Diet of a sigmodontine rodent assemblage in a Peruvian montane forest

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Knowledge of feeding habits of small rodents is necessary for understanding food webs, trophic structure, and plant–animal interactions in Neotropical forests. Despite several studies that have investigated community structure and feeding behavior of rodents, large gaps remain in our understanding of their guild occupancy. Our objective was to investigate the diets of 7 species of small (< 100 g) sympatric sigmodontine rodents in a high (3,500 m) Andean montane rainforest in Peru. We qualitatively and quantitatively assessed diet items in fecal samples from livetrapped rodents from 2009 to 2012. Frequency data for 4 diet categories indicated that all 7 species of rodents contained 4 diet categories in fecal samples: arthropods (88%), remains of leaves and fibers from plants (61%), intact seeds (with or without fruit pulp; 50%), and mycorrhizal spores (45%). Omnivory was found to be a strategy used by all species, although contingency table analysis revealed significant differences among and within species in diet categories. Cluster analysis showed 2 main groupings: that of the *Thomasomys* spp. plus *Calomys sorellus* group which included high amounts of intact seeds and plant parts in their fecal samples, and those of the genera *Akodon*, *Microryzomys*, *Oligoryzomys*, which included a greater proportion of arthropods in their fecal samples, but still consumed substantial amounts of fruit and plant parts. Intact seed remains from at least 17 plant species (9 families) were found in fecal samples. We concluded that this assemblage of sigmodontine rodents is omnivorous but that they likely play an important role as frugivores and in seed dispersal in tropical montane forests in Peru.

El conocimiento de los hábitos alimenticios de roedores pequeños es necesario para comprender cadenas alimenticias, estructura trófica, e interacciones planta-animal en los bosques neotropicales. A pesar de que numerosos estudios han investigado la estructura de comunidades y el comportamiento de forrajeo en roedores, aún existen grandes vacíos en nuestra comprensión de sus gremios tróficos. Nuestro objetivo fue investigar las dietas de siete especies de pequeños (< 100 g) roedores sigmodontinos simpátricos en un bosque montano andino a 3.500] m en Perú. Cualitativamente y cuantitativamente evaluamos la dieta en muestras fecales de roedores capturados entre el 2009 y el 2012. Datos de frecuencia para cuatro categorías de dieta indicaron que las siete especies de roedores consumieron cuatro categorías de dieta: artrópodos (88%), pedazos de hojas y fibras de plantas (61%), semillas intactas (con o sin pulpa de frutos; 50%), y esporas de micorrizas (45%). Omnivoría fue la estrategia utilizada por todas las especies, aunque el análisis con tablas de contingencia reveló diferencias significativas entre y dentro de especies en categorías de dieta. El análisis de agrupación presentó 2 grupos principales: el grupo *Thomasomys* spp. y *Calomys sorellus*, que incluye una gran proporción de semillas intactas, y partes de plantas en las muestras fecales y el grupo que incluye los géneros *Akodon*, *Microryzomys* y *Oligoryzomys*, el cual incluyó una proporción mayor de artrópodos en sus muestras fecales, pero con niveles altos de semillas intactas. Semillas intactas de al menos 17 especies de plantas (9 familias) fueron encontradas en las muestras fecales. Concluimos que este ensamble de roedores sigmodontinos es omnívoro y que probablemente las especies juegan un rol importante como frugívoros y en la dispersión de semillas en los bosques montanos tropicales en el Perú.

Knowledge of food habits and trophic structure of rodent assemblages are crucial for understanding ecosystem function and plant–animal interactions in Neotropical forest habitats. In the Neotropics, where rodents are diverse and abundant (Voss and Emmons 1996; Pacheco et al. 2009), in desert (Marquet 1994), Andean (Pizzimenti and De Salle 1981; Novillo and Ojeda 2014), and rainforest habitats (Fonseca 1989; Patterson et al. 1998; Solari et al. 2006; Pacheco et al. 2009, 2011), knowledge of rodent feeding habits can facilitate understanding not only the ecology of their habitats but also provide information necessary for management, conservation, and restoration of forest rodent populations (Pacheco et al. 2013; Salas et al. 2013). For North America, a rich literature exists regarding the ecology and dietary habits of small desert-dwelling rodents (Brown and Lieberman 1973; Reichman 1975; Meserve 1981; Wolff et al. 1985; Kotler and Brown 1988; Brown 1989; Kelt et al. 2004; Stevens and Tello 2009; Meserve et al. 2011; Lobo et al. 2013; Stevens and Anderson 2014). A general consensus from these studies is that rodents, through their seed consumption, seed predation, scatter-hoarding, and caching behavior, elicit profound influences on plant reproductive success and community structure (Ostfeld et al. 1997; Kelt 2011).

