

**DIET OF THE ANDEAN FROG *RANITOMEYA VIROLINENSIS*  
(ATHESPHATANURA: DENDROBATIDAE)**

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**UNIVERSIDAD INDUSTRIAL DE SANTANDER  
FACULTAD DE CIENCIAS  
ESCUELA DE BIOLOGÍA  
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## RESUMEN

**TITULO:** DIETA DE LA RANA ANDINA, RANITOMEYA VIROLINENSIS (ATHESPHATANURA:DENDROBATIDAE).\*

**AUTOR:**

Mercedes Valderrama Vernaza\*\*

**Palabras claves:** Rana venenosa de Santander, Andes de Colombia, dieta, ácaros, hormigas, ontogenia.

### DESCRIPCIÓN

Los factores filogenéticos y ecológicos alteran los patrones alimenticios. En el presente estudio se analizan los efectos de la ontogenia y la estacionalidad en la dieta de *Ranitomeya virolinensis*. Las categorías de presas más importantes son Acari, Formicidae, larvas holometabolos y Collembola. No hay diferencias en el contenido total del tracto digestivo en el tiempo, pero el consumo de Formicidae y Collembola varió con respecto al tiempo. La importancia de Formicidae se incrementó en Mayo, (IRI, hembras = 4836 y machos = 4125) en relación con los otros meses del año, mientras que la importancia de Collembola se incrementó en Marzo (IRI, hembras = 571 y machos = 483). Los tractos digestivos de machos presentan un número y volumen de presas significativamente menor que el de las hembras. En particular Acari y Formicidae son significativamente más frecuentes en hembras que en machos. Hay un cambio ontogenético en el tamaño promedio de las presas y en el número de presas con el tamaño corporal. El volumen de Acari se redujó con el tamaño del cuerpo, mientras, el volumen de Formicidae se incremento. Los juveniles de tamaño intermedio tienen más presas en número y volumen, Acari y Formicidae en particular son significativamente mayores en volumen en las ranas de tamaño intermedio. El consumo de acaros está ligado a la ontogenia, al sexo, pero son consumidos por todo el año. Las hormigas también están ligadas a la ontogenia y al sexo de las ranas; sin embargo su consumó varió a lo largo del año. La dieta de esta especie puede estar relacionada a factores filogenéticos y ecológicos. Formicidae no son la presa más importante como ha sido descrito previamente para otras especies de Dendrobatidae. La presa más importante en *R. virolinensis* es Acari, como en especies también pequeñas y de linajes cercanos.

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## ABSTRACT

**TITLE:** DIET OF THE ANDEAN FROG *RANITOMEYA VIROLINENSIS* (ATHESPHATANURA: DENDROBATIDAE) .\*

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**Key Words:** Santander Poison Frog, Colombian Andes, diet, mites, ants, ontogeny.

### DESCRIPTION

Feding patterns are influenced by phylogenetic and ecological factors. We studied the effects of sex, ontogeny, and season on the diet of *Ranitomeya virolinensis*. The most important prey items were Acari, Formicidae, Holometabolous larvae, and Collembola. There were no differences in total prey gut content over time; but, consumption of Formicidae and Collembola did decrease or increase over time. Formicidae importance increased in May, the peak of the rainy season (IRI; females=4836 and males=4125) in relation to other months, while Collembola importance increased in March (IRI; females= 571 and males=493) at the beginning of one of the rainy season. Males had significant less prey in their guts than females. Acari and Formicidae particularly had significant larger volume in females than in males. Though the diet of this species is composed mainly of small prey, there is an ontogenetic shift in prey number and volume and the average prey size increased with body size. The volume of Acari decreased with body size, while the volume of Formicidae increased. Juveniles of intermediate size had more prey in number and volume, and Acari and Formicidae were significantly higher in the frogs of this size. Mites are linked to ontogeny and sex, but are consumed throughout the entire year. Ants are also linked to the ontogeny and sex of frogs; however their consumption changes throughout the year. The diet of this species might be related to phylogeny and ecological factors. Formicidae are not the most important prey as has been described previously for other dendrobatid species, but instead Acari are the most important prey, as in other small and closely related species.

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## INTRODUCTION

Dendrobatoidea is a monophyletic taxon (Vences et al., 2000; Haas, 2003; Grant et al., 2006), which includes dart poison frogs, family Dendrobatidae and non poison frogs, family Aromobatidae (Grant et al., 2006). Certain dendrobatoid frogs are characterized by territorial behavior (Roithmair, 1994; Lima et al., 2002; Lima and Keller, 2003; Gardner and Graves, 2005; Pröhl, 2005), parental care (Caldwell and Oliveira, 1999; Wijngaarden and Bolaños, 1992), and the presence of alkaloid skin secretions that are used as a chemical defense against predators (Daly et al., 1987; Daly, 1995; Daly, 1998; Mortari et al., 2004; Daly et al., 2005). Alkaloids in poison frogs are accumulated directly from diet (Daly et al., 1994a, b; Daly, 1998) and are stored in specialized skin glands located in the skin (Neuwirth et al., 1979; Toledo and Jared, 1995). Recent studies have hypothesized an evolutionary correlation between aposematism and toxicity at the species level (Summers and Clough, 2001; Santos et al., 2003). Although there are interpopulational differences in frog toxicity and coloration, there is no apparent correlation between toxicity and color of frogs among populations (Daly and Myers, 1967). It has been further proposed that a specialized diet of

ants may be linked to these two features (Caldwell, 1996; Santos et al., 2003; Darst et al., 2005). However, there are many ecological factors influencing the relationship between frog diet and toxicity, including the distribution of the studied species and availability of alkaloid-containing arthropods at these locations (Biavati et al., 2004; Toft, 1980b; Saporito et al., 2006; Saporito et al., in press). The effects of long term accumulation of alkaloids, and spatial and temporal variation in alkaloids among arthropod prey also change the toxic profile of frogs (Smith and Jones, 2004; Saporito et al., 2004, 2007; Saporito et al., in press). Ants are an important dietary source of alkaloids in dendrobatids (Jones et al., 1999; Saporito et al., 2004); however mites have recently been shown to be the largest source of alkaloids at least in one species, *Oophaga pumilio* (Saporito et al., 2006, 2007; Takada et al., 2005). Other dietary sources of alkaloids include millipedes (Saporito et al., 2003) and beetles (Dumbacher et al., 2004). It is crucial to gain a further understanding of the importance of certain prey items in the diet of dendrobatids and their relationship with intrinsic factors such as phylogeny, morphology and ontogeny and extrinsic factors such as seasonality, prey availability and sex, before inferring relationships between diet and toxicity.

