Typical coloration of an adult *Craugastor underwoodi* (Boulenger, 1896) from Estación Biológica Río Macho, Distrito de Orosí, Paraíso de Cartago, Provincia de Cartago, Costa Rica; this species, however, can be highly polymorphic. In the following article the authors report on the density, phenology, and biomass of *C. underwoodi* at the above locality, as well as in the nearby Parque Nacional Tapanti.

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Density, biomass, and phenology of *Craugastor underwoodi* (Boulenger, 1896) from mid-elevation forests in the Valle de Orosi, Costa Rica

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**ABSTRACT:** We report data on the density, phenology, and biomass of *Craugastor underwoodi* from Parque Nacional Tapanti (PNT) obtained in 1994–95, and from Estación Biológica Río Macho (EBRM) in 2012–13. We sampled large frogs and froglets using transects of defined width along Sendero La Oropéndola (SLO) at PNT, and quadratic sampling in an old-growth forest (OF) and a secondary forest (SF) at EBRM. In both areas we found large frogs and froglets active day and night throughout the year. The density of large frogs differed slightly between SLO (0.98 ± 0.78 ind/ha) and EBRM (OF = 0.39 ± 0.19 ind/ha; SF = 0.13 ± 0.20 ind/ha), but was similar in froglets between SLO (0.24 ± 0.18 ind/ha) and EBRM (OF = 0.29 ± 0.23 ind/ha; SF = 0.23 ± 0.22 ind/ha). The estimated biomass in EBRM was 54.73 ± 46.30 g/ha for large frogs and 7.29 ± 2.58 g/ha for froglets. We found the density values much lower than those reported for *C. bransfordii*, a sister species found in the Costa Rican lowlands; however, the values for density and biomass were similar to those reported for morphologically equivalent craugastorids from the Brazilian Atlantic Forest. In both areas, differences in detection, seasonality, leaf litter accumulation, and even climatic oscillations (e.g., La Niña) might explain the variation in our reported densities through time. Even when comparing data obtained from two different sampling methods, we cannot discard the hypothesis that *C. underwoodi* in these areas has undergone a decline, as reported for other craugastorids in Costa Rica. Additional monitoring at EBRM, PNT, and in similar forest types is necessary to further understand the population dynamics of this species.

**Key Words:** Craugastoridae, Lower Montane Tropical Forest, Premontane Tropical Forest, Río Macho Biological Station, Tapantí National Park, Terrarana

**RESUMEN:** Reportamos datos de la densidad, fenología y biomasa de *Craugastor underwoodi* en Parque Nacional Tapanti (PNT) obtenidos en 1994–95, y de Estación Biológica Río Macho (EBRM) en 2012–13. Muestreamos ranas grandes y juveniles pequeños usando transectos con banda definida a través de Sendero La Oropéndola (SLO) en PNT, y muestreo cuadrático en bosque maduro (OF) y crecimiento secundario (SF) en EBRM. En ambos sitios encontramos ranas grandes y juveniles pequeños, activos de día y noche, a través del año. La densidad de ranas grandes disfirió ligeramente entre SLO (0.98±0.78 ind/ha) y EBRM (OF = 0.39 ± 0.19 ind/ha; SF = 0.13 ± 0.20 ind/ha), pero fue similar en juveniles pequeños entre SLO (0.24 ± 0.18 ind/ha) y EBRM (OF = 0.29 ± 0.23 ind/ha; SF = 0.23 ± 0.22 ind/ha). La biomasa
estimada en EBRM para las ranas grandes fue $54.73 \pm 46.30$ g/ha, y $7.29 \pm 2.58$ g/ha para los juveniles pequeños. Encontramos valores de densidad mucho menores a los reportados para *Craugastor bransfordii*, una especie hermana encontrada en tierras bajas de Costa Rica; sin embargo, los valores de densidad y biomasa fueron similares a los valores reportados para craugastóridos morfológicamente equivalentes del Bosque Atlántico Brasileño. En ambos sitios, diferencias en detección, estacionalidad, acumulaciones de hojarasca e incluso oscilaciones climáticas (e.g., La Niña) podrían explicar la variación en nuestras densidades reportadas a través del tiempo en ambas áreas protegidas. Incluso cuando comparamos datos obtenidos por dos métodos de muestreo distintos, no podemos descartar la hipótesis que nuestra especie ha sufrido un declive, como el reportado para otros craugastóridos en Costa Rica. Monitoreo adicional en EBRM, PNT y bosques similares es necesario para entender sus dinámicas poblacionales de esta especie.