In the South American Neotropics, diet and seed dispersal in rodents have been primarily studied in larger rodents belonging to the genera *Cuniculus*, *Dasyprocta*, *Myoprocta* (Smythe 1978; Forget 1990; Henry 1999; Forget et al. 2002; Dubost and Henry 2006), and *Proechimys* (Adler 1995; Mangan and Adler 2002). These studies showed that impacts by rodents are wide and far ranging; for example, rodents of the genus *Proechimys* consume and disperse mycorrhizal spores (Janos et al. 1995; Mangan and Adler 2002), and act as seed predators and possibly seed dispersers via scatter-hoarding (Forget and Milleron 1991; Forget 1993; Adler 1995; Forget 1996; Jansen and Forget 2001). Rodents belonging to the genus *Dasyprocta*, *Myoprocta*, and *Cuniculus* include fruit in their diets (Smythe 1978; Henry 1999; Dubost and Henry 2006) and can consume scatter-hoarded seeds as well as germinating seedlings (Forget and Milleron 1991).

The subfamily Sigmodontinae (Cricetidae) includes approximately 400 species in some 86 genera and 9 tribes of small rodents (12–500 g—D'Elía et al. 2007; Salazar-Bravo et al. 2013; D'Elía and Pardiñas 2015). They range from North to South America, inhabiting deserts, highlands, and tropical forests. They are ubiquitous and diverse, with a high degree of endemism (D'Elía and Pardiñas 2015). The natural history, feeding behavior, and ecological roles of these small rodents in Neotropical forests are for the most part unknown, hampering our understanding of ecosystem structure and function in lowland and highland tropical forests.

Some recent studies of sigmodontines in the Neotropics indicate that they exhibit flexible diet strategies. Sigmodontine rodents were omnivorous, granivorous, or herbivorous in the Monte Desert in Argentina (Campos et al. 2001; Giannoni et al.

2005). *Akodon* spp. were found to be omnivorous in the temperate forests of Chile (Meserve et al. 1988). In the Brazilian Atlantic forest, sigmodontine rodents were recorded consuming fruits in captivity (Viera et al. 2003, 2006). In southern Brazil, rodent species were generalist in relation to diet composition (Caella and Caceres 2006). Stomach contents of 5 species of sigmodontine rodents from the montane forests of Huánuco, Peru, were recorded and arthropod consumption was found for *Akodon orophilus*, omnivory for *Microryzomys altissimus* and *M. minutus*, and herbivory (plant remains and seeds) for *Thomasomys notatus* and *T. kalinowskii* (Noblecilla and Pacheco 2012). Given the captive feeding experiments for Brazilian rodents and seeds found in stomach contents from *Thomasomys* spp. from montane forests in Peru, fruit consumption by sigmodontine rodents may be more common than previously thought. If this is true in Neotropical forests, then a reassessment of the guild occupancy of small-rodent communities, ecological roles, as well as niche occupancy relative to other, better studied taxa Neotropical forests such as birds, bats, and primates may be useful. However, for both lowland and montane rainforest, data on rodent diets are incomplete.

Herein, we document the diet of sigmodontine rodents found in a tropical montane forest in Ayacucho, Peru. Montane forests host many endemic species, including rodents (Gentry 1992; Leo 1995; Olson and Dinerstein 1998; Pacheco 2002; Pacheco et al. 2009) that are highly threatened by human activity such as road-building, agriculture, logging, and climate change (Young 1994; Foster 2001; Kintz et al. 2006). We addressed the questions: what is the diet composition of 7 species of sympatric sigmodontine rodents in a tropical montane forest? What are qualitative and quantitative differences in diet among species of rodents? and, is there evidence of frugivory within this assemblage of rodents?

MATERIALS AND METHODS

Study site.—As part of a larger study to determine potential impacts of a natural gas pipeline on rodent populations, we collected fecal samples of rodents caught in Sherman live traps (Pacheco et al. 2013; Salas et al. 2013). Our study site was located near Chiquintirca, Department of Ayacucho, in the province of La Mar (13°03′34″S, 73°42′25″W). It is near the upper limit of montane forests of the Apurimac River valley ranging in elevation from 3,200 to 3,500 m. This area is cataloged as belonging to the Pluvial Montane Subtropical Forest (Instituto Nacional de Recursos Naturales 1995), upper montane pluvial forest of the yungas (Josse et al. 2007), and the Apurimac river valley montane forest ecotone (Langstroth et al. 2013).

