Resource partitioning between Microlophus occipitalis and Stenocercus puyango (Sauria: Tropiduridae) in Cerros de Amotape National Park, Tumbes, Peru

Repartición de recursos entre Microlophus occipitalis y Stenocercus puyango (Sauria: Tropiduridae) en el Parque Nacional Cerros de Amotape, Tumbes, Perú

Abstract
Activity, microhabitat use, and diet are patterns commonly used to define the saurian community structure, because of differential exploitation allowing coexistence at the same time and place. We analyze resource partitioning between two sympatric saurian species, Stenocercus puyango and Microlophus occipitalis, in the transitional area of the Pacific Tropical Forest and the Dry Forest inside Cerros de Amotape National Park (PNCA) in Tumbes, northwestern of Peru. Microlophus occipitalis and S. puyango both showed a unimodal activity pattern with higher activity around 13:00 h, with a mean body temperature of 34.83 °C and 32.17 °C respectively, observing a significant relationship between body and environmental (air and substrate) temperatures. Rocks and tree trunks were the most frequent microhabitats used by M. occipitalis while S. puyango were registered more frequently over leaf litter. The diets of both tropidurids were composed by arthropods, ants, and insect larvae mainly. Similarities in activity times (temporal niche) and diet (trophic niche) should be related to phylogenetic relationship and environmental characteristics of PNCA (seasonality, vegetal composition) meanwhile differences in space use and microhabitat thermal quality will be related to thermal quality in the area.

Resumen
Los horarios de actividad, el uso de microhábitat y dieta, son patrones comúnmente utilizados para dilucidar la estructura de una comunidad de saurios, ya que estos hacen un uso diferenciado de los recursos que explotan, lo que les permite coexistir de forma adecuada en el mismo tiempo y lugar. Analizamos la repartición de recursos entre dos especies simpátricas de saurios, Stenocercus puyango y Microlophus occipitalis, en la zona transicional entre el Bosque Tropical del Pacífico y el Bosque Seco en el Parque Nacional Cerros de Amotape (PNCA), departamento de Tumbes, analizando el solapamiento del nicho espacial, temporal y trófico entre ambas especies, incluyendo algunos aspectos de sus ecologías termales. Microlophus occipitalis y S. puyango presentaron un patrón de actividad unimodal con un pico de actividad hacia las 13:00 horas y una temperatura corporal promedio de 34.83 °C y 32.17 °C respectivamente, registrándose una relación significativa entre la temperatura corporal y las temperaturas ambientales (aire y suelo). Los microhábitats más utilizados por M. occipitalis fueron los troncos caídos y rocas, mientras que S. puyango fue registrado principalmente sobre hojarasca. La dieta de ambos tropíduros estuvo compuesta por artrópodos, principalmente hormigas y larvas de insectos. Las similitudes encontradas tanto en los horarios de actividad (nicho temporal) como en la dieta (nicho trófico), estarían asociadas a su parentesco filogenético y a características ambientales propias dentro del PNCA (estacionalidad, composición vegetal), mientras que las diferencias en el uso del espacio y temperaturas corporales entre ambas especies estarían relacionadas a la calidad térmica de los microhábitats presentes en el área.

Keywords:
Ecology; lizards; dry forests; ecological niche; Peru.

Palabras clave:
Ecología; lagartijas; bosques secos; nicho ecológico; Perú.
Introduction

Species coexistence inside a community has been attributed to ecological factors (competition and predation; Schoener 1974, 1975); however other explanations are suggested: morphological differences and physiology (Chase et al. 2002), foraging mode (Huey 1979), reproduction patterns (Colli et al. 1997), allopatric characteristics (Huey & Pianka 1977, Huey 1979), among others. Based on its historic context (phylogeny), these species should present differences due to their evolutionary history rather than competitive pressures (Huey 1979, Vitt et al. 1999, Losos 2000, Pérez 2005). Otherwise, recent studies demonstrated that differential partitioning of biotic and abiotic resources is the principal factor for community structure (Mesquita & Colli 2003, Mesquita et al. 2006), overall, on areas where resources are scarce (Pérez 2005, Jordán 2010).

