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The Geographic Distribution of Parasite-Induced Fruit Mimicry in *Cephalotes atratus* (Formicidae: Myrmicinae)

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ABSTRACT: Parasite distributions fundamentally depend on the distributions of their hosts but may be more restricted than their hosts. Host–parasite symbioses tend to be spatially aggregated, and widely distributed host–parasite relationships are rare. Here, we combine field observations with published collection data to document the current known distribution of the nematode, *Myrmeconema neotropicum*, which infects the Neotropical canopy ant *Cephalotes atratus*. We report 6 new records from different Brazilian ecosystems, bringing the total number of independent observations of this interaction to 11. The broad distribution of these data points suggests that *M. neotropicum* infects *C. atratus* throughout its geographic range, although possible disturbance effects and specific habitat associations of the interaction remain unknown.

In relatively heterogeneous environments, host–parasite symbioses tend to be spatially aggregated on biogeographic scales (Gregory, 1990; Poulin 1998), possibly reflecting differential effects of abiotic and geographic factors on the lifestyles of hosts and parasites (Poulin, 1995; Morand and Krasnov, 2010). In contrast, parasite distributions are expected to match the distribution of their hosts in relatively homogeneous environments (Poulin, 1998). Thus, partly as a consequence of increasing environmental heterogeneity at larger spatial scales, the distribution of host–parasite interactions, the degree of host specificity, and other ecological parameters should vary across the landscape (Krasnov et al., 2005).

Recently, a case of morphological and behavioral change in the Neotropical canopy ant *Cephalotes atratus* (L.) (Formicidae: Myrmicinae), parasitized by the tetradonematid nematode *Myrmeconema neotropicum* Poinar and Yanoviak (Nematoda: Tetradonematidae), was reported in tropical forests of Peru and Panama (Poinar and Yanoviak, 2008; Yanoviak et al., 2008). Ants infected with the nematode exhibit several behavioral and morphological differences from uninfected individuals, the most conspicuous being the change of the gaster color of infected workers from black to red. This color change causes gasters to resemble ripe fruits of various forest plants, including species of *Hyeronima*, *Psychotria*, and *Trema*, that are consumed by birds (Yanoviak, 2010; S. Yanoviak, unpubl. obs.). The working hypothesis for this apparent mimicry complex is that it fools frugivorous or omnivorous birds into eating infected gasters, thereby transmitting the parasite to other ant colonies via their feces (Yanoviak et al., 2008). Since its discovery, this parasitic relationship has generated many questions regarding its origins, effects, and mechanisms (Hughes et al., 2008; Shik et al. 2011; Verble et al., 2012). Here, we compile historical collection records and field data to summarize the current known distribution of the interaction.

Cephalotes atratus ranges from Panama south to Argentina and is widely distributed in different ecosystems (from primary forest to urban settings) and among different elevations; however, records of *C. atratus* parasitized by *M. neotropicum* are limited to a few sites in Brazil, Colombia, Peru, and Panama (de Andrade and Baroni Urbani, 1999; Yanoviak et al., 2008). Poinar and Yanoviak (2008) proposed that the interaction between *C. atratus* and *M. neotropicum* occurs throughout the distribution of *C. atratus*. However, detecting infected workers in the field can be difficult because the infection frequency among colonies, and the number of workers with red gasters within infected colonies, tend to be low (ca. 5%; Yanoviak et al., 2008). Consequently, this interaction can easily be overlooked.

Here, we present 6 new records of *C. atratus* workers parasitized by *M. neotropicum* in Brazilian ecosystems and evaluate the potential distribution of this interaction. Data were obtained from 3 sources: (1) direct observation of red-gastered *C. atratus* workers during field expeditions conducted during 2005 and 2010 in different Brazilian ecosystems (see Yanoviak et al., 2008), (2) references to "red gaster" in published collection records for *C. atratus* (de Andrade and Baroni Urbani, 1999), and (3) examination of red-gastered specimens in the myrmecological collection of the Museu de Zoologia of Universidade de São Paulo, Brazil (MZSP) (Fig. 1; Table I).

Host–parasite interactions are complex, and various factors can affect their coevolutionary dynamics (Poulin, 1995; Duffy and Sivars-Becker, 2007). The geographic distributions of specialized host–parasite interactions tend to be more restricted than those of generalist parasites (Price, 1990; Poulin, 1998). Generalists tolerate a wider range of physical and environmental barriers and are thus capable of parasitizing a wider range of taxa (Tella et al., 1999; Tripet et al., 2002; Krasnov et al., 2005). Indeed, there are few cases where highly specialized parasite–host interactions are widely distributed (Krasnov et al., 2005). All information that we have gathered to date indicates that the interaction between *M. neotropicum* and *C. atratus* is very specialized, consistently results in the distinctive red gaster, and occurs throughout the geographic range of *C. atratus* as proposed by Poinar and Yanoviak (2008). However, other parasites and pathogens occasionally cause localized reddening of the *C. atratus*