Rodent capture and sample collection.—In 2009–2010, 8 sampling plots 20×150 m in size were established to evaluate the small mammal community and potential influence of construction of a

pipeline (Pacheco et al. 2013; Salas et al. 2013). Each plot consisted of 2 parallel lines separated by 15–20 m, and each line had 16 sampling stations 10 m apart. We placed 2 Sherman traps at each sampling station. When possible, 1 of the traps at each station was placed on a branch of a shrub or tree, 1–2 m above ground. Plots were evaluated 3 times during the rainy season for 5 nights each (November 2009–March 2010) and 3 times in the dry season (August–November 2010), for a total of 14,400 trap nights (Pacheco et al. 2013; Salas et al. 2013). In 2011–2012, 9 sampling plots were sampled for 4 nights prior to the rainy season (October–November 2011) and after the rainy season (May 2012) for a total of 6,912 trap nights. Traps were baited late in the afternoon, left open at night and evaluated in the morning. All traps were washed with a small amount of powdered laundry detergent in between captures. Rodents captured were identified to species, aged (juvenile or adult), weighed, tagged, and released. Animal capture and handling followed ASM guidelines (Sikes et al. 2011) and was approved by The Smithsonian National Zoological Park-Institutional Animal Care and Use Committee (NZP-IACUC #09-39).

Plant species richness and fruit availability.—In 2011, plant species richness and abundance was recorded in the rodent sampling grids. In addition, 13 modified Whittaker plots of 0.1 ha were sampled. Seven of these were located in the pipeline right-of-way (RoW), 3 in long-term "control" plots, and 3 alongside the RoW that included forest and shrub habitat. For each sample plot, the number of plant species and individuals per plant species was recorded. Leaves, stems, fruits, and seeds in the plant study grids were collected and used as reference. These were deposited in the herbarium collection of the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos. These data were tabulated and a list of plant species found at our study site was compiled. This was used to complement the plant species list and fruit availability data compiled by Servat et al. (2013).

Fruit availability was recorded May 2012. A 90-m-long line-transect was established in each rodent sampling grid, with 10×2-m-long perpendicular transects every 10 m ($n = 10$). We recorded the number of plants with fruits on each transect, and estimated the number of fruits per shrub and tree by counting the total number of fruits in 3 infructescences (shrubs) or branches (trees), and by multiplying the average number of fruits by the number of branches or infructescences with fruits on each individual plant. We then calculated the number of fruits per species/m^2. Rainfall data were obtained from a pluviometer at the study site.

Diet analysis of rodents.—Diet was determined via analysis of fecal remains of captured rodents (Meserve 1981; Cortes et al. 2002a, 2002b; Lopez-Cortes et al. 2007). After a captured rodent was measured, tagged, identified, and released, feces found in the trap were collected and placed in 2-ml-labeled plastic cryovial tubes with 70% ethanol. A total of 554 samples were collected from 2009 to 2012. We did not have recaptures in the same trapping night but did have recaptures within a trapping session (5 nights). We utilized these in our diet analyses. Twelve fecal samples from each tube were placed in a 140×20 mm petri dish that was placed atop grid paper with 1×1 mm squares. Ten observational fields of 10×10 mm were chosen randomly, and frequency (presence/absence) of arthropods, intact, undamaged seeds (with or without fruit pulp), plant parts (leaves, stems,

shoots), and mycorrhizal spores were recorded using a 20× Leica RX and a 7× zoom lens stereoscope. A 40–100× Labomed microscope was utilized to identify fragments and mycorrhizal spores. Four diet categories (2009–2012) and items (2009–2010; see below) were identified via a reference collection of insects, plants, fruits, and seeds from this study and a previous habitat analysis (Servat et al. 2013). Seeds were identified to family, genus, and species level when possible, using identification keys found in Gentry (1993), Ponte (1998), and Caceres (2004). Histological analysis of plant remains was not conducted.

For arthropods, parts of exoskeletons of adults were identified whenever possible to lowest taxonomic level (Tripplehorn and Johnson 2005). In 2009–2010, 7 diet categories were recorded: 1) arthropod larvae, 2) adult arthropods, 3) monocotyledon plant parts, 4) dicotyledon plant parts, 5) monocotyledon fruit remains, 6) dicotyledon fruit remains, and 7) mycorrhizal spores. Intact seeds in fecal samples with or without fruit pulp were considered as evidence of fruit consumption.

Analysis of data.—Using frequencies of occurrence for arthropods, intact seeds, plant remains, and mycorrhizal spores from 2009 to 2012, contingency table analysis was utilized to determine whether: 1) observed values of diet categories were different from expected; 2) species were associated with diet category; and 3) season was associated with diet category among and within species. Association between diet and year was not calculated due to different sampling dates and effort among years. A Bray–Curtis dissimilarity index was calculated for frequency of occurrence data from 2009 to 2012, and utilized in a cluster analysis to visualize grouping patterns according to diet.

Statistical analyses were conducted using SPSS version 21 and PAST version 7.

