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Nocturnal multi-species roosts of Cicindelidae (Coleoptera)  
in a Neotropical lowland rainforest

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Nocturnal multi-species roosts of Cicindelidae (Coleoptera)  
in a Neotropical lowland rainforest

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**Abstract.** Tiger beetles (Coleoptera: Cicindelidae) are frequent predators on the forest floor of the Amazon rainforest. We report on five diurnal sympatric tiger beetle species belonging to the genera *Odontocheila* Laporte de Castelnau and *Poecilochila* Rivalier in a terra firme rainforest in South Venezuela. We observed adult beetles for a full year and monitored their nocturnal roosts along two forest paths during the rainy season in 1998.

We found up to four species communally roosting on low vegetation along the paths during the night. Multi-species roosts were more often observed than conspecific communal roosts. Although the individual composition of the nocturnal roosts changed frequently, distinct plants were used for several days to weeks. The most individual-rich roosts comprised 10 or 11 adult tiger beetles roosting on one leaf. Observed nocturnal roosts were dominated by *O. angulipenis* W. Horn and *O. margineguttata* (Dejean). Most mixed roosts included *O. confusa* (Dejean), *O. angulipenis* and *O. margineguttata*.

Low abundances and size differences possibly facilitate the coexistence of these five tiger beetle species. The advantage of communal roosting during the rainy season is probably the reinforcement of their chemical defense.

**Key words.** Biodiversity, Amazonas, aggregation behavior, communal roosts, coexistence, seasonality, tiger beetles, Venezuela.

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## Introduction

The family of tiger beetles (Cicindelidae Latreille, 1802) currently includes 2897 species (Wiesner 2020). The Neotropics is the second richest biogeographical region of the world with about 634 species (Wiesner 2020). Fifteen Neotropical genera are recognized within the subtribe *Odontocheilina* W. Horn, 1899 (Wiesner 2020). The most species-rich genus within this subtribe is *Odontocheila* Laporte de Castelnau, 1843 comprising 78 described species, while the genus *Poecilochila* Rivalier, 1969 includes 11 species (Moravec 2019, 2020; Wiesner 2020).

Cicindelidae are primarily diurnal predators on insects and spiders with most species hunting on bare ground (Pearson and Vogler 2001; Rewicz and Jaskuła 2018) and a few species that are arboreal (Marohomsalic et al. 2021). Most species of Cicindelidae show narrow habitat specialization (Pearson 1985; Zerm and Adis 2001; Jaskuła et al. 2019). Forest species are principally diurnal and fly to temporary roosts in the low vegetation to escape floor predators (Pearson and Anderson 1985). Several species have been found roosting on the leaves of undergrowth bushes during the night (Cassola and Pearson 2001). In Carabidae and Cicindelidae, aggregations of several thousand individuals have been observed during inactive periods in winter quarters or hiding places (Arndt et al. 2005).

Roosting and aggregate perching behavior in tiger beetles is a readily observed and quantifiable pattern in tropical forest habitats (Pearson and Anderson 1985; Bhargav and Uniyal 2008). To investigate this roosting behavior of tiger beetles, we monitored forest floor species in a terra firme rainforest in southern Venezuela for a full year. We provide detailed data on communal roosts along two forest paths during the rainy season in 1998.

## Materials and Methods

**Study site.** The study site is in the upper Orinoco region (Venezuela, state of Amazonas) close to the black water river Surumoni (3°10'N, 65°40'W; 105 m asl). Anhuf et al. (1999) described the weather pattern as a mean annual rainfall of about 3100 mm (with year-to-year fluctuations of about 500 mm). There is a strong peak in the annual precipitation from May to July and a lower peak in September and October. The average annual temperature in the study area is ca. 26°C, usually with slight variations between the coolest month (25°C) and the warmest month (26.5°C). Maximum daytime temperatures reach 30.5°C and drop to 20–21°C during the night.