Anuran diet can be modified by shifts in dietary resources, such as geographic and seasonal shifts in arthropod availability (Toft, 1980 a, b; Biavati et al., 2004). Ants are the main prey items identified in the diet of the dendrobatid frogs studied in Amazonian and Central American wet forests (Toft, 1980a, b; Caldwell, 1996). However, ants may not be a crucial dietary component in dendrobatid frogs in the Cerrado biome. For example, *Ameerega flavopicta*, a toxic species that inhabits the Cerrado biome, is not an ant specialist as their Amazonian and Central America relatives (Biavati et al., 2004). The dietary importance of ants or other prey items in Andean amphibian species is poorly known (Piñero-Bonilla and La Marca, 1996). *Ranitomeya virolinensis* (Ruiz-Carranza and Ramírez-Pinilla, 1992), commonly known as Santander Poison Frog, is a small (up to 18.9 mm SVL) dendrobatid frog distributed throughout the northern montane wet forests of the western slope of the Cordillera Oriental of Colombia (Ruiz-Carranza and Ramírez-Pinilla, 1992). Its distribution ranges throughout the Departaments of Boyacá, Cundinamarca, and Santander. This studied focused on the diet of *R. virolinensis* and the goals of the research tried to answer: (1) Is *R. virolinensis* an ant specialist, as has been suggested for most of the

studied lowland dendrobatids? (2) What is the annual feeding pattern of this Andean species? and (3) Are there any changes in the diet of *R. virolinensis* associated with differences in sex, ontogeny, and reproductive condition? Diet is not solely linked to phylogeny, and in many Neotropical anuran species it changes over time, linked to seasonal fluctuations in prey resources (Toft, 1980 a, b; Donnelly, 1991). In addition, because behavioral activity is directly associated with reproduction, there may be temporal changes in the energetic investments of frogs (Girish and Saidapur, 2000). If this is true, then other factors that are restricted by morphology and behavior may be important in understanding the trophic ecology of anurans, such as ontogeny (Lima and Moreira, 1993), sex (Donnelly, 1991), and reproduction (Biavati et al., 2004). To address these questions, we investigated a population of *R. virolinensis* in a montane wet forest on the western slope of the Cordillera Oriental of Colombia.

## **MATERIALS AND METHODS**

This study was conducted in a secondary wet forest located at approximately 6°6' N, 73°13' W, on the western slope of the Cordillera

Oriental of Colombia. This area is known as Costilla del Fara, Corregimiento de Virolín, Santander, Colombia. This zone has an annual mean temperature of 18.4°C and a mean annual rainfall of 2916 mm. Rainfall follows a seasonal pattern (Fig. 1) that is characterized by a first rainy season from March to May, a rainfall decrease from June to July, a second rainy season from August to November, and a dry season from December to February (Hijmans et al., 2005). The vegetation of the site is characteristic of low montane forest (Holdridge, 2000). The site is located on a steep hill with a small stream, at an elevation of 1803 m. The roots of trees and rocks covered by leaf litter are used by males of *R. virolinensis* as territories for calling.

Frog sampling was conducted once every two months from July, 2005 to May, 2006, in order to collect data from the different seasons. Within the boundaries of a pre-established 2300 m<sup>2</sup> area (see Gil, 2005), frogs were collected from 08:00 through 16:00 h for three days during each sampling period. A minimum of 20 postmetamorphic individuals were collected per month by searching the leaf-litter, old vegetation on the ground, and inside rocks and root caves where calling males and courtship couples can be found (Gil, 2005). Given the small

size of these frogs (mean SVL = 16.01 mm, range 9.05 mm - 18.44 mm), we could not stomach flush individuals to obtain dietary items. Therefore, specimens were euthanized with 10% ethanol and immediately fixed in 10% formalin to preserve gut contents with minimum digestion. In the laboratory, specimens were transferred to 70% ethanol for storage. All of the collected specimens are housed in the Colección Herpetológica, Museo de Historia Natural UIS (UIS-A-3584 to UIS-A-3750).

Snout-vent length (SVL) and mouth width (MW) were recorded to the nearest 0.02 mm in the laboratory with a Vernier caliper. Adult females (SVL mean  $\pm$  SD = 17.38  $\pm$  0.53 mm) were significantly larger than adult males (16.72  $\pm$  0.54;  $t_{124} = 6.91$ ,  $P < 0.001$ ). There were no significant differences in mouth width (MW) between females and males ( $t_{124} = 0.53$ ,  $P = 0.596$ ). Juveniles had a mean SVL of 12.61  $\pm$  2.03.

Specimens were dissected, and the sex and size of gonads were recorded for each individual. The complete reproductive and digestive tracts were also dissected and stored separately in 70% ethanol. The diameter of the largest follicles and oviduct convolution of females were also recorded. Macroscopic features of gonads were used to determine

the age of sexual maturity and reproductive stage in females. In addition, histological slides of ovaries and testes were prepared for adults and juveniles to further confirm sexual maturity and reproductive condition. Given the small size of testes in males (mean  $\pm$  SD = 1.24  $\pm$  0.24 mm, N = 72 mature and immature males), sexual maturity and reproductive status was only determined using histology. The smallest SVL for females possessing vitellogenic oocytes and convolute oviducts was regarded as the minimum size for sexual maturity; therefore, all collected females with a SVL equal or greater to this value were considered adults. The same was done for males, in which the smallest male possessing sperm within testes was considered the minimum size for sexual maturity. Females reached sexual maturity minimum size at 15.95 mm and males at 15.54 mm, SVL.

The development of follicles and oviducts of all frogs were also examined, given that size is a gross way of indicating sexual maturity and establishing reproductive categories. This species had a continuous reproductive pattern and there was not a representative sample of nonreproductive females to compare with reproductive females (Valderrama-Vernaza et al., unpubl. data).