RESULTS

Rodent community.—A total of 554 captures of 7 species of sigmodontine rodents were obtained during this study. Species captured (sample size of adult rodents, and average mass [g] ± *SD* in parenthesis) were the cloud forest grass mouse, *Akodon torques* ($n = 44$ adult females, $\bar{X} = 25.93 \pm 7.39$; $n = 74$ adult males, $\bar{X} = 27.40 \pm 3.79$); the Peruvian vesper mouse, *Calomys sorellus* ($n = 9$ females, $\bar{X} = 23.04 \pm 3.70$; $n = 11$ males, $\bar{X} = 22.12 \pm 3.77$); the forest small rice rat, *Microryzomys minutus* ($n = 23$ adults, both sexes, $\bar{X} = 17.59 \pm 3.48$); the Andean pygmy rice rat, *Oligoryzomys andinus* ($n = 5$ adults, both sexes, $\bar{X} = 29.0 \pm 3.7$); the golden *Thomasomys*, *Thomasomys aureus* ($n = 9$ adults, both sexes, $\bar{X} = 91.2 \pm 11.5$); Kalinowski's *Thomasomys*, *Thomasomys kalinowskii* ($n = 26$ females, $\bar{X} = 44.65 \pm 6.95$; $n = 13$ males, $\bar{X} = 52.50 \pm 4.23$); and the montane fairy *Thomasomys*, *Thomasomys oreas* ($n = 27$ females, $\bar{X} = 32.79 \pm 5.43$; $n = 34$ males, $\bar{X} = 37.97 \pm 6.80$). Adult rodents ranged in average mass from 17.6 g (*M. minutus*) to 91.2 g (*T. aureus*).

Diet.—From 2009 to 2012, all of the 7 species of rodents captured contained 4 diet categories in fecal samples; arthropods, intact seeds, plant parts, and mycorrhizal spores. Frequency of occurrence of each diet category tabulated for each species indicated differences in feeding strategies (Table 1). Differences among species and within diet categories were significant

Table 1.—Proportion frequency of occurrence of diet category for 7 species of sigmodontine rodents, 2009–2012, at Chiquintirca, Ayacucho, Peru. All 7 rodent species contain each diet category in fecal samples which is highly indicative of omnivory in this assemblage. *Thomasomys aureus* samples contain the highest frequency of intact seeds and plant parts and the lowest frequency of arthropods. *Akodon torques* samples contain the lowest frequency of intact seeds and plant parts and the highest frequency of arthropods.

Species	*N*	Diet category			
		Arthropods	Intact seeds	Plant parts	Mycorrhizal spores
All species	554	0.88	0.61	0.50	0.46
Akodon torques	283	0.93	0.39	0.33	0.40
Calomys sorellus	47	0.89	0.83	0.51	0.26
Microryzomys minutus	46	0.91	0.52	0.71	0.60
Oligoryzomys andinus	11	0.91	0.45	0.73	0.36
Thomasomys aureus	19	0.53	0.95	1.0	0.42
Thomasomys kalinowskii	57	0.81	0.94	0.56	0.67
Thomasomys oreas	91	0.80	0.96	0.77	0.55

($n = 554$, $d.f. = 6$, $\chi^2 = 35.59$, $P < 0.001$, arthropods; $n = 554$, $d.f. = 6$, $\chi^2 = 152.34$, $n = 554$, $d.f. = 6$, $P < 0.001$, intact seeds; $n = 554$, $d.f. = 6$, $\chi^2 = 91.86$, $P < 0.001$, plant parts; $n = 554$, $d.f. = 6$, $\chi^2 = 29.98$, $d.f. = 6$, $P < 0.001$, mycorrhizal spores) indicative of diet differences or variable access to resources among rodent species.

