	20/7.2	0.06 ± 0.09 (13)	2.5 ± 3.7 (13)
Various				0.03 ± 0.04 (17)	2.2 ± 3.2 (17)				0.03 ± 0.02 (19)	1.1 ± 0.7 (19)
Mineral material				0.09 ± 0.08 (8)	1.1 ± 0.8 (8)				0.05 ± 0.05 (5)	2.0 ± 1.5 (5)
Detritus				0.24 ± 0.19 (19)	11.9 ± 14.3 (19)				0.23 ± 0.29 (20)	7.3 ± 6.2 (20)

[a]The item weight was not determined because it was less than 0.005 g in all the cases, then the weight percentage was not calculated (Nc).
*Cultivated species.

icant sexual differences were detected for the 67 articles consumed by Darwin's Nothuras (χ^2_{66} = 51.36, P = 0.91), nor for the 60 articles consumed by Ornate Tinamous (χ^2_{59} = 51.98, P = 0.73).

Similarly to the analysis for species, these analyses produced high percentages of cells with expected frequencies less than five (87% for Darwin's Nothuras, and 90% for Ornate Tinamous). Therefore, the analyses were made for the six most frequent items for each species. These also demonstrated independence among the items consumed by each sex in each species (Ornate Tinamou: χ^2_5 = 1.37, P = 0.93; Darwin's Nothura: χ^2_5 = 3.24, P = 0.66). The data of relative consumption frequency of each food item show a high value of interspecific feeding niche overlap (O = 0.88).

From the 81 food items, 25 were recorded as present only, because their individual biomass in crops was less than 0.005 g. The data for weight and weight percentage in relation to the total weight in crops for the remaining 56 articles for each species are shown in Table 1.

The weights of total crop contents of both species together ranged from 0.04 g to 14.85 g (4.22 ± 3.80 g). Darwin's Nothuras showed higher values (between 0.15 g and 14.85 g), but a lower average (3.87 ± 3.64 g) than Ornate Tinamous (4.58 ± 4.04 g, range between 0.04 g and 11.78 g). The crop of one Ornate Tinamou was empty.

Very few items were consumed in high proportion. Those with the highest average dry weight consumed by Ornate Tinamous (i.e., those with an average > 1 g) were *Hordeum vulgare* (barley), *Bromus* and Leaves 2 (succulents). Those consumed by Darwin's Nothuras were *H. vulgare*, *Chenopodium quinoa* and *Trifolium*. In the latter, two of the three items are cultivated species, and of these *H. vulgare* was observed in both species. It should be noted that the food items with greatest frequency do not necessarily correspond to those with greatest relative proportion in weight. This is due to differences in the biomass of each item; for example, a *H. vulgare* grain weighs around 30 times more than that of *Trifolium*.

The Kolmogorov-Smirnov test demonstrated a significant difference only for *Trifolium*, with a very marginal rejection value of the null hypothesis (Z = 1.36, P = 0.05). This item was more consumed by Darwin's Nothuras (Table 1). The other items were consumed by both species in a weight proportion that did not differ significantly.

Overlap of feeding habitats. For the quantitative study, a total of 728 direct and indirect observations were recorded with certainty of species identification: 420 for Ornate Tinamous and 516 for Darwin's Nothuras.

The altitudinal distribution of Ornate Tinamous in the localities here studied was between 3830 m to 4200 m a.s.l., and most of the observations were between 3850 to 4050 m a.s.l. (82%). This species was more frequently observed in the mountain and hill areas (41% and 48%, respectively), but was not detected in the plains (Fig. 2, Table 2). The specific habitats frequented by Ornate Tinamous were rocky areas, dense shrubs and bushes, but this species was also observed in open areas (including some which were almost denuded by cattle), fallow and potato fields up to 3900 m a.s.l. (Table 2).

Darwin's Nothura was observed between 3710 m and 4150 m a.s.l. However, it was very rarely observed above 4000 m, and was particularly frequent between 3800 and 3950 m a.s.l. (77%) in the piedmont and hill areas (35% and 40% respectively) (Fig. 2, Table 2). This species was observed more frequently in bush areas of *Stipa ichu* and *Festuca* spp. growing between cultivated fields and houses in the piedmont, hill and plains areas (Table 2). It was also observed in dense shrubs, fallow

TABLE 2. Number of field observations of Ornate Tinamou and Darwin's Nothura in the habitat units of the northern Bolivian highlands. In parenthesis the percent of total observations for each species.