For all gut samples, prey items were separated, counted, identified to the lowest possible taxonomic category, and measured for length and width (to the nearest 0.01 mm) with a digital caliper under a dissecting stereomicroscope. The volume of intact prey was estimated with the formula for  $\text{Prey volume} = \frac{4\pi}{3} \left( \frac{\text{prey length}}{2} \right) \left( \frac{\text{prey width}}{2} \right)^2$  a prolate spheroid: To describe the importance of each arthropod item consumed ( $t$ ), the index of relative importance (Pinkas et al., 1971) was calculated as  $\text{IRI}_t = \%O_t (\%N_t + \%V_t)$ , where  $\%O_t$  is the occurrence percentage (i.e., the number of guts containing each  $t$  item),  $\%N_t$  is the percentage of the number of  $t$  items in all guts, and  $\%V_t$  is the percentage of the volume of  $t$  items in all guts. Niche breadth was calculated for females, males, and juveniles separately to compare the utilization of prey species using Levins standardized formula (Hurlbert, 1978):  $B_A = \frac{(1/\sum p_i^2) - 1}{n - 1}$  where  $p_i$  = the proportion of occurrence of each prey species in each age-sex category of *R. virolinensis* diet;  $n$  = the number of prey species in the frogs diet.  $B_A$  ranges from 0 to 1, and a value of 1 for  $B_A$  means that all of prey were used in equal proportions, whereas a value near zero for  $B_A$  means that only one or a few categories were used in high proportions and that most prey were used in low proportions.

The average prey volume of prey items was correlated with the SVL of frogs to evaluate changes of prey size with ontogeny. Multiple regressions were employed to evaluate the relationship between frog size and total prey volume or number. The volume of the four prey items with highest IRI (which were the ones with a representative N, of volume and number of each prey item to make statistics comparisons) was analyzed separately to see if there is a shift in these prey items with SVL. To ensure normality of the data for all regression analyses, volumetric and numeric data from the four most important prey items, the total volume and number content and SVL were transformed using  $\text{LOG}_{10}(X+1)$ . Juveniles were arranged in five size-age category classes (<10 mm (N=5); 10.1-12 (N=10); 12.1-14 (N=13); 14.1-16 (N=12) and frogs with a SVL greater than 16 mm (N=125). A Kruskal Wallis test was employed to compare the differences in total prey volume and volume of Acari, Collembola, Formicidae and Holometabolous larvae. When necessary, a residual analysis was performed to eliminate the effect of frog size on prey number and volume of prey items. Given the small sample sizes, Holometabolous larvae were treated as a single unit, including Coleoptera, Lepidoptera, and non identified larvae. To assess

the effects of time periods and sex on the volumetric and numeric data of the four major prey items and on total prey contents a two way Kruskal Wallis (Sokal and Rohlf, 1995) was used, sampling months were used as time periods. July 2005 corresponds to the sample of the first dry period, September 2005 to the beginning of the rainy season, November 2005 to the peak of the rainy season, January 2006 to the second and driest period, March 2006 to the beginning of the rainy season and May 2006 to the peak of the second rainy period (Fig.1 and Fig.4) To check if changes with time were related to amount of rain, we employed a Spearman Rank Correlation between rain and prey volume from the total content and from the four major prey items.

## RESULTS

We analyzed 166 specimens of *Ranitomeya virolinensis* (61 adult males, 66 adult females and 39 juvenile frogs). All of the frogs examined contained at least one complete prey item in their guts ( $X = 56 \pm 37.63$ ). A total of 8993 prey items were analyzed, representing 13 prey categories (Table 1). The Relative Importance Index showed that the diet of *R. virolinensis* in both sexes and juveniles was dominated by

Acari, which was true for females, males, and juveniles (Fig. 1.). After Acari in order of significance, Formicidae, Holometabolous larvae (Coleoptera, Lepidoptera, and Non Identified larvae; Table 1) and Collembola were also important prey categories. Dietary niche breadth of *R. virolinensis* was close to zero, suggesting that this species tends to concentrate on a select group of prey items (juveniles  $B_A = 0.020$ , females  $B_A = 0.046$ , and males  $B_A = 0.039$ ).

There is an ontogenetic shift in volume of prey items (Table 2). There was a negative relationship between number of prey and SVL ( $r^2 = 0.058$ ,  $P = 0.002$ ,  $N = 165$ ). The average prey size increased with frog body size. Acari consumption decreased ( $r^2 = 0.1059$ ,  $P < 0.01$ ,  $N = 165$ ) while Formicidae consumption increased with respect to SVL ( $r^2 = 0.0391$ ,  $P = 0.0109$ ,  $N = 165$ ) (Fig. 2). However, there is no significant relationship between total volume content and frog body size. Intermediate juveniles ate the largest number of prey, when both accounting and without accounting for size effect (Fig. 3a). Intermediate juveniles (size age-class of SVL = 12.1-14 mm) consumed the highest amount of Acari ( $H_{5,165} = 10.65$ ,  $P = 0.0307$ ) and Formicidae ( $H_{3,160} = 8.74$ ,  $P = 0.0313$ ) when accounting for size effect (Fig. 3b, c).

Ontogenetic differences in prey consumption could be biased by the low sample size of the age-size categories with respect to adults sample size. The first age category was not comparable for Formicidae and Holometabolous larvae because of the low sample of these prey items in this size age category. There were no significant differences in Collembola ( $H_{5,165} = 2.99$ ,  $P = 0.5594$ ) or larvae ( $H_{5,165} = 4.58$ ,  $P = 0.3330$ ) content among size age categories.

Adult males and females do not consume the same volume of prey, we do not correct for body size in this analysis because there was not a significant relationship ( $P > 0.05$ ) between prey volume and SVL when only adults were accounted in the analysis. Females total volume prey content was significantly higher than males (Mann-Whitney U test,  $Z_{126} = -3.14$ ,  $P = 0.0016$ ) (Fig. 4). Females had higher volume content of Acari (Mann-Whitney U test,  $Z_{125} = 3.34$ ,  $P = 0.0008$ ) and Formicidae (Mann-Whitney U test,  $Z_{125} = 2.09$ ,  $P = 0.0362$ ) than males. There were no significant differences in other prey categories between sexes (Mann-Whitney U test,  $P > 0.05$ ).