Association between season (summer, autumn, winter, spring) and diet category for all species combined was significant for 4 categories: arthropods, intact seeds, plant parts, and mycorrhizal spores ($n = 554$, $d.f. = 3$, $\chi^2 = 23.019$, $P < 0.001$; $\chi^2 = 23.861$, $P < 0.001$; $\chi^2 = 40.259$, $P < 0.001$; $\chi^2 = 56.994$, $d.f. = 3$, $P < 0.001$). A contingency table analysis for season by species revealed that *A. torques* differed significantly among seasons for all diet categories ($n = 283$, $d.f. = 3$, $\chi^2 = 19.2$, $P < 0.001$, arthropods; $\chi^2 = 21.94$, $P < 0.001$, intact seeds; $\chi^2 = 41.94$, $P < 0.001$, intact seeds; $\chi^2 = 71.29$; $P < 0.001$, mycorrhizal spores) whereas *C. sorellus* did not differ among seasons in the presence/absence of arthropods, plant remains, or mycorrhizal spores ($n = 47$, $d.f. = 3$, $\chi^2 = 1.35$, $P = 0.72$, arthropods; $\chi^2 = 2.54$, $P = 0.47$, plant remains; $\chi^2 = 3.3$, $P = 0.35$, mycorrhizal spores) but differed significantly among seasons in intact seed occurrence ($n = 47$, $d.f. = 3$, $\chi^2 = 10.82$, $P = 0.013$). *M. minutus* did not show significant differences among seasons for diet items except for the presence of mycorrhizal spores ($n = 46$, $d.f. = 3$, $\chi^2 = 4.34$, $P = 0.23$, arthropods; $\chi^2 = 6.03$, $P = 0.11$, intact seeds; $\chi^2 = 1.97$, $P = 0.58$, plant parts; $\chi^2 = 9.72$, $P = 0.021$, mycorrhizal spores). *T. kalinowskii* showed significant differences among season only for intact seed consumption ($n = 57$, $d.f. = 3$, $\chi^2 = 3.47$, $P = 0.33$, arthropods; $\chi^2 = 16.89$, $P = 0.001$, intact seeds; $\chi^2 = 0.61$, $P = 0.89$, plant parts; $\chi^2 = 6.45$, $P = 0.09$, mycorrhizal spores) whereas *T. oreas* showed significant differences among seasons only for arthropods but not for fruits and seeds ($n = 91$, $d.f. = 3$, $\chi^2 = 9.52$, $P = 0.02$, arthropods; $\chi^2 = 2.81$, $P = 0.42$, intact seeds; $\chi^2 = 3.08$, $P = 0.379$, plant parts; $\chi^2 = 9.216$, $P = 0.27$, mycorrhizal spores). Due to small sample sizes, we were not able to reach conclusions regarding diet and seasonality for *O. andinus* and *T. aureus*.

Diet composition.—Diet composition, determined for samples collected in 2009–2010, indicated that all species (except for *T. aureus* [59%; Table 2]) had high frequency of occurrence of arthropods (between 90% and 100%). Arachnids were an infrequent diet item, although *A. torques* was found to consume spiders and scorpions. Within the class Insecta, coleopterans were the most common diet item, found most frequently in *C. sorellus* and *A. torques*, but absent from *T. aureus*. *A. torques* had the highest diversity of insects in its diet, with coleopterans, hemipterans, hymenopterans, isopterans, orthopterans, and other unidentified invertebrates present in fecal samples. *C. sorellus* was found to include at least 3 orders of insects (Coleoptera, Hemiptera, Hymenoptera); *M. minutus* 2 orders (Coleoptera, Hymenoptera); *O. andinus* 2 orders (Coleoptera, Hymenoptera); *T. kalinowskii* 2 orders (Coleoptera, Hemiptera); and *T. oreas* 3 orders (Coleoptera, Hymenoptera, Orthoptera).

Nine plant families and 17 plant morpho-species belonging to a minimum of 10 genera were identified by intact seeds occurring in rodent fecal remains. Based on identification of intact seeds, rodents consumed fruits that occur in families that are most commonly associated with small trees or shrubs that likely produce berries with small seeds. Positively identified families in the diets included Annonaceae (*Guatteria* sp.), Bromeliaceae (*Greigia* sp.), Brassicaceae (sp. 1, sp. 2), Ericaceae (*Gaultheria* sp. 1, *Gaultheria* sp. 2, *Demosthenesia* sp.); (Solanaceae sp. 1–4), Melastomataceae (*Miconia* sp. 1 and sp. 2), and Myrtaceae (*Myrteola* sp.). These represent approximately 13% of the plant families identified thus far at the study site but is likely a conservative estimate, as we were not able to identify all fruit pulp occurring in fecal samples.

Monocotyledon plant, fruit, and intact seed remains were found much less frequently than dicotyledon plant items in all species. Among the monocots, seeds belonging to the genus *Greigia* (Bromeliaceae) were found only in *T. kalinowskii* fecal samples. Seeds from the genus *Miconia* sp. 1 and sp. 2 (Melastomataceae) were found in 5 species and 3 genera of rodents (*Akodon*, *Microryzomys*, *Thomasomys* spp.). Seeds from the genus *Gaultheria* (sp. 1 and/or sp. 2; Ericaceae) were found in samples from all species of rodents. Seeds belonging to the Solanaceae family were found infrequently in *T. kalinowskii* and *T. aureus* feces. *Demosthenesia* sp. 1 (Ericaceae) seeds were found at low frequencies in *T. kalinowskii* and *T. oreas* fecal samples as were unidentified seeds belonging to the Rosaceae (sp. 1) and Rubiaceae (sp. 1 and sp. 2). Mycorrhizal spores belonging to the genus *Glomus* were frequent in samples from all species of rodents. *T. kalinowskii* had the highest percent occurrence of *Glomus* sp. spores, followed by *O. andinus*.