The Surumoni area is within the Japura/Negro moist forests ecoregion that extends from Brazil to southern Venezuela, Colombia, and Peru (Dinerstein et al. 1995). The vegetation is that of a moist lowland tropical rain forest classified as terra firme (Prance 1979). The upper canopy ranges from 25 to 27 m in height. Only a few emergent trees rise to a height of 35 m. The forest here is frequently interrupted by light gaps, thus the canopy is not completely closed. Altogether 316 species of higher plants were identified in the 1.4 ha study plot belonging to 202 genera from 76 families (Wesenberg 2004). The Surumoni study plot is average in tree species richness for the area. The herb layer is well developed due to sufficient radiation transmission to the ground. It is dominated by ferns of the families Hymenophyllaceae and Metaxiaceae as well as small palms of the genera *Geonoma* Willd. and *Bactris* Jacq. ex Scop. Other dominant plants include: Rubiaceae (*Psychotria* L. spp. and *Faramea* Aubl.), Melastomataceae and Maranthaceae (*Ischnosiphon* Körn. spp.) as well as Heliconiaceae (Wesenberg 2004).

**Beetle sampling and observations.** Sampling and observation of adult tiger beetles was conducted three times from 1997 to 1999 (August–November 1997; April–August and December 1998; January–March 1999) and combined include a full year. Voucher specimens of each tiger beetle species were collected by hand or with an entomological net along two forest paths and in the surrounding forest in all months of their occurrence. To prevent an influence on the abundances, adults were collected only in at least 10 m distance from the monitored paths during June and July 1998. Except for *Odontocheila bipunctata* (Fabricius, 1792), some adults were captured also with pitfall traps installed at the study site. The beetles are stored in Museo del Instituto de Zoología Agrícola ‘Francisco Fernández Yépez’ (MIZA), Maracay, Venezuela.

During the rainy season, tiger beetles most regularly congregated at nocturnal roosts on leaves of herbs. These nocturnal aggregations were observed between 31 May and 2 August 1998 using a flashlight. The roosting aggregations of Cicindelidae were monitored as far as possible every second night along two different forest paths at the study site. Each path was about 75 m long and separated from each other by 5 m. The preceding frequently used path 1# was up to 80 cm broad, the following occasionally walked path #2 up to 50 cm. The period of monitoring was from 7 June to 2 August on path #1 (Fig. 1) and from 31 May to 21 July on path #2. Roosting tiger beetles along each forest path were counted and communal roosts were marked with colored tapes. Except for the very similar *Odontocheila angulipenis* W. Horn, 1932 and *Odontocheila margineguttata margineguttata* (Dejean, 1825), specimens were visually assigned to the species epithet. The sex was noted as well. Because visual distinction of *O. angulipenis* and *O. margineguttata* in the field is difficult, both species were treated as a single taxon. To clarify the identity of both species, the adults of some randomly selected communal roosts were captured and identified in the laboratory. They were released at their nocturnal roost in the morning.

## Results

**Cicindelidae community.** In total, five diurnal tiger beetle species were observed along clearings or paths of the rainforest in the study area. Adults of *Poecilochila lacordairei* (Gory, 1833) were found year-round except for December and January. The number of collected vouchers was 30 ( $N = 6$ : February–March 1999;  $N = 12$ : April–July 1998;  $N = 12$ : August–November 1997). Adults of *O. bipunctata*, *Odontocheila confusa* (Dejean, 1825), and *O. margineguttata* were found between March and November. *Odontocheila bipunctata* was collected with 14 individuals ( $N = 2$ : March 1999;  $N = 6$ : April–June 1998;  $N = 6$ : August–November 1997), *O. confusa* with 15 individuals ( $N = 1$ : March 1999;  $N = 10$ : April–July 1998;  $N = 4$ : September–November 1997), and *O. margineguttata* with 16 specimens ( $N = 2$ : March 1999;  $N = 8$ : April–July 1998;  $N = 6$ : August–November 1997). Adults of *O. angulipenis* were observed between March and August and collected with 16 voucher specimens ( $N = 2$ : March 1999;  $N = 13$ : May–July 1998;  $N = 1$ : August 1997).