The total number of prey was relatively similar among time periods for females, males, and juveniles (Fig 4a), and there were no significant differences among time periods ( $H_{5,125} = 2.67$ ,  $P = 0.751$ ) or the interaction of sex and time periods ( $H_{10,125} = 2.73$ ,  $P = 0.742$ ). Prey volume was apparently higher for females in January 2006 and May 2006 (Fig. 4b), but this difference was not significant among time periods or their interaction with sex ( $H_{10,125} = 6.31$ ,  $P = 0.277$ ). This apparent increase in volume was probably due to the effect of two frogs that had two large Lepidoptera larvae. The total gut content did not change over time, however the consumption of Formicidae ( $H_{5,125} = 14.47$ ,  $P = 0.013$ ) and Collembola ( $H_{5,125} = 13.44$ ,  $P = 0.019$ ) did change over time. The consumption of Formicidae was higher in the months with more rain, such as November and May (Fig 5a, b). All females from May 2006 had at least one ant in their guts but there was not a significant difference for the interaction of sex and time ( $H_{10,125} = 4.53$ ,  $P = 0.476$ ). March was the month where consumption of ants was lowest; this was also the month with the highest consumption of Collembola (Fig 5 c, d). Acari and Holometabolous larvae consumption did not change over time (Kruskal-Wallis test,  $P > 0.05$ ). However the only prey that was significantly correlated with rain (mm) was larvae

(Spearman Rank Correlation  $r_s = -0.1763$ ,  $P = 0.02$ ,  $N=165$ ), and total prey content or other prey items was not significantly correlated with rain (Spearman Rank Correlation,  $P > 0.05$ )

## DISCUSSION

This study illustrated that *Ranitomeya virolinensis* is a species whose diet is composed of small sized prey. Niche breadth and IRI values showed that this species has a narrow diet, with Acari as the most important prey item in adults and juveniles. This is consistent with other studies of small anurans from different regions; including Central American (Donnelly, 1991), Amazon forests, a montane moss forest of Papua New Guinea, Oceania (Simon and Toft, 1991), a moist forest from Malawi, Africa (Blackburn and Moreau, 2006), and in montane forests of the Andean Region of Argentina (Bonansea and Vaira, 2007).

Acari are a common prey in small frogs such as some Dendrobatids (Donnelly, 1991; Simon and Toft, 1991; Saporito et al., 2006; Saporito et al., 2007). Although information related to the ecology of mites in South America is poor, mites are related to bromeliads, leaf-

litter, and soil (Santos and Albuquerque, 2006). *R. virolinensis* is found in these same microhabitats, which may explain in part why mites are a common prey item in this species. Mites also contain a wide variety of alkaloids, many of which are the same alkaloids found in dendrobatid frogs (Takada et al., 2005, Saporito et al., 2007). Simon and Toft (1991) found that mites are the most important item for juveniles and small SVL anurans and that they were consumed in larger proportions than expected based only on body size. *R. virolinensis* had an high consumption of mites in comparison with other prey items (Fig.1). Mites could be more common in guts of this species due to the high percentage of chitin that affects negatively the gut passage time of food and the long-term rate assimilation of energy (Díaz and Carrascal, 1993). The high proportion of chitin is common in prey like Acari and Formicidae where the surface to volume results in small size and large surface area, making these preys only profitable for small frogs (Simon and Toft, 1991).

The number of prey items decreased with body size, whereas the average size of prey items increased with body size in *R. Virolinensis*. Size distribution of arthropod types might cause changes in arthropod prey items among frogs of different snout-vent length (Lima and Moreira,

1993). With respect to prey composition, there was a decrease in the volume of Acari and an increase in Formicidae consumption with increasing body size (Fig. 2) that could be due to the change in mean size of prey consumed. Lima and Magnusson (1998) also found a reduction in mites and increase of ants related to size. Although adults of *R. virolinensis* consumed large amounts of mites and ants, intermediate juveniles (12.1-14 mm) had significantly more mites and ants than smaller and adult frogs. However, this could be due to the fact that intermediate juveniles had a larger volume of preys in their stomach than the other size-age categories. Intermediate juveniles could be eating more to facilitate rapid growth prior to the start of reproduction (Christian, 1982). The diet of *Oophaga pumilio* changes ontogenetically, and mites are consumed in higher proportions in juvenile frogs than adults (Donnelly, 1991). *O. pumilio* had low variation of prey size with respect to other anurans studied for the same site in Costa Rica (Whitfield and Donnelly, 2006). This could also be the case for *R. virolinensis* in which there is only a slight shift in prey size with frog body size (Fig. 2). These ontogenetic shifts of prey size are expected in dendrobatids and non dendrobatids (Lima and Moreira, 1993; Hirai and Matsui, 2002). *R. virolinensis* did not omit small prey items such as

mites and collembolans when they become adults, but the importance of other prey items that are not eaten by juveniles, such as ants increased (Fig. 2).

The total number and volume of prey in guts was not different among time periods, but ants and collembolans did vary (Fig.5). Collembola consumption was highest when ant consumption was lowest, which occurred during March, that is the transition month between the wet and dry season (Fig 4). Arthropods are positively associated with moisture content in the leaf litter among seasons and sites (Leving, 1983; Leving and Windsor, 1984; Pearson and Derr, 1986). Moreover, arthropod fluctuations are independent among taxa (Whitfield and Donnelly, 2006) for instance, the proportional occurrence of ants is strongly affected by litter moisture content when compared to that of other arthropods groups (Leving, 1983). High moisture content sites have more active arthropods (Janzen and Schoener, 1968; Pearson and Derr, 1986). Fluctuations in the abundance of ants among months may be due to reduced activity in terrestrial ants responses to desiccation stress between seasons and among sites within a season (Kaspari and Weiser, 2000; Hahn and Wheeler, 2002). However, there