Table 2.—Diet composition and proportion frequency of occurrence of diet items for 2009–2010 at Chiquintirca, Ayacucho, Peru. Starred items were found only in 2011–2012 samples, have the corresponding *n* next to frequency, and are included here to complete our diet composition list for plants.

Species	Akodon torques	Calomys sorellus	Microryzomys minutus	Oligoryzomys andinus	Thomasomys aureus	Thomasomys kalinowskii	Thomasomys oreas
	n = 162	n = 21	n = 34	n = 7	n = 17	n = 23	n = 64
Invertebrata	1.00	1.00	1.00	1.00	0.59	1.00	0.91
Arachnida							
Araneae	0.006		0.03				
Scorpiones	0.02						
Insecta							
Coleoptera	0.80	0.90	0.44	0.71		0.61	0.36
Hemiptera	0.09	0.05				0.04	
Hymenoptera	0.20	0.10	0.03	0.14			0.05
Isoptera	0.01						
Orthoptera	0.10						0.02
Unidentified larvae	0.60	0.42	0.38	0.29	0.35	0.39	0.42
Plantae							
Plant parts	0.85	0.95	0.97	1.00	1.00	1.00	0.97
Monocotyledoneae	0.10		0.06		0.18	0.04	0.06
Dicotyledoneae	0.29	0.61	0.59	0.57	0.94	0.65	0.73
Seeds							
Monocotyledoneae							
Bromeliaceae							
Greigia sp.						0.39	
Dicotyledoneae							
Annonaceae							
Guatteria sp.					0.59	0.04	0.02
Brassicaceae							
Brassicaceae sp. 1	0.01		0.03		0.29	0.04	0.03
Brassicaceae sp. 2							0.03
Ericaceae							
Gaultheria sp. 1	0.17	0.52	0.32	0.28	0.23	0.30	0.30
Gaultheria sp. 2	0.03	0.05					0.06
Demosthenesia sp.	0.01					0.13	0.03
Melastomataceae							
Miconia sp. 1	0.14		0.06		0.59	0.43	0.26
Miconia sp. 2	0.03				0.18		0.06
Myrtaceae							
Myrteola sp.							0.02
*Rosaceae sp. 1	11 (0.09)						
*Rubiaceae sp. 1							3 (0.33)
*Rubiaceae sp. 2						4 (0.25)	
Solanaceae							
Solanaceae sp. 1					0.59		
Solanaceae sp. 2					0.59	0.09	
Solanaceae sp. 3					0.59	0.04	
Solanaceae sp. 4						0.13	
Unidentified seeds	0.02	0.05			0.12	0.22	0.06
Fungi							
Glomeromycetes							
Glomerales							
Glomus sp.	0.58	0.57	0.71	0.57	0.47	0.74	0.59

Bray–Curtis index of dissimilarity.—A cluster analysis utilizing a Bray–Curtis dissimilarity index showed 2 main clusters according to diet. The genus *Thomasomys* plus *C. sorellus* formed a group with *T. aureus* being the most dissimilar of this group. The 2nd cluster was formed by *O. andinus*, *A. torques*, and *M. minutus*, with *A. torques* being the most dissimilar of this group (Fig. 1).

Plant species richness and fruit production.—A total of 172 species and morpho-species (54 families, 94 genera) were recorded at the study site. Rodents were found to pass whole, undamaged seeds from 17 species (10% of plant species registered). Plant families and genera in the diet of rodents primarily are associated with small trees and shrubs as well as the bromeliad *Greigia*, which commonly is found along the ground in montane cloud forest. We were not able to confirm the identity of all fruit pulp found in feces, so the number of fruit-bearing plants consumed may be larger than that reported for whole seed consumption and passage.

In May 2012, after the rainy season (Fig. 2), 57 species of plants were producing fruits (21 families and 33 genera) and 9 species of intact seeds were identified in feces (16% of fruiting species). Total fruit production at this time was 136 fruits/m^2 in forest habitat and 142.35/m^2 in shrub habitat.

DISCUSSION

The 7 species of sigmodontine rodents in our study area have flexible diet strategies with all species being omnivorous. Due to the high presence of intact seeds, we believe that fruit
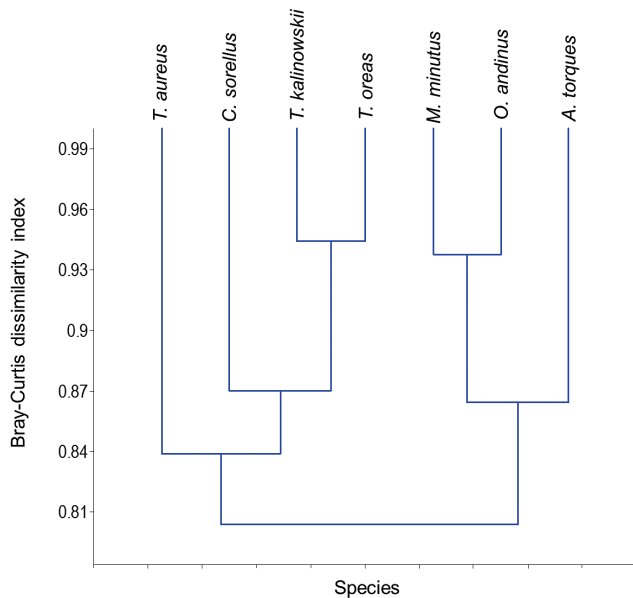