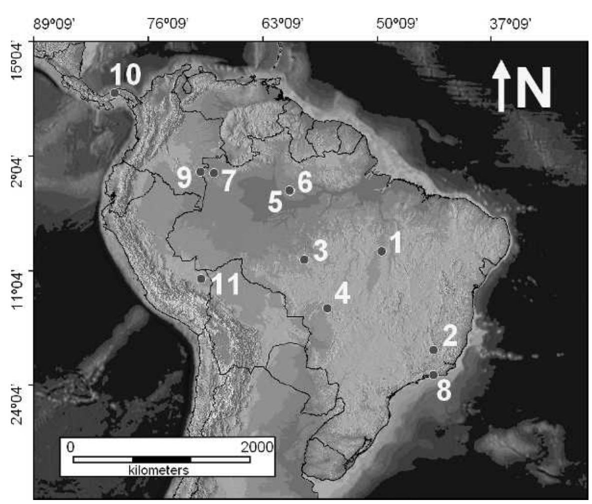

FIGURE 1. Records of *Cephalotes atratus* (Formicidae: Myrmicinae) parasitized by *Myrmeconema neotropicum* (Nematoda: Tetradonematidae) in Central and South America. *Cephalotes atratus* ranges from central Panama to northern Argentina and Uruguay.

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TABLE I. Records of the neotropical canopy ant *Cephalotes atratus* (Formicidae: Myrmicinae) parasitized by *Myrmeconema neotropicum* (Nematoda: Tetradonematidae). Records 1 and 2 are from examination of museum specimens and 3–6 are from field data; all others are from published information.

Record	Country	Locality	Date	Coordinates* and elevation	Ecosystem	Citation
1†	Brazil	ca. Araguacema, Tocantins	2005	08.874°S, 49.372°W, 214 m	Savanna	This study
2†	Brazil	Caraça range, Minas Gerais	unkn.	20.083°S, 43.466°W, 1,546 m	Montane meadow	This study
3‡	Brazil	ca. Juruena River, Cotriguaçu, Mato Grosso	2010	09.866°S, 58.206°W, 206 m	Tropical rainforest	This study
4	Brazil	ca. Marimbondo Waterfall, Chapada dos Guimarães, Mato Grosso	2010	15.334°S, 55.634°W, 454 m	Savanna (gallery forest)	This study
5	Brazil	ca. road AM-240, Presidente Figueiredo, Amazonas	2008	02.042°S, 59.834°W, 88 m	Tropical rainforest	This study
6	Brazil	ca. Mutum Waterfall, Presidente Figueiredo, Amazonas	2008	01.984°S, 59.906°W, 181 m	Tropical rainforest	This study
7	Brazil	ca. Rio Uaupés, Taracua, Amazonas	1964	00.050°N, 68.517°W, 98 m	Tropical rainforest	de Andrade and Baroni Urbani (1999)
8†	Brazil	Rio Grande Reservoir, Piraí, Rio de Janeiro	1966	22.916°S, 43.466°W, 810 m	Tropical rainforest	de Andrade and Baroni Urbani (1999)
9†	Colombia	ca. Bellavista city and Tiquie River, Dept. of Vaupés	unkn.	00.150°N, 70.017°W, 182 m	Tropical rainforest	de Andrade and Baroni Urbani (1999)
10	Panama	Barro Colorado Island, Gigante Peninsula, and Camino de Cruces, Canal Zone	2005–6, 2012	09.155°N, 79.847°W, 113 m	Tropical rainforest	Yanoviak et al. (2008) and Yanoviak unpub. obs.
11	Peru	Los Amigos (CICRA) field station 100 km W of Puerto Maldonado	2007	12.577°S, 70.070°W, 343 m	Tropical rainforest	Yanoviak et al. (2008)

* Coordinates and elevation are approximate for records with unknown collection dates (unkn.) or collection dates prior to 2005.
† Deposited in the Museu de Zoologia da Universidade de São Paulo, Brazil (MZSP).
‡ Deposited in the Setor de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso, Brazil (CEMT).

exoskeleton (Verble et al., 2012). Such cases are exceedingly rare and not repeated among workers in a colony and, thus, are unlikely to be confused with *M. neotropicum* infection (S. Yanoviak, unpubl. obs.). Also, 2 other *Cephalotes* species apparently are infected by *Myrmeconema* with similar effects on gaster color (de Andrade and Baroni Urbani, 1999; Verble et al., 2012), but the species identity of the parasite remains unknown in both cases.

Cephalotes atratus is a relatively common and conspicuous ant that inhabits trees in forests as well as in highly disturbed settings (e.g., Weber, 1957; Corn, 1976; Yanoviak et al., 2005). Although we show that *M. neotropicum* infects *C. atratus* at sites representing different elevations and forest types, the effects of disturbance on this interaction remain unknown and would be an appropriate extension of this work. Specifically, whereas *C. atratus* often inhabits disturbed sites, the appropriate paratenic vectors of the parasite (presumably birds) may not. Clearly, direct determination of the paratenic host is an essential next step.

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