	Rocky areas	Dense shrubs	Open shrubs	Bush areas	Fallow fields	Cultivated fields	Total
Alluvial plain area							
Ornate Tinamou			0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Darwin's Nothura			14 (2.7)	27 (5.2)	17 (3.3)	9 (1.7)	67 (12.9)
Piedmont area							
Ornate Tinamou		11 (2.6)	14 (3.3)	6 (1.4)	8 (1.9)	9 (2.1)	48 (11.3)
Darwin's Nothura		32 (6.2)	27 (5.2)	52 (10.1)	46 (8.9)	24 (4.6)	181 (35)
Hill area							
Ornate Tinamou	33 (7.9)	46 (11)	17 (4.1)	37 (8.8)	34 (8.1)	32 (7.6)	199 (47.5)
Darwin's Nothura	7 (1.4)	49 (9.5)	35 (6.8)	54 (10.5)	31 (6)	28 (5.4)	204 (39.6)
Mountain area							
Ornate Tinamou	36 (8.6)	34 (8.1)	29 (6.9)	33 (7.9)	22 (5.2)	19 (4.5)	173 (41.2)
Darwin's Nothura	0 (0)	23 (4.5)	8 (1.6)	19 (3.7)	14 (2.7)	0 (0)	64 (12.5)

TABLE 3. Student t analysis for ten external morphometric variables (mm) of Ornate Tinamou and Darwin's Nothura.

	Ornate Tinamous						Darwin's Nothuras					
	Males		Females		t-test		Males		Females		t-test	
Variables	Mean ± SD	n	Mean ± SD	n	t	*P*	Mean SD	n	Mean ± SD	n	t	*P*
Weight	457.69 ± 44.82	26	552.31 ± 54.24	39	7.37	< 0.001	226.13 ± 21.98	23	255.92 ± 23.30	13	3.82	0.001
Flat wing length	192.67 ± 4.12	27	202.12 ± 13.4	42	3.55	0.001	142.65 ± 3.56	23	146.46 ± 4.72	13	2.74	0.010
Bill length	31.79 ± 1.93	25	34.78 ± 2.17	40	5.63	0.000	20.20 ± 1.08	21	20.41 ± 0.83	13	0.62	0.539
Head diameter	20.88 ± 1.45	24	21.16 ± 1.54	40	0.71	0.479	17.68 ± 0.62	21	18.34 ± 0.94	13	2.48	0.018
Bill height	8.79 ± 0.79	25	9.74 ± 0.80	40	4.69	< 0.001	6.86 ± 2.26	21	6.50 ± 0.58	13	0.55	0.586
Tarsus length	49.54 ± 1.60	27	51.63 ± 1.58	41	5.30	< 0.001	38.37 ± 1.25	22	38.11 ± 1.16	13	0.60	0.551
Tarsus width	4.39 ± 0.28	26	4.64 ± 0.27	39	3.70	< 0.001	3.65 ± 0.26	21	3.63 ± 0.22	13	0.29	0.771
Medium toe length	36.95 ± 1.65	26	39.00 ± 1.97	39	4.38	< 0.001	28.67 ± 1.46	21	28.70 ± 0.85	13	0.05	0.960
Medium toe width	4.05 ± 0.36	26	4.33 ± 0.35	39	3.00	0.004	3.13 ± 0.19	21	3.33 ± 0.20	13	2.86	0.007
Claw length	9.47 ± 1.08	26	10.15 ± 1.52	40	1.98	0.052	6.11 ± 0.59	21	6.03 ± 0.54	13	0.36	0.724

fields and active crops where even broods were spotted.

The index of habitat overlap using the height ranges was O = 0.75, and the corresponding result for habitat category was O = 0.70. Therefore, there was a considerable degree of overlap in the use of altitudinal ranges for both species, and also both species foraged in the same habitats in each range. This finding is consistent with the fact that the two species can take off with "explosive flights" from the same places.