**Palabras Claves:** Bosque Tropical Montano Bajo, Bosque Tropical Premontano, Craugastoridae, Estación Biológica Río Macho, Parque Nacional Tapantí, Terrarana

**INTRODUCTION**

Several studies on leaf litter plots located in South America and Costa Rica have provided estimated densities or the biomass of leaf litter anurans in Lowland or Premontane Tropical Forest, thereby allowing a comparison of anuran faunas among sites or across time (Scott, 1976; Lieberman, 1986; Whitfield et al. 2007; Siqueira et al., 2009). As a direct or indirect result of these efforts, species such as Bransford’s Litter Frog, *Craugastor bransfordii*, have been studied extensively in places like La Selva and its surrounding areas in northwestern Costa Rica. Information on the habitat use of this species (Scott, 1976; Lieberman, 1986; Whitfield et al., 2007; Hilje and Aide, 2012), how its populations have declined since the 1970s, and how species respond to changes in leaf litter depth have been reported by Whitfield et al. (2007, 2014); Donnelly (1999) and Watling and Donnelly (2002) also described the reproductive phenology of *C. bransfordii*.

Unfortunately, such detailed information is lacking for most areas, including some forests belts in Costa Rica. Thus, the ecology of many amphibians that inhabit Premontane and Lower Tropical Montane Forest is among the least studied in the country, when compared with species from lower elevations (Acosta-Chaves et al., 2015). For example, little information is available on the natural history of Underwood’s Litter Frog, *C. underwoodi* (Savage, 2002; Pounds et al., 2004). Once considered a synonym of *C. bransfordii*, this robber frog occurs in a broad range of habitats in Costa Rica and western Panama at elevations from 920 to 1,800 m, and is among the most abundant amphibian species in Lower Montane Tropical Forest in the Cordillera de Talamanca (Savage, 2002; Acosta-Chaves et al., 2015). Herein we report data on the density, phenology, and biomass of *C. underwoodi* from two sites in the Valle de Orosi, in the province of Cartago, Costa Rica, with studies at each site conducted during a different time period, to provide baseline information for future comparisons and monitoring.
MATERIAL AND METHODS

Study Areas

Estación Biológica Río Macho (EBRM).—We chose two plots for this study area, of which the first measured 11.62 ha and was located in young (ca. 17 years old) secondary forest (SF) (9°45’50.70”N, 83°51’44.75”W; datum WGS 84; elev. 1,715 m), and the second measured 21.26 ha and was located in old-growth (> 50 years old) forest (OF) (9°45’28.41”N, 83°51’23.09”W; datum WGS 84; elev. 1,750m). Acosta-Chaves et al. (2012, 2015) provided detailed information on the biological and climatic conditions at EBRM and the plots we selected.

Parque Nacional Tapantí (PNT).—We sampled Premontane Moist Forest at Sendero La Oropéndola (SLO) (9°44’53”N, 83°46’55”W; datum (WGS 84); elev. 1,200 m), located in Sector Tapanti, Parque Nacional Tapanti. The trail cuts across disturbed riparian and primary forest habitats (Atlas Digital ITCR, 2014). The biological and climatic conditions are similar to those at EBRM; Sánchez (2002) provided details about the park and trail system.

Field Sampling

EBRM.—Our sampling units consisted of 14 randomly-selected subplots measuring 10 × 10 m, seven in each type of forest, which we conducted randomly during 11 sampling sessions (day and night) from January of 2012 to January of 2013. Acosta-Chaves et al. (2015) described the sampling method, the capture of individuals, and the species identification process. For call identification, when males were calling we compared the calls with the descriptions in Savage (2002), as well as with those provided by A. García-Rodríguez et al. (unpublished).

PNT.—We sampled a transect measuring ca. 1,200 m long × 1.5 m wide along SLO, and recorded all of the Craugastor underwoodi observed along the trail. Two people accompanied by at least one of the authors (FB, GC) sampled the ground monthly from January of 1994 to June of 1995 from 0700 to 0900 h. Individuals were classified as froglets (smaller juveniles) and large frogs (larger juveniles and adults) according to the criteria of the researchers.

Body Mass and Estimate of Age Status

EBRM.—We determined the body mass of the captured animals with a 5g Medio-Line Spring Scale (Pesola®). We did not determine the sex or minimum reproductive size of individuals, because they were not sacrificed to check the status of the gonads (Donnelly, 1999; Watling and Donnelly, 2002), and both sexes are similar in external appearance (Savage 2002). We classified the animals with a body mass below 0.8 g as froglets because of their tiny size, whereas the rest were classified as large frogs to include the larger juveniles and adults.