Usually, species partitioned their resources over three dimensions of the ecological niche: temporal, spatial and trophic niche. So, species differs in their activity patterns, spaces where they exploit resources and prey consumption allowing the coexistence of several species on a community (Hutchinson 1957, MacArthur 1972, Pianka 1973, Dunham 1980, 1983, Vitt et al. 1999, Vanhooydonck et al. 2000).

Lizard species are “ideal models” for ecological research because they display several characteristics (i.e. thermoregulation, high site fidelity, low dispersal rate, territorial behavior) that had been well studied (Cowles & Bogert 1944, Pianka 1973, Huey & Pianka 1981, Huey et al. 1983, Vitt & Pianka 1994, Vitt et al. 1999, 2003). Lizard resource use patterns have been studied widely in Australian desertic ecosystems (Pianka 1973, Huey & Pianka 1977, Pianka 1986, Vitt 1991) while research on interactions inside lizard community structures had been increasing on Neotropical ecosystems (Colli et al. 1992, Vitt & Colli 1994, Vitt & Zani 1998, Vitt et al. 1999, Mesquita & Colli 2003, Mesquita et al. 2006, Rocha et al. 2009) specially on Teiids and Tropidurids in Central and South America (Rocha & Bergallo 1990, Vitt & Colli 1994, Vitt & Zani 1998, Faria & Araujo 2004, Rocha et al. 2009, Ribeiro 2010).

The tropidurid lizards *Microlophus occipitalis* (Peters 1871) and *Stenocercus puyango* (Torres-Carvajal 2005) are distributed on northwestern Peru and southwestern Ecuador, using a broad variety of habitats as rocky boulders, bushes, and algarrobo trees (*Prosopis* sp.) (Dixon & Wright 1975, Torres-Carvajal 2005). Regardless of their broad distribution range (Carrillo & Icochea 1995, Torres-Carvajal 2005, 2007), few studies consider ecological traits for both species (Watkins 1996, 1997, 1998, Jordán & Pérez 2012) which occupy in syntopy a narrow area inside Cerros de Amotape National Park.

Cerro de Amotape National Park holds the most important ecoregions of northwestern Peru: Equatorial Dry Forest and Pacific Tropical Forest (Brack-Egg 1986), showing a high endemism rate and connectivity for wildlife between both ecosystems (SERNANP 2012), and had been considering a “biodiversity hotspots” (“Tumbes-Chocó-Magdalena”; Mittermeier et al. 2005). Regardless of these characteristics, few herpetological studies had been done inside this protected area (Tello 1998, Jordán 2006, 2010, 2011a, 2011b, Jordán & Pérez 2012). The goal of this study is to analyze differences or similarities at the temporal, spatial, trophic niche, and thermal characteristics between *Stenocercus puyango* and *Microlophus occipitalis* which allows them to coexist in syntopy in Cerros de Amotape National Park.

Material and methods

**Study area**- Data collection was done between El Caucedo and La Angostura localities (Fig. 1) in the transitional area of the Pacific Tropical Forest and the Dry Forest inside Cerros de Amotape National Park (PNC) in the northwestern region of Tumbes (SERNANP 2012) between August and September of 2012. The climate is relatively mild with an average annual temperature of 26 °C showing a highly marked seasonality with a dry season ranging from May to November and a wet season ranging from December to April with an annual average precipitation of 1450 mm (Ponte 1998).

**Data Collection**- Data were collected by three herpetologists (360 man-hours) during 20 days at the dry season through visual encounter surveys (VES) (Crump & Scott 1994) with 30 minutes duration between 08:00 and 18:00 hours.

**Activity pattern and thermal ecology**- For each observed individual, sighting hour was recorded and a histogram was elaborated from this data. A Kolmogorov-Smirnov test was used to determine possible differences in activity patterns for each species. Body, air, and substrate temperatures (°C) were registered for each captured individual after Vitt & Carvalho (1995). Temperatures were recorded with a cloacal thermometer Miller and Weber® to the nearest 0.2 °C. The relationship between body and environmental temperatures were analyzed by simple and multiple regressions as well as differences in temperatures for age, sex, and species with a variance analysis (ANOVA). The exposure degree to the sun (exposed: totally exposed to sunlight; filtered: exposed to scattered sunlight; shaded: under total vegetation cover) for each observed individual were registered and analyzed with an ANOVA with exposure degree as factors (Vitt et al. 1995).