Fig. 1.—Cluster analysis for rodent species based on Bray–Curtis dissimilarity index for frequency of occurrence of 4 diet categories at Chiquintirca, Ayacucho, Peru. Two clusters are apparent; one is comprised of *Thomasomys* spp. but also includes *Calomys sorellus* due to the high levels of intact seeds and plant parts in fecal samples. The 2nd cluster is comprised of *Akodon torques*, *Microryzomys minutus*, and *Oligoryzomys andinus* which are omnivorous, but have lower proportions of intact seeds and plant remains in samples as compared to the 1st group.

consumption is an important component of the diet for this rodent assemblage. All 7 species consumed arthropods, fruits, plant remains (stems, leaves, shoots), and mycorrhizal spores. Campos et al. (2001) and Giannoni et al. (2005) reported flexibility in the sigmodontine diet in montane and desert habitats, but did not report fruit as part of their diet. Viera et al. (2003, 2006) found that captive sigmodontine rodents ate fruit when it was offered. Omnivory was found in *Akodon* spp. in a temperate rainforest (Meserve et al. 1988). Noblecilla and Pacheco (2012) found intact seeds in stomach contents of *T. kalinowskii* and *T. notatus*, indicative of fruit consumption.

As expected, the frequency of occurrence of diet categories among genera and species was significantly different, suggestive of diet preferences among taxa and/or differential access to resources. Within rodent species, frequency of occurrence of diet categories also was significantly different, also suggestive of diet preference. Variation in diet categories among seasons is also significant, indicating variable access to resources over time. Although we do not have plant phenology recorded over the entire course of this study, rainfall data at our study site are indicative of pronounced rainy and dry seasons. Smythe (1978) found seasonal consumption of fruit pulp by *Dasyprocta punctata* and variable consumption of seeds and plant parts were found for *D. leporinae* (Henry 1999). Seasonal variation was found in fruit pulp consumption versus seed consumption in *Dasyprocta* spp. and *Myoprocta* spp. (Forget et al. 2002). Mangan and Adler (2002) found seasonal consumption of mycorrhizal spores by *Proechimys semispinosus*, whereas Janos et al. (1995) found seasonal occurrence of mycorrhizal spores in *Proechimys* and *Oryzomys* spp. fecal samples. Additional data on resource seasonality at our study site throughout the year would be useful for differentiating between resource availability and foraging strategies.

Akodon torques had the highest frequency of occurrence for arthropods and the lowest frequency of occurrence for fruits. Solari (2007) found that in the Andean highlands, *A. torques* and *A. subfuscus* were primarily insectivorous; in the montane forests of Huanuco, Peru, *A. orophilus* also exhibited a
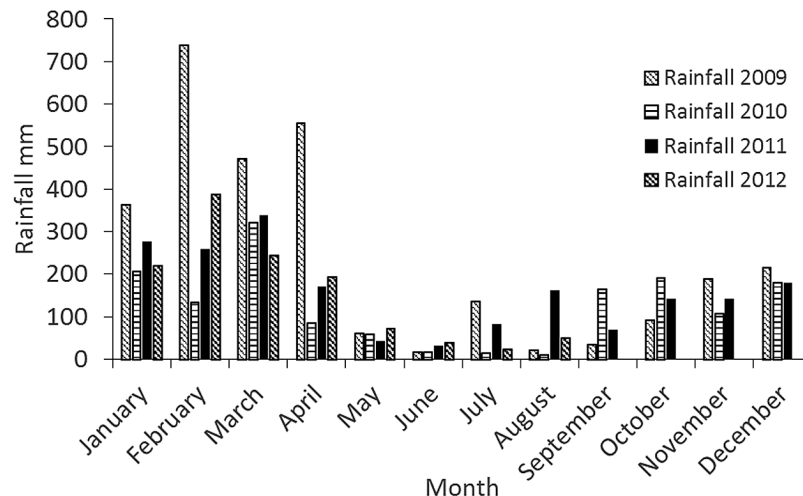

Fig. 2.—Rainfall for 2009–2012 from the study site at Chiquintirca, Ayacucho, Peru, illustrating variability in precipitation within and between years. For 2012, data from September through December are missing.

high degree of insectivory (Noblecilla and Pacheco 2012). Pizzimenti and de Salle (1980) found that *Akodon* was primarily insectivorous, with only one species *A. jelskii*, being principally herbivorous. *Akodon* spp. were found to be omnivorous in a Chilean temperate rainforest and consumed fruit (Meserve et al. 1988). In our study, *A. torques* fed principally on coleopterans, although spiders and scorpions also were included in its diet. Nonetheless, plant parts were a common item in its diet, as were fruits and mycorrhizal spores.