Data Analysis

We compared the means of abundance in SLO before May of 1994 and after using a Mann Whitney U test (W), and the mean density during the day for large frogs and froglets among OF, SF, and SLO using Kruskall-Wallis Tests (Z). We compared the mean of biomass estimate for OF and SF using W. We conducted the analysis using the software Statgraphics Centurion XVI v.15.1.02 (Stat Point Inc., 1982–2006).

RESULTS

In EBRM, a major proportion of the individuals detected were large frogs and froglets captured during the day, mainly in the OF plot (Table 1). Moreover, almost one-third of the detected adults were males calling at night (Table 1). Large frogs and froglets were detected throughout the year (Fig. 1A), but males were heard calling only from April to August. Similarly, in SLO, the majority of detected animals were large frogs (253 individuals), whereas the froglets (57) also were present throughout the year (Fig. 1B). Despite the similar patterns in both sites throughout the year, an apparent decline in frog detection was observed in SLO after May of 1994 (Fig. 1B; W = 22.5, P < 0.01).

During the day, densities of Craugastor underwoodi between SF (large frogs = 0.39 ± 0.19 ind/ha, froglets= 0.29 ± 0.23 ind/ha, n = 10), OF (large frogs = 0.13 ± 0.20 ind/ha, froglets = 0.23 ± 0.22 ind/ha, n = 10) in EBRM, and SLO (large frogs= 0.98 ± 0.78 ind/ha, froglets= 0.24 ± 0.18 ind/ha, n = 18) were slightly different for large frogs (Z = 6.023, P = 0.05), but similar for froglets (Z = 2.90, P = 0.23) (Fig. 2). In EBRM, the body mass of large frogs
Density, biomass, and phenology of *Craugastor underwoodi*

ranged from 0.8 g to 6 g, and there was no significant difference between OF (\(n = 18, 1.79 \pm 1.47 g\)) and SF (\(n = 6, 1.43 \pm 1.26 g\)) (\(W = –10, P = 0.5\)). The body mass of froglets was similar between OF (\(n = 11, 0.23 \pm 0.08 g\)) and SF (\(n = 6, 0.18 \pm 0.06 g\)) (\(W = –10, P = 0.25\)); thus, an estimated biomass for large frogs was 54.73 ± 46.30 g/ha, and 7.29 ± 2.58 g/ha for froglets.

**Table 1.** Individuals of *Craugastor underwoodi* detected visually or acoustically during the sampling period at Estación Biológica Río Macho in old-growth forest (OF) and secondary forest (SF).

<table>
<thead>
<tr>
<th>Detection</th>
<th>Age/Type of forest</th>
<th>Diurnal</th>
<th>Nocturnal</th>
<th>Total</th>
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<tbody>
<tr>
<td></td>
<td>Age/Type of forest</td>
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<td>SF</td>
<td>OF</td>
</tr>
<tr>
<td>Call</td>
<td>Large frogs</td>
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<td>0</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>Froglets</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<td></td>
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<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td>40</td>
<td>20</td>
<td>13</td>
</tr>
</tbody>
</table>

**Fig. 1.** (A) Abundance of *Craugastor underwoodi* in Estación Biológica Río Macho. (B) Abundance of *Craugastor underwoodi* in Sendero La Oropéndola, Parque Nacional Tapantí.
DISCUSSION AND CONCLUSIONS

Savage (2002) referred to *Craugastor underwoodi* as a diurnal frog, but in our study we found that this species performs acoustic activity during the evening, which could be associated with reproductive behavior. Additionally, a related species, *C. stejnegerianus*, recently was reported to be active at night in Guanacaste province (Gómez-Hoyos et al., 2016). The poorly known calling activity for this species, and its cryptic appearance (Savage, 2002), makes it almost impossible to distinguish individuals at night on a dark background, which might explain why it was considered active only during the day. This also might explain why similar numbers of frogs were captured at night in OF and SF. Males of *C. underwoodi* detected calling at night might be responding to a mixture of environmental variables (e.g., temperature, rainfall, humidity, moonlight) that induced calling activity (Wells, 2007), and not necessarily to a restricted breeding season. The presence of froglets during the year in EBRM and PNT suggests that *C. underwoodi* breeds throughout the year, similar to *C. bransfordii* at La Selva (Donnelly, 1999; Watling and Donnelly, 2002).