was no significant correlation between rain and Formicidae or Collembola found in guts of this species. Although the volume of these prey items changes over time, so it could be that ants change their availability due to factors different to rain or to the fact that this site has high humidity even during the dry season. We found that ants were more common in the guts of *R. virolinensis* during November and May, the months of the peak of the two rainy seasons though the reason for ants to be more common in the stomachs of frogs is not clear because there is no correlation with the volume of ants in stomach contents and rain. These results contrast with other anuran diet studies (Toft 1980 a; Donnelly 1991; Whitfield and Donnelly 2006), where ants were less common in the guts of frogs during the wet season. In other Neotropical localities there were no changes in diet of several species of anurans and reptiles among months, for instance the diet of Amazonian savanna lizards were similar along different seasons (Magnusson and Viera Da Silva, 1993) and the index of most important prey categories of *Ameerega flavopicta* does not change seasonally, but frogs collected during the dry season had significantly more prey in their guts (Biavati et al., 2004). There were no differences in the total number or volume of prey in guts of *R. virolinensis* and we had no complete empty guts. Total

availability of arthropod prey is not limited seasonally, but preferred arthropod types become seasonally less abundant (Whitfield and Donnelly, 2006). The lack of total diet decline could be due to this issue, *R. virolinensis* frogs ate more of other prey items such as Collembola when ants were not available (Fig. 5). The overgeneralization that food is more limiting during the wet season due to deterioration of leaf litter (Toft, 1980 a), should be seen with caution because arthropod patterns change from site to site and arthropod taxa are independent from each other as seen in the present study. Other factors, such as reproductive condition and age cannot be discarded as a possible cause for differences in annual feeding patterns of anurans.

Most studies on diet do not account for the reproductive effect on diet (Toft, 1980 a, b; Whitfield and Donnelly, 2006). Reproduction is also an important factor that can change the diet of anurans in time. It is likely that this is due to increased energy uptake by females during vitellogenesis when their energetic needs are higher (Biavati et al., 2004). Changes in the behaviour of individuals who invest more time in reproductive activities such as mating, courtship, and transport of larvae instead of foraging during the time of reproduction are also plausible

explanations for changes in diet (Roithmair, 1994). There is a seasonal reproductive pattern, where the reproductive season is associated with the rains in some of the studied dendrobatid species of the Amazonian and Central America forests; eg. *Allobates marchesianus* (Lima and Keller, 2003) and *Oophaga pumilio* (Donnelly, 1989). Therefore reproduction is a factor that may affect the diet pattern over time that was not accounted for in previous diet studies of these species.

*Ranitomeya virolinensis* is a continuous breeder with gravid females throughout the year. Therefore, if reproductive stage in *Ranitomeya virolinensis* has an effect on the diet of this species, it will influence individuals uninterruptedly, with no seasonal or time differences. If age distribution of the population changes with time this could also have an effect on the diet given the differences in number, volume and type of prey consumed by juveniles and adults (Lima and Moreira, 1993; Lima and Magnusson, 1998; Whitfield and Donnelly, 2006). However, there were no changes in age structure of this population of *R. virolinensis* over the time period of this study (Valderrama-Vernaza et al., unpubl. data). Hence this is likely not a factor influencing the diet of this species over time.

Females of *R. virolinensis* had more prey items in number and volume than males, and they consumed more Acari and Formicidae than males. These results contrast with those in *Ameerega flavopicta* (Biavati et al., 2004) and *Aromobates alboguttatus* (Piñero-Bonilla and La Marca, 1996), where no differences in diet composition between sexes were found. Donnelly (1991) suggested that females have more time to forage than males because they do not invest in territorial maintenance and need to meet energetic requirements associated with reproduction. Males of *R. virolinensis* transport tadpoles to pools of water in bromeliads (Ruiz-Carranza and Ramírez-Pinilla, 1992); therefore, the main energetic requirements of *R. virolinensis* females might be vitellogenesis. Calling activity, territory defense, courtship, and offspring transport by males could involve higher energetic costs (Roithmair, 1994) than those invested by females in vitellogenesis.

There are differences in mobility between males and females (Roithmair, 1994) which might also cause variation in the diet. Males of this species are very territorial, this could restrict foraging activity of males to those sites and they might not be able to seek for aggregate resources such as ants or mites.

*Ranitomeya virolinensis* most important prey item were not ants as has been shown for other dendrobatid species in tropical lowland wet forests. Mites were the most important prey item in this Andean species. These results could be linked to the size of this frog and to the availability of this prey item in the habitats, wet montane forests, where it is found. Its diet pattern could be to its closely related lineages that inhabit Central America. *Ranitomeya minuta* and *Ranitomeya fulgurita* were the only true mite specialists studied by Simon and Toft (1991), who found that mite number, was inversely correlated with ants. However, studies about the diet of its closely related species: *R. bombetes* and *R. opisthomelas* found in the Colombian Andes are needed. Both ants and mites are an important resource as in other related species, but their importance depends on the time of the year when frogs are sampled, the sex and the age of frogs. There are differences in alkaloid composition within dendrobatid frog species among different seasons and localities (Saporito et al., 2006; Saporito et al., in press), which appear to be related to variation in diet. Other factors such as ontogeny and sex could be also influencing the diet pattern. Diet is strongly influenced by ecological relationships over

evolutionary relatedness among species (Simon and Toft, 1991; Donnelly, 1991; Biavati et al., 2004). Therefore, *Ranitomeya virolinensis* diet might be linked to phylogeny and ecological factors such as seasonality and prey availability. Mites are important sources of alkaloids in some poison frogs (Saporito et al., 2007) and their importance in an evolutionary and ecological context remains unstudied. It will be of interest in the future to study the diet of mite specialist species with other evolutionary traits such as aposematism and chemical defense.

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**TABLE 1.** Diet of *Ranitomeya virolinensis* from a montane rainforest at the Cordillera Oriental of Colombia. N = Number of prey of each item, N%= Percentage of N, V= Volume of Prey of each prey item, V% = Percentage of V, F= Frequency of each prey item, F%= Percentage of F, IRI = Index of Relative Importance (Pinkas et al., 1971).