Microryzomys minutus and *O. andinus* showed a preference for arthropods but also consumed fruits, plants, and mycorrhizal spores, concurring with Noblecilla and Pacheco (2012) who noted that *M. minutus* and *M. altissimus* were also omnivorous in montane tropical forests. Solari (2007) noted that *Oligoryzomys* sp. B showed tendencies toward omnivory in the high grasslands of Manu National Park. *M. minutus* consumed primarily coleopterans, as did *O. andinus*, and both consumed fruits, although *M. minutus* had a higher percent volume of mycorrhizal spores in fecal samples.

Calomys sorellus also had a high frequency of occurrence of arthropods in samples, but this frequency of occurrence was almost equal to its consumption of plant remains and fruits, similar to *T. kalinowskii*. Pizzimenti and De Salle (1980) stated that *C. sorellus* was atypical for its genus by being small and insectivorous, but this study indicated that its diet is more flexible than previously noted and could be habitat dependent.

The genus *Thomasomys* was notable for its high frequency of occurrence of intact seed remains in fecal samples as well as plant remains, mycorrhizal spores, and arthropods. *T. aureus*, the largest rodent in our study, had the highest frequency of occurrence of intact seeds plus plant remains and the lowest frequency of occurrence of arthropod remains. Our study indicates that *T. aureus* appeared to specialize on fruits (as evidenced by consumption of intact seeds) and plant parts.

Thomasomys oreas had a very high frequency of occurrence of intact seeds and arthropods in its diet. *T. kalinowskii* was the most generalist species of the assemblage studied. Its diet included both a high frequency of intact seeds as well as arthropods and mycorrhizal spores. Noblecilla and Pacheco (2012) found that *T. kalinowskii* had the largest niche width of the rodent assemblage studied in Huanuco, Peru. Lopez-Arevalo et al. (1993) found that for *T. laniger*, diet was composed of fruits, seeds, and insects, with an increase of insects in the wet season. For *T. niveipes*, the diet was composed mainly of young leaves and other plant remains.

Thomasomys kalinowskii was the only species of rodent that was found to have *Greigia* sp. seeds in its feces. *Gregia* sp. is a bromeliad that often grows at ground level and exhibits a red, berry-like fruit. Troya et al. (2004) found that Andean bears, which inhabit montane rainforest, also include *Greigia* in their diet. *Gaultheria* spp. (Ericaceae) were consumed by all 7 species of rodents, ranging from 17% to 52% frequency of occurrence. *Gaultheria* species (of which there are at least 4 at our study site) are usually found as shrubs, producing fleshy berries with numerous small seeds.

Phenology data, taken shortly after the rainy season, indicated that during at least 1 portion of the year, fruits are plentiful and are not likely limiting. However, without year-round data on phenology and fruit consumption by potential competitors such as bats and birds, we cannot make conclusions as to whether fruit resources are limiting throughout the year.

Biological significance.—The rodent assemblage we studied is similar in diversity at the generic level and number of species to sigmodontine communities found in other montane tropical forests (Pacheco et al. 2013). We can hypothesize that similar diet patterns may be found for small rodents in tropical montane forests, with omnivory being common, and certain taxa specializing on either arthropods or fruit and plant parts. Two distinct clusters existed according to diet in our study; one that was comprised of the *Thomasomys* spp. + *C. sorellus* group and specializes more on plants (fruits, leaves, stems), and the 2nd one which consisted of genera that while omnivorous, consumed equal or higher quantities of arthropods in their diet.

Fruits consumed generally belong to taxa that are commonly associated with shrubs and produce berries with small-seeded fruits. All species of rodents consumed mycorrhizal spores belonging to the genus *Glomus*, in accord with several other studies that indicate rodents are dispersers of vesicular–arbuscular mycorrhizal fungi in tropical forests (Janos et al. 1995; Mangan and Adler 2002). Thus, the pattern shown in this study showed us a range of feeding strategies which varied from a high degree of arthropod specialization (*A. torques*) to arthropod-preferring omnivores, plant-preferring omnivores, and a tendency toward fruit specialization (*T. aureus* and *T. oreus*). Therefore, these sigmodontine rodents likely play important ecological roles in montane tropical forests, not only as arthropod predators but also as frugivores and seed dispersers.

ACKNOWLEDGMENTS

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