Alimentary tract. The statistical analyses carried out on the morphometric measurements demonstrate high sexual dimorphism in Ornate Tinamous, expressed as significant differences in all the variables studied, except head diameter and claw length of the medium toe (Table 3). Our results show that females are larger than males. Darwin's Nothuras showed lower sexual dimorphism because only four variables exhibit significant differences. Similarly, in Darwin's Nothuras, females were also larger (Table 3).

Weight was the only variable that showed a significant difference with $P < 0.001$ in both species. Rising & Somers (1989) determined this variable to be that which best represents bird size, a variable which is even better than wing size, a favorite for many ornithologists. For this reason weight was used to correct for the effect of size of each individual in each species by linear regression of the transformed $\log_{10}$ variables. Table 4 shows the means for the measurements of gastrointestinal variables in each sex of both species. Table 5 shows the parameters of the lineal regressions of the same 10 measurements. All these variables show a significant correlation with weight ($P \leq 0.001$), but some regression indexes denote the accumulation of less than 50% of the variability, e.g., proventriculus diameter and intestine length. However, given that most of the variables show relatively high regression indexes, the use of the residuals of these regressions as morphometric values corrected for individual size was considered appropriate.

The results of the ANOVAs carried out with the residuals of the linear regressions shown that no component of the digestive tract significantly differed between the two species (Table 5).

DISCUSSION

Generalism and opportunism. The presence of only one empty crop demonstrates that the winter diet analysis of Darwin's Nothuras and Ornate Tinamous was a sample of daily consumption. The finding of 81 distinct food items, without counting the arthopod taxonomic groups, is an indication of the wide trophic spectrum of these birds, which appears larger in Darwin's Nothuras. On the other hand, only a low proportion of consumption involved food of animal origin. Our results characterise the Bolivian highland tinamous as mainly granivorous, and occasionally folivorous and insectivorous, at least in winter. This is consistent with Dorst & Vuilleumier (1986), who considered tinamous as large terrestrial granivorous-insectivorous birds of the tropical Andes.

Practically all the studies on tinamous demonstrate wide diet spectra (Mosa 1997, 2000; Jimbo 1957, Bonetto *et al.* 1960, Bump & Bump 1969, Grigera 1973, Silva & Sander 1981, Cabot 1992). The family was qualified as opportunistic, with more consumption of food of plant origin, and less of animal origin (Cabot 1992).

Although the wide range of food items consumed indicates a generalist feeding strategy, one of the most important findings of this study is that very few articles are consumed with greater frequency and abundance. This also indicates an opportunistic strategy, since some of the more frequent items were

TABLE 4. Descriptives of ten morphometric gastrointestinal tract variables of Ornate Tinamou and Darwin's Nothura.

	Ornate Tinamous				Darwin's Nothuras			
	Males		Females		Males		Females	
Variables	Mean ± SD	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD	n
Esophagus length	118.83 ± 12.58	12	125.50 ±13.98	14	90.77 ± 6.37	13	93.73 ± 8.00	11
Proventriculus length	21.88 ± 1.99	14	23.53 ± 3.35	15	17.59 ± 1.30	16	17.88 ± 1.77	11
Proventriculus diameter	9.72 ± 1.36	14	9.93 ± 1.08	15	8.65 ± 0.79	16	9.57 ± 0.88	11
Gizzard length	37.41 ± 2.63	14	40.08 ± 2.90	16	31.58 ± 2.14	16	33.53 ± 1.67	12
Gizzard heigth	31.66 ± 2.09	14	33.70 ± 2.45	16	27.95 ± 1.86	16	29.51 ± 1.60	12
Gizzard width	20.21 ± 1.44	14	21.49 ± 2.04	16	17.81 ± 1.20	16	18.89 ± 0.85	12
Gizzard walls width	28.60 ± 3.80	14	31.75 ± 3.99	15	19.79 ± 3.01	16	21.50 ± 2.35	12
Intestine length	731.43 ± 46.44	14	746.60 ± 90.77	15	516.60 ± 45.15	15	547.50 ± 49.65	12
Ceca length	364.00 ± 42.80	14	383.33 ± 48.55	15	273.94 ± 23.41	16	290.58 ± 27.90	12
Rectum plus cloaca length	86.43 ± 7.31	14	84.13 ± 9.99	15	74.25 ± 7.97	16	76.92 ± 5.87	12

cultivated grains that remained in the fields after reaping. Therefore, Ornate Tinamous and Darwin's Nothuras feed on reaped fields to take maximum advantage of these resources. Similar results were reported for the Red-winged Tinamou (*Rhynchotus rufescens*) in Brazil (Sander 1982), the Darwin's Nothura and Andean Tinamou (*Nothoprocta pentlandii*) in Argentina (Mosa 1997, 2000), and for the Spotted Nothura in Argentina (Bump & Bump 1969, Silva & Sander 1981).