**Microhabitat Use**- Eight microhabitats categories were identified in the study site for the study species: (1) leaf litter (substrate covered by leaf litter totally), (2) soil (substrate without leaf litter), (3) gravel (<5 cm), (4) sand, (5) tree branches, (6) trunks, (7) vegetation (crawling, herbs, shrubs), and (8) stones (>5 cm). Potential differences in microhabitat use between age, sex, and species were assessed with a Chi-square test.

**Diet**- All captured lizards were sacrificed immediately with Halatal® and preserved on 70° alcohol. Stomachs were dissected and analyzed under a stereomicroscope identifying prey items to order level (including broad categories as insect larvae). A Kolmogorov-Smirnov test was used to determine differences in diet composition consumed by lizard species.
Niche breadth.- We compute niche breadth (spatial, temporal, and trophic) using the inverse of Simpson’s diversity index formula of Simpson (Simpson 1949, Pianka 1973, Vitt & Zani 1996):

\[ B = \frac{1}{\sum_{i=1}^{n} p_i^2} \]

Niche breadth value range from 1 to n, where low values indicate a restricted use of resources while high values indicate an intensive use (Vitt & Zani 1996). The overlapping degree of the spatial, temporal and trophic niche was evaluated with the symmetric overlap index \( \Phi_{jk} \) where values near to 0 indicate a low overlap while values near or equal to 1 indicate a high overlap on the resource used (Pianka 1973, 1986):

\[ \Phi_{jk} = \frac{\sum_{n=1}^{n} p_{ij} p_{lk}}{\sum_{i=1}^{n} p_{ij}^2 \sum_{l=1}^{n} p_{lk}^2} \]

We generated 1000 repetitions using EcoSim 700 software (Gotelli & Entsminger 2004) and comparing “real” data matrix (observed) with “simulated” matrix (simulated) through a Monte Carlo analysis using R3 algorithm (Pianka 1973, 1986) to determine if overlap on any niche dimension (trophic, spatial, temporal) is a real structure or a random result (Winemiller & Pianka 1990, Gotelli & Entsminger 2004, Rouag et al. 2007). The recommended R3 algorithm retains niche breadth (or specialization degree) of each species in the simulated matrices but “allow” the potential use of other unexploited resources (Winemiller & Pianka 1990, Gotelli & Entsminger 2004, Rouag et al. 2007).

Statistical analysis.- We used PAST ® Version 3.0 (Hammer et al. 2001) with a significance level (\( \alpha \)) ≤ 0.05 for statistical analysis. Normality was verified through an Anderson-Darling test before parametric or non-parametric statistics were applied; variance homogeneity was analyzed with the Levene test. Data means appear ±1 SD in text. All collected individuals were deposited on the Department of Herpetology, Natural History Museum, Universidad Nacional Mayor de San Marcos.

Results

Activity pattern.- A total of 408 sightings of both species *Stenocercus puyango* and *Microlophus occipitalis* (Fig. 2) were registered between 8:00 and 16:00 hours (216 and 192 respectively).

A higher proportion of *Stenocercus puyango* sightings (52.9%) were registered between 10:00 and 15:00 hours while 47.1% of *Microlophus occipitalis* sightings were registered between 10:00 and 13:00 hours (Fig. 3). No significant differences between activity patterns for both species were registered (\( \text{D}_{\text{max}} = 0.18 \), p>0.05), indicating both species exhibit a unimodal activity pattern.

Thermal ecology.- Average body temperature of *Microlophus occipitalis* was higher than *Stenocercus puyango* average body temperature as well as the related environmental (air and substrate) temperatures (Table 1). Body temperatures of each species differ significantly (\( F_{1,113} = 35.84 \); p<0.05), indeed air (\( F_{1,113} = 5.28 \); p<0.05) and substrate temperatures (\( F_{1,113} = 10.32 \); p<0.05).