Prey type	N	N%	V	V%	F	F%	IRI
Acari	7766	84.79	72.83	25.18	165	100	10997.44
Hymenoptera							
Non Formicidae	68	0.74	3.65	1.26	45	27.27	54.62
Formicidae	328	3.58	74.48	25.75	103	62.42	1831.14
Total Holometabolous larvae	264	2.88	67.15	23.22	80	48.48	1265.43
Coleoptera larvae	210	2.29	29.25	10.11	64	38.78	481.23
Lepidoptera larvae	9	0.10	33.70	11.65	8	4.84	56.97
Non identified larvae	18	0.20	5.47	1.89	8	4.84	10.12
Collembola	488	5.33	18.79	6.50	118	71.52	845.74
Diptera	34	0.37	3.52	1.22	18	10.91	17.33
Coleoptera	91	0.99	32.09	11.10	61	36.97	446.98
Pseudoscorpiones	23	0.25	0.91	0.32	9	5.45	3.09
Tisanoptera	44	0.48	2.00	0.69	23	13.94	16.34

Gastropoda	18	0.20	7.82	2.70	11	6.67	19.34
Myriapoda	15	0.16	3.07	0.01	12	7.27	1.27
Aranae	20	0.22	2.90	0.01	14	8.48	1.94

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**TABLE 2.** Prey contents significant differences among size-age categories (<10 mm; 10.1-12mm; 12.1-14 mm; 14-16 mm and > 16 mm). Significant Kruskal Wallis comparisons are denoted by **Table 2.** Prey contents significant differences among size-age categories (<10 mm; 10.1-12mm; 12.1-14 mm; 14-16 mm and > 16 mm). Significant Kruskal Wallis comparisons are denoted by \*

Prey item	Number data		Volume data	
	$H_{5,164}$	$P$	$H_{5,164}$	$P$
Acari	2.51	0.6415	10.65	0.0307*
Formicidae	2.97	0.3967	8.85	0.0313*
Collembola	2.84	0.5853	2.99	0.5594
Larvae	4.58	0.3330	3.21	0.5232
Total prey	11.80	0.0189*	4.92	0.2956

## FIGURE LEGENDS

Fig. 1. Relative Importance Index (IRI) expressing annual seasonal pattern and monthly diet (from July 2005 to May 2006) of five major prey items in *Ranitomeya virolinensis*. A) juveniles B) males C) females. □, Acari; ■, Formicidae; □ larvae; ▨, Collembola; ■, other taxa. Line graph describes rain pattern.

Fig. 2. Volume of stomach contents for each prey item in relation to the SVL of the frogs. a) Acari ( $r^2 = 0.1059$ ,  $P < 0.01$ ,  $N = 165$ ), b) Volume of Formicidae, ( $r^2 = 0.0391$ ,  $P = 0.0109$ ,  $N = 165$ ), c) Volume of Collembola ( $r^2 = 0.0039$ ,  $P = 0.4278$ ,  $N=165$ ), d) Volume of larvae ( $r^2 = 0.0046$ ,  $P = 0.3873$ ,  $N = 165$ ), e) Total volume ( $r^2 = 0.0123$ ,  $P = 0.1558$   $N = 165$ ), f) Average prey size ( $r^2 = 0.0655$ ,  $P < 0.01$ ). Data are  $\log_{10}(X + 1)$  transformed.

Fig. 3. Comparison of gut contents among sex-age categories: a) Total number of prey accounting for size effect, b) Volume of Acari accounting for size effect, c) Volume of Formicidae accounting for size effect. Letters denote Nemenyi test significance at  $P < 0.05$ .

Fig. 4. Average of total preys in guts of *Ranitomeya virolinensis* frogs from July 2005 to May 2006 and annual seasonal pattern. ■, Juveniles; □, Males; □, Females. Line graph describes rain pattern.

Fig. 5. Comparison of prey items that differ in number and volume among time periods. a) number of Formicidae, b) volume of Formicidae, c) number of Collembola, d) volume of Collembola. Letters denote Nemenyi test significance at  $P < 0.05$ .