**Figures 1–3.** 1) Forest path #1 at the study site in lowland terra firme Venezuelan rainforest, February 1999. 2) Communal roost of *Odontocheila* Laporte de Castelnau spp. (*O. confusa* (Dejean) and *O. angulipennis* W. Horn/*O. margineguttata* (Dejean)) at the study site in lowland terra firme Venezuelan rainforest, June 1998. 3) Communal roost of *Odontocheila* Laporte de Castelnau spp. (*O. confusa* (Dejean) and *O. angulipennis* W. Horn/*O. margineguttata* (Dejean)) at the study site in lowland terra firme Venezuelan rainforest, May 1998.

From counts based on the nocturnal roosts, the maximum number of adult beetles was 63 individuals on path #1. Maximum numbers include five specimens of *P. lacordairei*, two specimens of *O. bipunctata*, 16 specimens of *O. confusa*, and 40 specimens of *O. angulipennis*/*O. margineguttata*. On the narrower path #2, the maximum number of adult beetles was only 34. *Poecilochila lacordairei* was represented at most with five specimens, *O. bipunctata* with one specimen, *O. confusa* with eight specimens, and both *O. angulipennis* and *O. margineguttata* with 20 specimens.

The number of males and females counted on the nocturnal roosts was noted along both paths. On path #1, *P. lacordairei* had two males and three females, *O. bipunctata* one male and one female, *O. confusa* eight males and eight females, and *O. angulipennis*/*O. margineguttata* 19 males and 21 females. Along path #2, the maximum number of *P. lacordairei* had three males and two females, *O. bipunctata* one male, *O. confusa* four males and four females, and *O. angulipennis*/*O. margineguttata* 11 males and nine females.

**Nocturnal aggregations.** Up to 48 adult tiger beetles were found roosting on the vegetation per night on the 75 m long path #1 from 7 June to 2 August 1998 (Table 1). Most beetles on path #1 were observed from 7 June to 9 July. From 10 July onwards, the number of observed nocturnal roosts and adult tiger beetles declined. In total, 101 communal roosts were observed during the observation period including up to 10 communal roosts per night. Only 13 single adults were observed on the vegetation. The highest number of individuals on a single nocturnal roost included 11 specimens with eight specimens of *O. angulipennis*/*O. margineguttata* and three specimens of *O.*

**Table 1.** Number of communal roosts and their cicindelid species composition along two forest paths in lowland terra firme Venezuelan rainforest, June–August 1998.

Species composition	Path #1 (7 June to 2 August)	Path #2 (31 May to 21 July)
<i>Poecilochila lacordairei</i>	1	5
<i>Odontocheila angulipenis</i> / <i>O. margineguttata</i>	30	26
<i>O. confusa</i>	1	2
<i>P. lacordairei</i> , <i>O.a./O.m.</i>	2	4
<i>O. confusa</i> , <i>O.a./O.m.</i>	57	25
<i>P. lacordairei</i> , <i>O. confusa</i> , <i>O.a./O.m.</i>	6	3
<i>P. lacordairei</i> , <i>O. bipunctata</i> , <i>O.a./O.m.</i>	2	2
<i>O. bipunctata</i> , <i>O. confusa</i> , <i>O.a./O.m.</i>	2	1

*confusa* as well as two roosts with 10 individuals each comprising nine *O. angulipenis*/*O. margineguttata* and one *O. confusa*. Conspecific communal roosts on path #1 (including the grouped *O. angulipenis*/*O. margineguttata*) amounted to 32 during the monitoring period. Fourteen of these roosts were occupied on the same plant in at least one the following nights. Sixty-nine roosts were comprised of different species. Forty-four out of the 69 mixed nocturnal roosts were found again on the same plant in subsequent nights. Most mixed communal roosts ( $N = 57$ ; 56.4%) consisted of *O. angulipenis*/*O. margineguttata* and *O. confusa* (Fig. 2, 3).