Body temperature of *Stenocercus puyango* was significantly related with air temperature (\( T_a \)) (\( R^2 = 0.53 \), \( F_{1,57} = 66.88 \); p<0.05; n=58) and substrate (\( T_s \)) (\( R^2 = 0.42 \), \( F_{1,57} = 40.83 \); p<0.05; n=58) (Figure 4 and 5). Also, body temperature of *M. occipitalis* was significantly related with air temperature (\( R^2 = 0.22 \), \( F_{1,57} = 15.57 \); p<0.05; n=56) and substrate (\( R^2 = 0.24 \), \( F_{1,57} = 17.9 \); p<0.05; n=57) (Figs. 4 and 5).
Table 1. Body temperature (Tb), air temperature (Ta) and substrate temperature (Ts) recorded for both species in Cerros de Amotape National Park. Mean ± standard deviation and range are showed.

| Species               | Tb (°C) | Range (max-min) | Ta (°C) | Range (max-min) | Ts (°C) | Range (max-min) |
|-----------------------|---------|-----------------|---------|-----------------|---------|-----------------|
| Stenocercus puyango   | 32.0 ± 2.65 | 24.8-37        | 28.6 ± 3.34 | 22.4-37.6      | 28.9 ± 3.76 | 22.4-39.2       |
| Microlophus occipitalis | 34.8 ± 2.23 | 27.4-38.2      | 30.1 ± 3.27 | 23.2-38.6      | 31.4 ± 3.84 | 24.0-43.0       |

Figure 2. (a) *Microlophus occipitalis* (adult male) and (b) *Stenocercus puyango* (adult male) in Cerros de Amotape National Park.

Figure 3. Activity pattern of *Microlophus occipitalis* and *Stenocercus puyango* in Cerros de Amotape National Park.

Figure 4. Relationship between body and air temperature of *Microlophus occipitalis* ($R^2=0.22$, $F_{1,55}=15.57$, $p<0.05$; n=56) and *Stenocercus puyango* ($R^2=0.53$, $F_{1,57}=66.88$, $p<0.05$, n=58).

Figure 5. Relationship between body and substrate temperature of *Microlophus occipitalis* ($R^2=0.24$, $F_{1,55}=17.9$, $p<0.05$; n=57) and *Stenocercus puyango* ($R^2=0.42$, $F_{1,57}=40.83$, $p<0.05$, n=58).
Multiple regression showed that environmental temperatures (T_a and T_s) influenced significantly over body temperature of *Stenocercus puyango* (R^2=0.52; F(2,53)=29.55; p<0.05; n=58) and *M. occipitalis* (R^2=0.23; F(2,54)=8.96; p<0.05; n=57).

A higher proportion of *Stenocercus puyango* was registered under filtered sun (n=148, 68%) follow by individuals exposed to sun (n=45, 21%) and shade (n=23, 11%), while *M. occipitalis* was recorded exposed to sun (n=113, 59%), and a lower proportion under filtered sun (n=66, 34%) and shade (n=13, 7%) (Fig. 6).

Microhabitat use.- Leaf litter was the most used microhabitat by *S. puyango* (n=216) (50.9% of all records) followed by trunks and stones (16.2% and 15.3%, respectively; Fig. 7). Individuals of *M. occipitalis* (n=192) were registered on trunks (34.9%), stones and grave (28.13% and 14.06%, respectively). Significant differences were found in microhabitat use among the eight identified categories by *S. puyango* and *M. occipitalis* (χ^2=155.78, p<0.05). Spatial niche breadth (Bs) for *S. puyango* and *M. occipitalis* were 2.49 y 3.39 respectively.

**Diet.-** Diet of *S. puyango* (n=55) and *M. occipitalis* (n=60) was composed of 17 and 15 different types of prey items, respectively (Table 2), where hymenopterans and insect larvae were the most consumed prey items by both species.

![Figure 6](image-url)  
**Figure 6.** Exposure degree to sun of *Microlophus occipitalis* and *Stenocercus puyango* in Cerros de Amotape National Park.

![Figure 7](image-url)  
**Figure 7.** Microhabitat use of *Microlophus occipitalis* and *Stenocercus puyango* in Cerros de Amotape National Park.