FIGURE 1

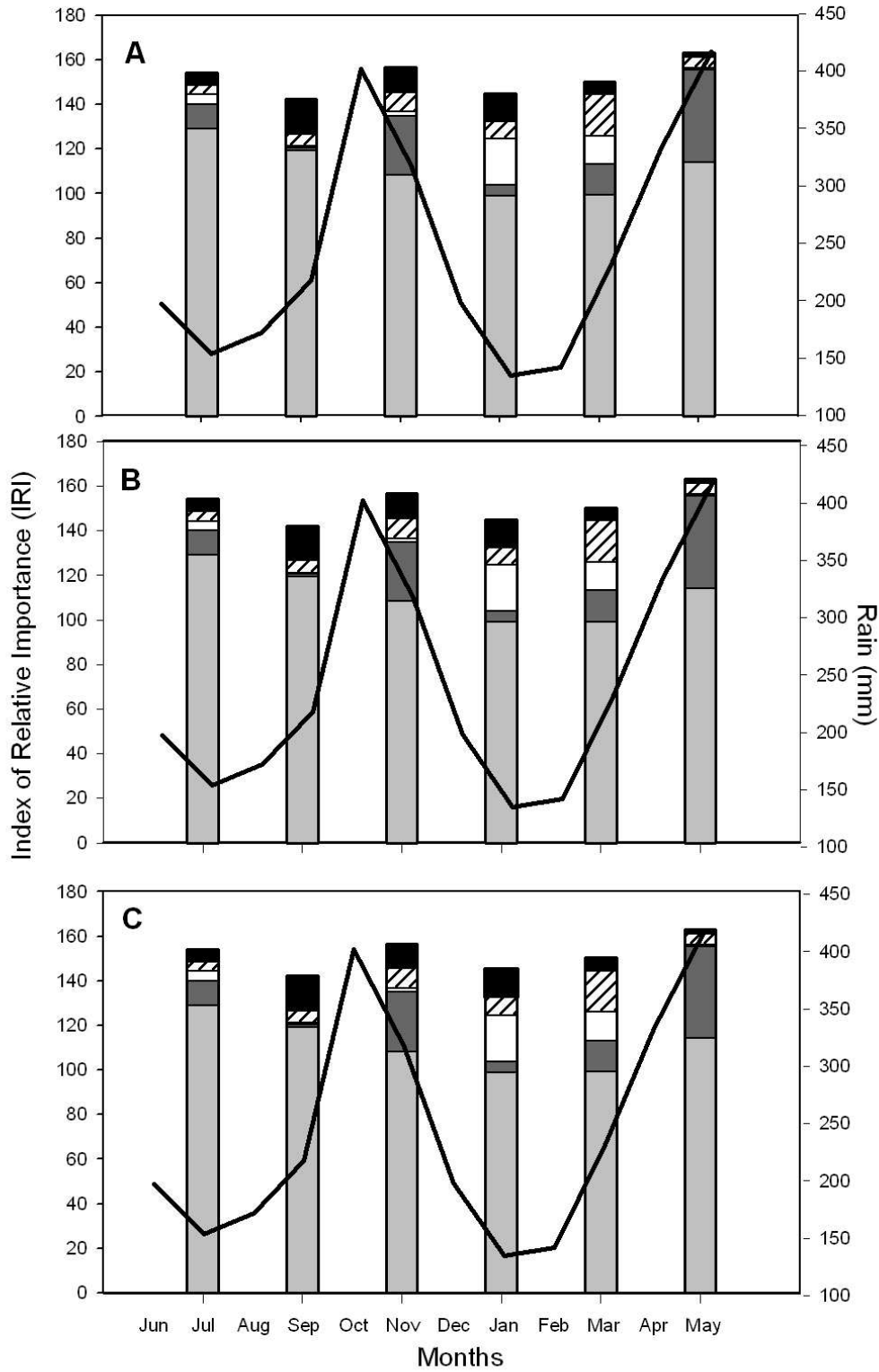
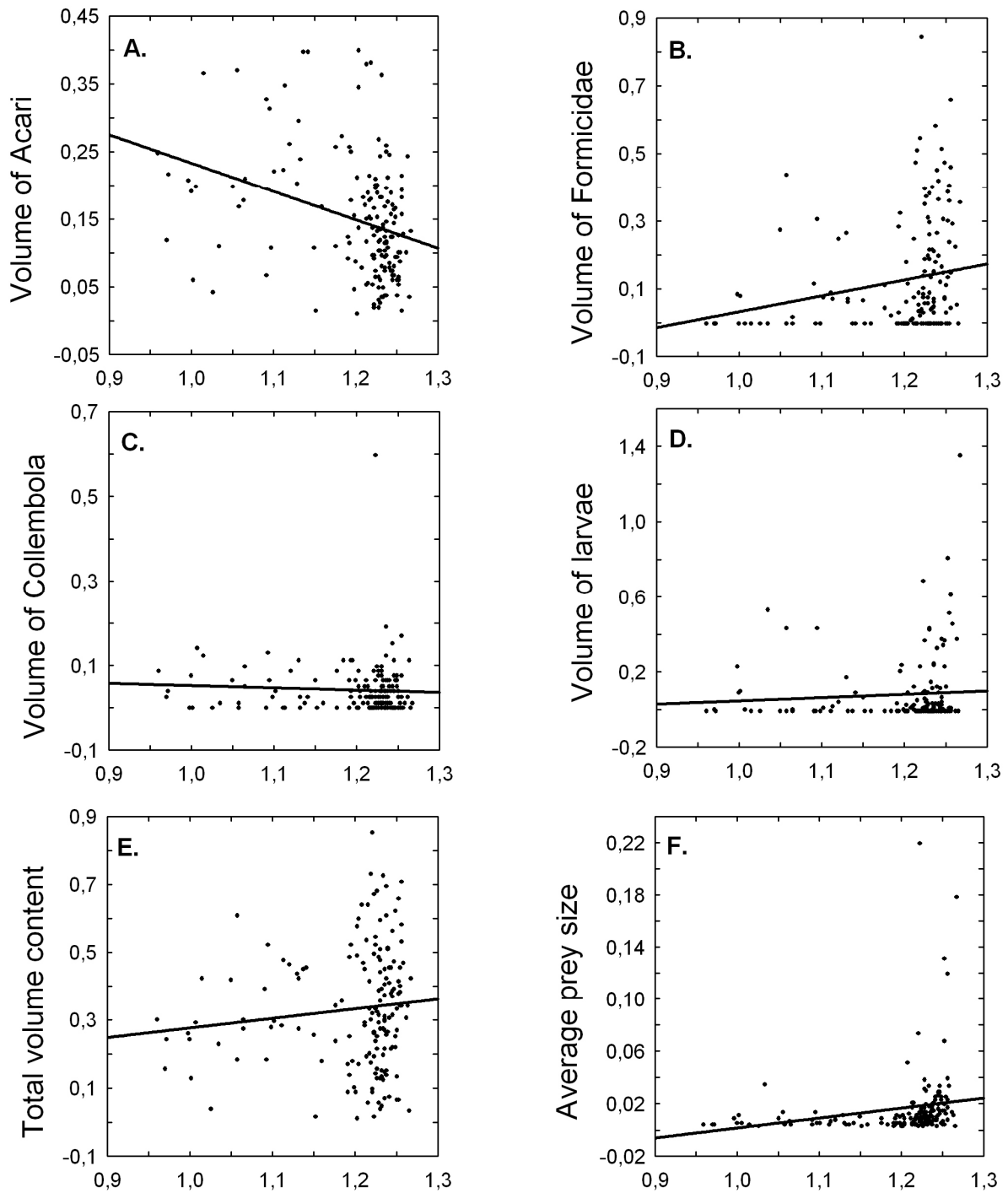