On path #2, between zero and 27 beetles were counted per night from 31 May to 21 July 1998 (Table 1). The adult beetles were found roosting in up to eight communal aggregations per night. In total, 68 communal roosts were observed, while only 23 specimens were observed roosting solitarily. The roost with the highest number of individuals included seven specimens of *O. angulipenis*/*O. margineguttata*. There were altogether 33 conspecific and 35 heterospecific roosts on path #2 during the monitoring period. Eight of the conspecific and five of the heterospecific roosts were found repeated on the same plant during one of the following nights. Most mixed communal roosts ( $N = 25$ ; 71.4%) consisted of *O. angulipenis*/*O. margineguttata* and *O. confusa*.

Some roosts on path #1 were occupied continuously up to 15 consecutive observation nights (7 June–9 July) (Table 2). The composition of species and sexes on the nocturnal roosting aggregations usually varied from night to night. Roost A and B were only about 2 m apart, and the third most frequented roost on path #1 was separated by 10 m from roost A. Roost B was on a palm leaf, roost C on a leaf of a Melastomataceae and roost A on an unidentified plant (Rubiaceae?).

## Discussion

**Coexistence of tiger beetles.** The co-occurrence of different diurnal species of *Odontocheila* and *Poecilochila* inhabiting the forest floor is well known from elsewhere in the Neotropics. In Peru, Pearson and Anderson (1985) found *P. lacordairei* to co-occur with *O. margineguttata* and two other species of *Odontocheila* in floodplain forests and three species of *Odontocheila* in terra firme forests. In central Amazon terra firme forests, Paarmann et al. (1998) report four species of *Odontocheila* and two species of *Poecilochila* including *O. bipunctata*, *O. margineguttata*, and *P. lacordairei* occurring in the shaded forest interior. In central Amazon inundation forests, *O. confusa* co-occurred with *P. lacordairei* (Adis et al. 1998), an occurrence regularly reported from other areas (Pearson 1985; Pearson and Anderson 1985; Pearson and Huber 1995; Wiesner 2020).

Several factors could facilitate the coexistence of the five cicindelid species on the forest floor in our study area. The adults of our five diurnal cicindelid species showed contemporaneous occurrence and clear seasonality. Adults of four cicindelid species were found in the rainy season from March to November. Only *O. angulipenis* was not collected later than August. Forest species in central Amazonia including *O. bipunctata* and *P. lacordairei* also showed strong and relatively synchronous change in seasonal abundance with high abundances during the rainy season (Paarmann et al. 1998). In concordance with this observation, the life cycle of *O. confusa* has been



found to be univoltine in central Amazon forests (Adis et al. 1998). The different sizes of our cicindelid species could limit their interspecific competition, as Pearson and Mury (1979) found that the average prey size of tiger beetle species corresponds to the size of the mandibles. The smallest species, *P. lacordairei*, is followed by similar sized *O. angulipenis* and *O. margineguttata*. The largest species is *O. bipunctata* with a body length of 15 mm next to *O. confusa* with maximal 13 mm. Some reduction in limiting similarity might be expected if abundances are low (Pearson 1980). Indeed, we counted fewer than one cicindelid adult per meter path in our study site. Still, Zerm et al. (2001) found in concordance with our observation that guilds of tiger beetles from terra firme forest floors exhibit wide niche overlap in the region of central Amazonas.

**Roosting behavior of tiger beetles.** Aggregations are known from different diurnal and nocturnal tiger beetles and often restricted to distinct periods. In some Indian species of Cicindelidae, diurnal roosts formed by many thousand adults were found on shrub plants, limited to the first monsoon months (Uniyal and Bhargav 2007). In central Amazon inundation forests, nocturnal *Tetracha sobrina punctata* Laporte hide aggregated during the day during the terrestrial phase (Adis et al. 1998). Adults of *Pentacomia egregia* Chaudoir pass the aquatic phase in groups and roost sometimes in groups on top of leaves on tree branches at night (Adis et al. 1998). In Peru, Pearson and Anderson (1985) observed *O. confusa* forming communal nocturnal roosts of up to nine individuals on bushes during the night in the early rainy season. In contrast to our study, communal roosts were found only in floodplain forests, while nocturnal roosts were occupied by single individuals in terra firme forests. Moreover, nocturnal roosts included only conspecifics in contrast to our study.