Table 2. Diet composition of *Microlophus occipitalis* (N=55) and *Stenocercus puyango* (N=60) in Cerros de Amotape National Park. N-number of prey items; %N-percentage of prey items consumed, F-frequency of prey items in stomachs, %F-percentage of prey items frequency.

| Prey items          | *Stenocercus puyango* (N=55) | *Microlophus occipitalis* (N=60) |
|---------------------|-------------------------------|---------------------------------|
|                     | N    | N%  | F     | F%   | N    | N%  | F     | F%   |
| Hymenoptera (Formicidae) | 80   | 26.58 | 0.183 | 18.274 | 87   | 33.33 | 0.229 | 22.9 |
| Larvas de insectos   | 64   | 21.26 | 0.162 | 16.244 | 79   | 30.27 | 0.200 | 20.0 |
| Orthoptera           | 39   | 12.96 | 0.152 | 15.228 | 24   | 9.2   | 0.193 | 19.3 |
| Coleoptera           | 32   | 10.63 | 0.142 | 14.213 | 33   | 12.64 | 0.129 | 12.9 |
| Hemiptera            | 26   | 8.64  | 0.102 | 10.152 | 10   | 3.83  | 0.071 | 7.1  |
| Araneae              | 22   | 7.31  | 0.096 | 9.645  | 4    | 1.53  | 0.029 | 2.9  |
| Diptera              | 12   | 3.99  | 0.056 | 5.584  | 4    | 1.53  | 0.029 | 2.9  |
| Lepidoptera          | 9    | 2.99  | 0.041 | 4.061  | 2    | 0.78  | 0.029 | 2.9  |
| Restos vegetales     | 5    | 1.66  | 0.010 | 1.015  | 1    | 0.38  | 0.014 | 1.4  |
| Isoptera             | 4    | 1.33  | 0.015 | 1.523  | 1    | 0.38  | 0.014 | 1.4  |
| Phasmatodea          | 2    | 0.66  | 0.010 | 1.015  | 3    | 1.15  | 0.014 | 1.4  |
| Blattodea            | 2    | 0.66  | 0.010 | 1.015  | 5    | 1.92  | 0.014 | 1.4  |
| Odonata              | 2    | 0.66  | 0.010 | 1.015  | 1    | 0.38  | 0.007 | 0.7  |
| Nematoda (silvestre) | 1    | 0.33  | 0.005 | 0.508  | 2    | 0.78  | 0.007 | 0.7  |
| Decapoda (exoquesleto) | 1   | 0.33  | 0.005 | 0.508  | 2    | 0.78  | 0.007 | 0.7  |
| Mantodea             | —    | —     | —     | —      | 2    | 0.78  | 0.007 | 0.7  |
| Escorpioidae         | —    | —     | —     | —      | 1    | 0.38  | 0.007 | 0.7  |
Stenocercus puyango consumed hymenopterans (26.58%), orthopterans (12.96%), coleopterans (10.63%), and hemipterans (8.64%), and a higher percentage of insect larvae (21.26%) both in frequency and numerically. Predominant preys in M. occipitalis diet were hymenopterans (33.33%), coleopterans (12.64%), orthopterans (9.2%), and elevated consumption of insect larvae (30.27%) with similar results in frequency (Table 1). Significant differences in numerical diet composition between both species were not found (Dmax = 0.18; p > 0.05).

Niche breath and niche and overlap.- Stenocercus puyango showed a wider temporal niche breadth (Bt) than M. occipitalis (Bt = 8.28 and Bt = 6.26, respectively) and the temporal niche overlap (Фjk) between both tropidurids was lower (Фjk = 0.54; p obs ≥ esp = 0.01) (Table 2). Spatial niche breadth (Bs) was wider for M. occipitalis (Bs = 6.65) than S. puyango (Bs = 3.15), however, both species showed a lower overlap on this niche axis (Фjk = 0.96; p obs ≥ esp = 0.001) (Table 3). Otherwise, trophic niche breadth was wider for Stenocercus puyango than for M. occipitalis (Bt = 6.26 and Bt = 4.35, respectively), with a higher trophic niche overlap (Фjk = 0.84; p obs ≥ esp = 0.001).

Table 3. Niche breadth and niche overlap between Microlophus occipitalis and Stenocercus puyango. Bs: Spatial niche breadth. Bt: temporal niche breadth. Bd: trophic niche breadth.

| Species                  | Bs  | Bt  | Bd  |
|--------------------------|-----|-----|-----|
| Microlophus occipitalis  | 6.65| 4.26| 4.35|
| Stenocercus puyango      | 8.28| 3.15| 6.26|
| Фjk                      | 0.84| 0.54| 0.96|

The values of the null modes (p observed ≥ simulated) were lower than the significance level established (p > 0.05) indicating the existence of a real structure for each ecological niche dimension for these lizard species.