FIGURE 2



**FIGURE 3**

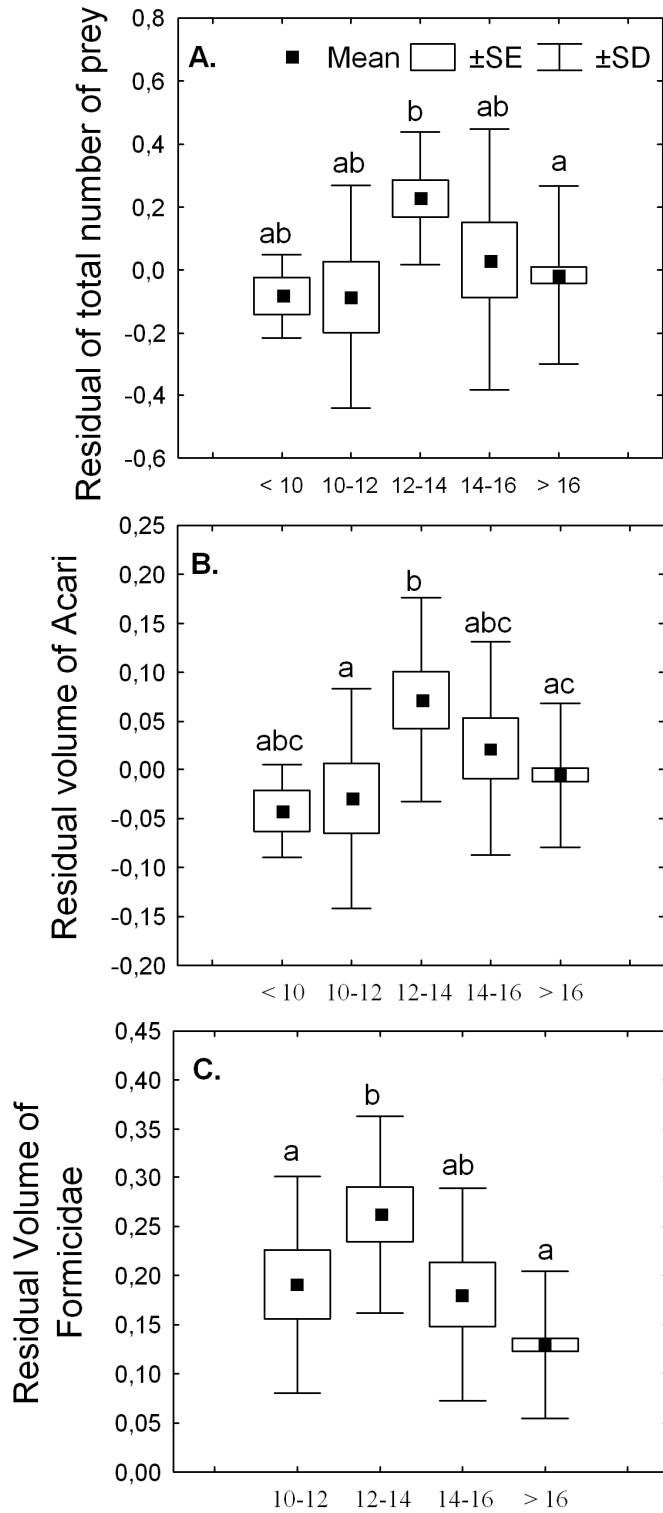
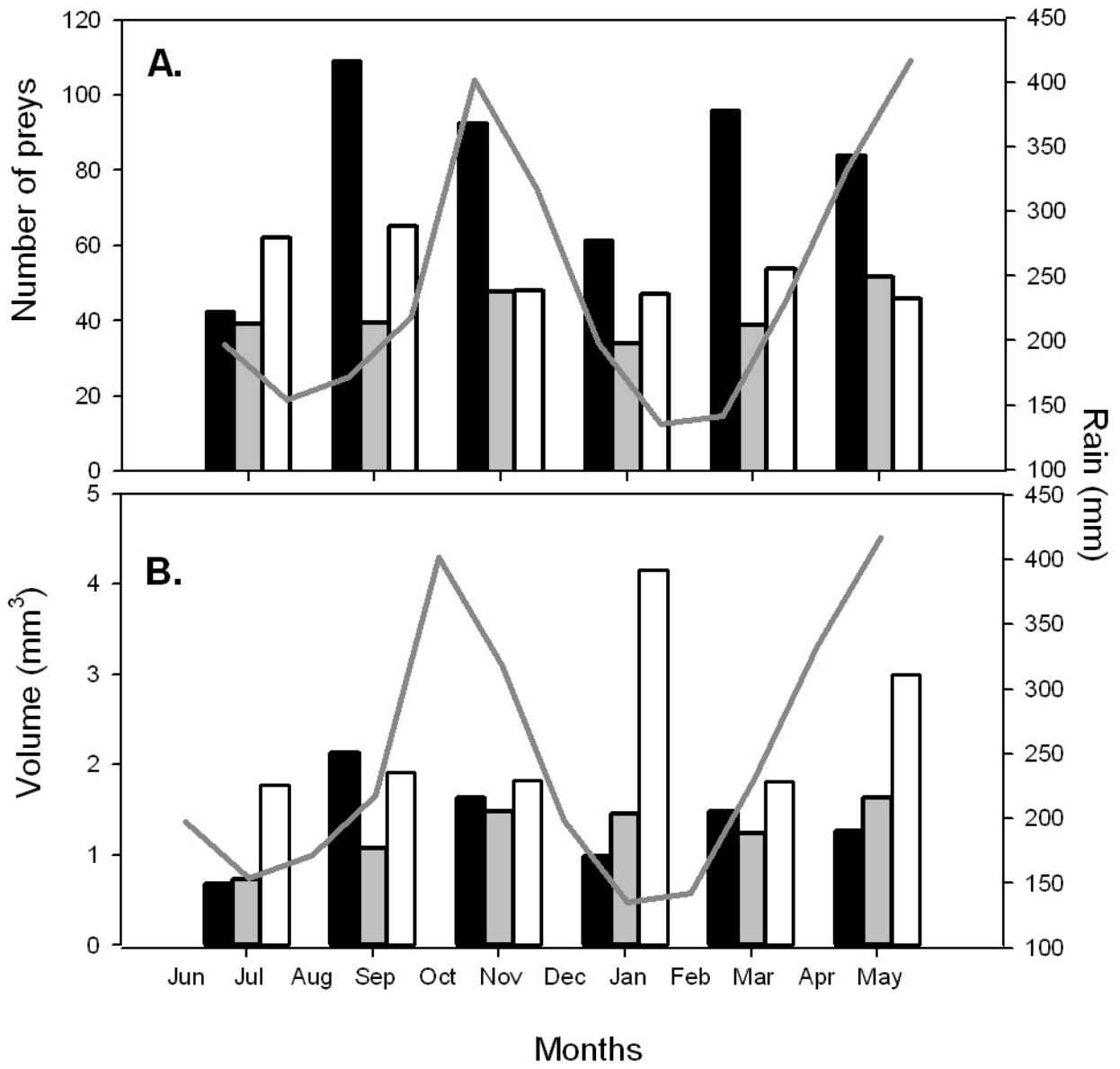


FIGURE 4



**FIGURE 5**