Generalistic and opportunistic strategies in tinamous are also evident from the frequent consumption of foods that demonstrate low selection capacity. This is the case of mouse excrements that are reported here for Tinamiformes for the first time. Similar low selection capacity has been reported in other studies (Bump & Bump 1969, Bohl 1970, Mosa 1993).

Food resources and habitat use. Both tinamous species of the Bolivian highlands showed high overlap in their winter qualitative use of food resources and foraging habitats, and no differences were observed in the amount of consumed biomass of the most frequent nutritious articles, except for *Trifolium*. Although the results show high values of habitat overlap, it is important to consider that there is a wide altitudinal overlap, but there are also areas which are mainly exploited exclusively by Darwin's Nothuras or by Ornate Tinamous (Fig. 2). The former has a larger range, which also coincides with the wider diet spectrum. Mosa (2000) conclude that the overlap degree between Darwin's Nothuras and Andean Tinamous in Argentina depends on the station of the year: in winter, the diet and space overlap is greater. The study of Menegheti (1983) with the Spotted Nothuras and Red-winged Tinamous in Brazil demonstrates a relatively low habitat overlap but a wider diet overlap.

High overlap levels in the use of food items and foraging habitats support the hypothesis that the Darwin's Nothuras and the Ornate Tinamous are generalists and opportunists in the Bolivian highlands, at least in winter. Mosa (2000) suggests that temporal variations of the niche amplitude and overlap degree between Darwin's Nothuras and Andean Tinamous result in temporal variations of the degree of opportunism and generalism of these species. May be, it is true in the Bolivian highlands and more studies are needed to confirm.

Menegheti (1983) emphasized the morphological difference among the bills of these species. The Red-winged Tinamou, like all the *Nothoprocta* species, has a longer, stronger and more curved bill than *Nothura* species, implying the potentiality for exploiting a wider diet spectrum (including tubers, bulbs and rhizomes). However, Spotted Nothuras were more abundant and prospering in the Brazilian fields. Menegheti (1983) attributed this phenomenon to a greater synantropic degree in Spotted Nothuras. Their distribution range increased following the substitution of natural habitats by agrosystems. Our results showed a very similar situation in the Bolivian highlands.

Gastrointestinal tract. The organization of the digestive tracts of Ornate Tinamous and Darwin's Nothuras corresponds to the descriptions of other tinamous (Chikilián & Bee de Speroni 1989, 1996; Morato & Bohórquez 1994). Intestine length and animal biomass in the two species matches the most frequent norm in birds, as indicated by the relationship suggested by McLelland (1979): Intestine length (cm) = $\sqrt[3]{\text{Body weight (g)}}$. The ceca of these species are highly developed; the cumulative length of both ceca is a little less than half the total length of the intestine (Table 4). The ceca differ morphologically from those

TABLE 5. Linear regression values between the log_{10} of weight and the log_{10} of the specified measurements. The two last columns show the ANOVA results obtained between the two tinamou species with the regression residuals. n = number of cases, F_1 = ANOVA Fisher's F value for the linear regression correlation, P_1 = their corresponding probability value, r^2 = linear regression value, F_2 = ANOVA Fisher's F for the analysis with both tinamou species using the regression residuals, P_2 = their corresponding probability value.