In Peru, *O. confusa* sit on the leaf surface with the heads usually up and facing the leaf petiole (Pearson and Anderson 1985). This upward position was observed often also in our nocturnal roosts (Fig. 3). Pearson and Anderson (1985) recaptured marked *O. confusa* on their nocturnal roosts or nearby the original sampling point in the succeeding night. The repeated assembly of tiger beetles on the same roosts is supported by our study (Table 2). Pearson and Anderson (1985) found that the size of the species and height of roosts during day were significantly correlated, and nocturnal roosts did not differ significantly from diurnal ones. The mean height of nocturnal roosts was 30 cm in *O. margineguttata* and 80 cm in *O. bipunctata*. However, in our mixed species roosts, different species often used the same leaves.

**Aggregation mechanisms.** Roosting aggregations of conspecifics or even interspecific aggregations can be found in different beetle taxa, but among carabid species aggregations seem to occur only rarely (Thiele 1977). Their predatory behavior could preclude such assemblies of conspecifics and different species. Commonly observed interspecific carabid aggregations often include aposematic and chemically protected species (Magistretti 1965; Novoa 1975; Bonacci et al. 2004; Schaller et al. 2018). Zetto Brandmayr et al. (2006) concluded that the adaptive significance of carabid beetle interspecific aggregation may be related to antipredatory strategies. Improved chemical defense might also be a cause for communal nocturnal roosts in Cicindelidae. The forest floor tiger beetle species in Neotropical rainforests produce the defense chemicals benzaldehyde (Moore and Brown 1971; Pearson et al. 1988), benzoyl cyanide (Blum et al. 1981), and pentadecane (Pearson et al. 1988) in their posterior pygidial glands (Forsyth 1970). Communally roosting beetles point their posteriors outward (Fig. 2) and thus, increasing the effect of chemical defenses against predators (Pearson and Anderson 1985; Brandmayr et al. 2009). As roosting aggregations in tiger beetles are often restricted to a few months during the rainy season, moisture could dilute the repellent effect of single roosting tiger beetles.

In addition, facing the leaf petiole may prove most effective against predation especially if potential predators approach the cicindelids on the leaf from its petiole (Pearson and Anderson 1985). Aggregations may enhance the collective environmental scanning as more sensors are added to the group (Vulinec and Miller 1989; Watt and Chapman 1998). Moreover, aggregations can reduce predation for the individual by dilution effects (Alcock 1979; Wcislo 1984; Pearson et al. 1988; Sillén-Tullberg and Leimar 1988; Zetto Brandmayr et al. 2006). Defense seems to be the main advantage achieved with gregariousness for most insects (Vulinec 1990). This particularly may apply to roosting aggregations of chemically defended species (Wautier 1971; Vulinec 1990; Bonacci et al. 2004).

The preconditions for aggregations are stimulations to join con- or even heterospecifics that are generated and regulated through complex interactions of chemical and mechanical as well as abiotic and biotic factors (Chapman 1998; Santiago-Blay et al. 2012). Many aggregations in the Coleoptera are chemically mediated (Eisner and Kafatos 1962; Wood et al. 1986; Peng and Weiss 1992; Al Abassi et al. 1998; Peng et al. 1999). Heterospecific



aggregations in Cicindelidae may occur because the cues for aggregations are similar or identical for the five closely related species in our Venezuelan study site. As abundances of the five cicindelid species and particularly for *O. confusa* or *O. bipunctata* are rather low, specimens of these species most probably join roosts of other closely related species.

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