The habitat of *C. underwoodi* apparently ranges from pastures with a border effect to dense forest (Pounds et al., 2004; Acosta-Chaves et al., 2015). For example, even when variation between OF and SF exists when comparing tree diversity (R. Cordero and D. Araya, unpublished), forest structure, phenology, soil parameters (e.g., nutrients, pH), leaf litter depth, biological communities (e.g., worms, amphibians, reptiles) and light patterns between plots (R. Cordero and F. Araya, unpublished; Barrientos, 2012, Pérez-Molina and Cordero, 2012; Guzmán and Rodríguez-Corrales, 2014; Acosta-Chaves et al., 2015), this was not the case for the estimated density and biomass of our studied species. In EBRM, *C. underwoodi* did not show a preference for a specific forest age, in accordance with the reported data for *C. bransfordii* in the Caribbean Lowlands (Hilje and Aide, 2012).

Our results for *C. underwoodi* densities in both EBRM and PNT were much lower than the values reported for *C. bransfordii* at La Selva by Scott (1976), Lieberman (1986), Heinen (1992), or Whitfield et al. (2007), mainly during the 1970s and 1980s, but also for this century (Whitfield et al., 2014). The densities for *C. bransfordii* ranged...
from 345 to 1,200 ind/ha, depending on the type of habitat or the time of year (Savage, 2002), but our expected
density for *C. underwoodi* for PNT or EBRM was significantly lower. Moreover, if we assume that the reported *C.
transforsidii* from Monteverde in the study of Fauth et al. (1989) from mid-1980s indeed were *C. underwoodi*, then a
significant difference probably existed in the densities between lowland and middle elevations of this species since
at least this decade. Compared with other Neotropical middle elevation forests, similar densities to the ones from
EBRM and TNP have been reported for morphologically equivalent craugastorids such as Girard’s Robber Frog,
*Ischnocnema parva* (0.5 ind/ha) or Steindachner’s Robber Frog, *I. guentheri* (0.8 ind/ha), found in the foothills of
the Brazilian Atlantic Forest (Siqueira et al., 2009). Additionally, the biomass values for *C. underwoodi* were similar
to the values reported for *I. parva* (56 g/ha) and *I. guentheri* (9.4 g/ha) from the foothills of the Atlantic Forest
(Siqueira et al., 2009).

Differences in detection, seasonality, leaf litter accumulation, and even climatic oscillations might explain
the high variation in the values of our reported densities in each place and time period—especially in PNT. For
example, 1994 and 2012 were years influenced by La Niña, a phenomenon that apparently produced changes in
the communities of similar leaf litter anurans in other Costa Rican localities, such as Las Cruces Biological Station
(Ryan et al., 2014, 2015). Although variation might occur when using two different sampling methods to compare
both time periods and places, especially because many forests have suffered a gradual decline in herpetoan fauna
diversity over the years (Whitfield et al., 2007; Abarca-Alvarado, 2012), we suggest that EBRM and PNT were
not exceptions based on our data from the mid-1990s, as well as from other studies in the area (Acosta-Chaves et
al., 2015) and personal observations. Whitfield et al. (2007, 2014) and Ryan et al. (2014, 2015) demonstrated that
changes in leaf litter depth could be associated with the decline in abundance of several leaf litter frogs, including
some closely related species of *Craugastor*. Additional studies characterizing the habitat and monitoring the density
of *C. underwoodi* in EBRM, PNT, and similar forest types are highly recommended to better understand the popu-
lation dynamics of this species, as well as whether populations are declining or recovering across time.

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**LITERATURE CITED**


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Gerardo Chaves Cordero is a biologist from the Universidad de Costa Rica (UCR). His Master’s degree thesis focused on “arribadas” of Olive Ridley turtles, but most of his professional work has been on the ecology and taxonomy of the Costa Rican herpetofauna. Gerardo has been working in the herpetological collection at the Museo de Zoología (UCR) since 1997. Since 1992, however, his research activities have focused on understanding amphibian decline in Mesoamerica, and filling inventory gaps in several areas of Costa Rica, primarily in the Cordillera de Talamanca. Based on his research, Gerardo has authored several papers in peer-reviewed journals, including the description of several new herpetofaunal species. His conservation efforts involve a project on the sustainable use of sea turtle eggs from “arribadas,” and he also has collaborated in IUCN Red List assessments for Costa Rican and Mesoamerican amphibians and reptiles. Currently, he serves as the Costa Rican chair for the IUCN Amphibian Specialist Group.