Variables	n	F_1	P_1	r^2	F_2	P_2
Esophagus length	50	137.17	0.000	0.74	0.04	0.840
Proventriculus length	56	81.65	0.000	0.59	0.04	0.837
Proventriculus diameter	56	12.04	0.001	0.17	0.25	0.618
Gizzard length	58	154.89	0.000	0.73	0.31	0.580
Gizzard width	58	98.42	0.000	0.63	0.73	0.396
Gizzard height	58	63.27	0.000	0.52	0.30	0.588
Gizzard walls width	57	121.67	0.000	0.68	0.04	0.833
Intestine length	56	183.50	0.000	0.77	0.17	0.679
Rectum plus cloaca length	57	28.08	0.000	0.33	0.11	0.738
Ceca length	57	114.08	0.000	0.67	0.01	0.905

of large ratites that have highly modified or reduced ceca (Beddard 1898, McLelland 1979). However, they are similar to the ceca of kiwis (Beddard 1898), which can be interpreted as the permanency of the most primitive morphology in these two palaeognathous groups. A function of the intestinal ceca in birds deals also with water reabsorption and fermentation of nitrogenic residuals excreted by the kidneys (Remington 1989). Thus, the relatively large intestinal ceca in the two tinamous species studied appears to be related to the optimization of nitrogen obtained from a granivorous diet as well as to reduce water expenditure in their habitats.

We did not observe large morphological differences between the gastrointestinal tract components of Darwin's Nothuras and Ornate Tinamous. Statistically, they are morphologically similar, given the difference in size between sexes and species. For other tinamous, a relative intra- and interspecific homogeneity in the digestive tract organization has also been reported, with slight morphometric and mucous surface variations (Chikilián & Bee de Speroni 1996). The structure of the gastrointestinal tract in birds is highly flexible (Starck 1999), and it is possible that this can vary in time and space regardless of the variations in diet. But our results suggest that the lack of difference in winter diet is related with a lack of difference in tract morphometry, which would support the generalistic diet strategy hypothesis.

Generalism and opportunism: Ecological adaptation or phylogenetic restrictions? Studies on specialization in the exploitation of trophic niches by animals have resulted in niche theories based on foraging optimization, ecomorphology, comparative morphology, and phylogeny (Sherry 1990). According to niche theories, natural selection favors "effective organisms" that can find enough food in time and space. Therefore, models of niche theory also predict that a generalist and/or opportunist feeding strategy is likely to be adaptive in variable habitats (Levins 1968).

In the Bolivian highlands, the inter-annual climatic variations, the prevalence of pioneer vegetable species with unpredictable phenologies, and the human establishment and handling of agricultural practices, are three dimensions resulting in environmental unpredictability in time and space for the tinamous. The basic adaptation expected in granivorous birds would be to take advantage of the unpredictable appearance of large amounts of certain seeds by consuming them rapidly, and by searching for other abundant food sources (Wiens & Johnston 1977). Unpredictability could therefore exert an important selective pressure that could explain the generalism, opportunism and relative synanthropy, with rapid changes in the diet according to the habitat offer, observed in the tinamous of the Bolivian highlands. Then, the use of the alimentary niche could be interpreted as adaptive.

However, according to Zweers *et al.* (1997), tinamous and ratites constitute a lineage that evolved with a palaeognathous rhynchokinetic skull, a primitive cranial type. Thus, they are in the tinamou-like browsers guild that take big mouthfuls with a low level of manipulation of the food in the bill. The rudimentary size of the tongue increases this relative cranioinertial feeding with little selectivity, and these characteristics are probably responsible for a low trophic radiation of the palaeognathes (Gussekloo & Zweers 1997, Tomlinson 1997a, 1997b). A corollary of the hypothesis of Zweers *et al.* (1997) is that the tinamous would have an evolutionary restriction that impedes specialization in the diet, also reflected in morphology, physiology and behavior.

All the characters studied here show that Ornate Tinamous and Darwin's Nothuras in the Bolivian highlands have a low degree of trophic specialization. Are generalism and opportunism adaptive strategies in tinamous to exploit their alimentary niche, or are they the reflection of phylogenetic restrictions? We hope that our study will result in the realization of more studies on the feeding biology and ecology of tinamous.

ACKNOWLEDGMENTS

The authors thank Ramiro López and Esther Valenzuela at the National Herbarium of Bolivia for their collaboration with the identification of plant material. Ernesto Hug and Oscar Aguilar, sport hunters of tinamous, allowed us access to their hunted animals. Robin Rycroft and Xavier Ruíz offered useful comments on a draft version, R. Rycroft corrected the English redaction too. Álvaro Garitano-Zavala thanks to the Spanish Agency of International Cooperation for the concession of a MUTIS scholarship to complete studies at the University of Barcelona (Spain).

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