DISCUSSION

Microlophus occipitalis and Stenocercus puyango showed a higher overlap on the temporal and trophic niche and lower overlap in spatial niche; in other words, they are active at the same hours and feeding on similar prey items, while the greater difference was observed on the spatial niche.

Ecological similarities such as their heliophilic and diurnal habits of both species may be related to their evolutionary similarity since both belong to Tropiduridae lizard family (Bergallo & Rocha 1993, Rocha et al. 2009) and reflecting the wide temporal niche breadth of both species, as well as their high temporal overlap. Diurnal activity patterns attributed to sunny hours for both species could be related to their thermal demands (Hatano et al. 2001), allowing them to develop their ecological activities (Bauwens et al. 1996, Smith & Ballinger 2001). This same diurnal activity pattern with a midday activity peak had been reported for other tropidurid species in the Peruvian coastal desert (M. peruviansus-Huey 1974, Catenazzi et al. 2005, Pérez & Balta 2007, M. tigris-Pérez 2005, Jordán 2011, M. theresiae and M. thoracicus-Pérez & Balta 2007).

A similar activity pattern, reflected by a high temporal niche overlap, may be an important factor for similar diet composition for both sympatric species because they could be exposed to the same preys set, explaining the high trophic niche overlap. This similarity on prey consumption could be related to seasonality (dry season in this case) due to reduced prey abundance and diversity related to limited availability of resources (vegetation) pushing lizards to prey over a similar and limited set of arthropods and other items. Ribeiro & Freire (2011) reported a similar case where a high trophic niche overlap was registered during the dry season between two tropidurid species (Tropidurus hispidus and T. semitaeniatus) in northeastern Brazil.

Foraging mode could influence diet similarity for both species. Lizards exhibiting an ambush foraging strategy eats mobile preys while active foraging lizards eats sedentary preys (Huey & Pianka 1981). Microlophus occipitalis and S. puyango showed an arthropod-based diet, a basal condition for Neotropical lizards (Vitt et al. 2003), where ants (Formicidae) and insect larvae were the more abundant and frequent consumed preys. The high mobile preys consumption should be related to their foraging mode (sit and wait foragers, Schoener 1971) however a significative proportion of insect larvae, a low/mobility preys, were found on stomachs. This result reflects an intermediate foraging mode dependent of prey item availability in their environment as had been pointed by Huey & Pianka (1981) for lizards and reported by other authors in tropidurines (Bergallo & Rocha 1993, Pérez 2005). A similar pattern was found by Ribeiro & Freire (2011) for Tropidurus hispidus and T. semitaeniatus diet in northeastern Brazil and Meira et al. (2007) in central Brazil for T. oreadicus, were a mixed diet composed by active (Formicidae and Orthoptera) and lumped or sedentary items (termites and insect larvae) were registered. This plasticity in foraging mode probably allows Stenocercus puyango and Microlophus occipitalis to eat a wide variety of prey items, saving time and energy intake while preying (Ribeiro 2010). Both species showed a wide trophic niche, like other peruvian tropidurid species, indeed occupying distinct habitats as beaches (Microlophus peruviansus, Quispitúpac & Pérez 2008), lomas (or foothills, Microlophus tigris, Pérez 2005), tropical dry forest (Microlophus theresiae, Pérez & Balta 2007) and desert (Microlophus thoracicus, Pérez & Balta 2007). Thus, S. puyango and M. occipitalis could be considered as generalist predators. However, Chávez-Villavicencio et al. (2018) reported a narrow niche breadth for Microlophus occipitalis (B = 0.13) explained by a high consumption of ants, around 58.9 % compared to the 26.6% of this study and a lower consumption of other items. This could be related to prey abundance and vegetation composition among sites where the study site of Chavez-Villavicencio et al. (2018) considered as “algarrobos” shows a minor vegetation complexity than the tropical dry forest in Tumbes.
In conclusion, differences in spatial use between *Microlophus occipitalis* and *Stenocercus puyango* would be related to differential resource use, allowing the coexistence of both species in sympatry inside of Cerros de Amotape National Park.

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