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SHORT COMMUNICATION

The structure of the parasite–host interactions between *Philornis* (Diptera: Muscidae) and neotropical birds

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Philornis is a neotropical, monophyletic genus of Muscidae (Diptera) (Couri *et al.* 2007) that includes many bird parasites (Skidmore 1985). The interaction system of *Philornis* and birds is very peculiar: fly adults are free-living and only larvae interact with birds (Couri 1985, 1999; Dodge 1963). Larval trophic habits are known for 22 of the 49 species (de Carvalho *et al.* 2005) and are divided into three groups: coprophagous (*P. aitkeni* and *P. rufoscutellaris*), free-living haematophagous (*P. falsificus*) and subcutaneous (18 spp.). *Philornis downsi* is unusual because the first and the early second instars display a subcutaneous phase, whereas the late second and third phases show a nest-dwelling haematophagous phase (Fessl *et al.* 2006).

Subcutaneous larvae preferentially parasitize nestling birds that depend on parental care and stay longer in the nest before fledging (Rabuffetti & Reboreda 2007, Teixeira 1999). After hatching, larvae burrow into the host integument and reside intradermically (Spalding *et al.* 2002), where they feed on serous fluids, tissue debris and blood of the host. This parasitism affects nestling growth, development and fledging success (Arendt 1985, Dudaniec & Kleindorfer 2006, Rabuffetti & Reboreda 2007). Within approximately 4–8 d, larval feeding and growth are complete and larvae leave the host to pupate inside the bottom of the nest (Dodge 1971).

Studies concerning *Philornis*–bird interactions have recurrently assumed that these flies are generalists (Amat *et al.* 2007, Couri 1985, Couri *et al.* 2005). This assumption was based on one central observation and three peripheral aspects: (1) *Philornis* parasitize more than 100 bird species (Teixeira 1999 and later records); (2) *Philornis* does not select hosts of a particular kind of nest, except for two coprophagous species that infest nest cavities with organic matter (Dudaniec & Kleindorfer 2006); (3) The larval period of *Philornis* is short and depends on the host's nestlings. This scenario would require that flies parasitize many species of bird with complementary breeding seasons (Dudaniec & Kleindorfer 2006, Teixeira 1999); (4) *Philornis* species share hosts (Dudaniec & Kleindorfer 2006). Distinct species with the same interaction habit (Higgins *et al.* 2005) and different interaction habits (Teixeira 1999) were found on the same individual host. Although it might indicate lack of specificity, this is not a straightforward argument for a generalist fly strategy.

Indeed, the main argument for generalism is related to high numbers of *Philornis* host species. However, this observation concerns a generic perspective: it considers the genus as the parasitic unit and neglected species information. It is possible that generalists and specialists coexist in an interaction system comprised many parasite species and many host species (Poulin 2007). This generic perspective fostered a bias on the interpretation of the *Philornis* interactions, which remains to date as an untested axiom.

The hypothesis of generalist and specialist coexistence has been corroborated in parasite–host systems (Poulin 2007) and the arrangement of generalists and specialists can follow a nested pattern (Vazquez *et al.* 2005). A nested structure is a kind of interaction that encompasses generalists and specialists in a particular pattern: generalists interact with many host species and specialists interact with one or few hosts; however, specialists tend to parasitize the same hosts as generalists whereas hosts with low parasite richness tend to interact mainly with a few generalist species (Vazquez *et al.* 2005). This structure is

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also seen in interactions such as animal–plant (Bascompte *et al.* 2003) and animal–animal mutualistic networks (Guimarães *et al.* 2007).

The *Philornis*–bird parasite–host system is still poorly understood (Couri *et al.* 2007) and an overall analysis of the interaction structure can reveal whether the system is based on strictly generalist parasites or not. In this study, I describe the structure of the parasite–host interaction in order to test the hypothesis of generalist and specialist coexistence.

A parasite–host database was compiled and used to construct a binary interaction matrix of *Philornis* vs. bird species. The matrix was used to draw a bipartite network using the software Pajek 1.20 (http://vlado.fmf.uni-lj.si/pub/networks/pajek/). The network pattern illustrated the overall structure of parasite–host interaction system. If *Philornis* species are strictly generalists, the expected network would be fully connected by lines, connecting many parasites to many hosts. On the other hand, if *Philornis* species are strictly specific, only parallel lines connecting one parasite to one host would be found.

Matrix temperature was calculated as a statistical test for nestedness. Matrix temperature is a parameter that characterizes nestedness entropy packing (Atmar & Patterson 1993). Zero degrees represents a perfectly nested matrix, whereas higher temperatures (maximum = 100°) represent an unstructured matrix. Temperature values were acquired in 'Nestedness Temperature Calculator' software (http://aics-research.com/nestedness/tempcalc) and tested against a Monte Carlo-derived probability of 3000 runs; as well as in 'Nestedness' software (http://www.uni.torun.pl/∼ulrichw) and tested against null models under fixed-fixed (FF) and fixed-equiprobable (FE) algorithms. Under the FF algorithm, the number of observed fly interactions and the number of fly species parasitizing bird species is maintained in the simulation, whereas under the FE algorithm the number of interactions is maintained and the flies were equally likely found parasitizing bird species.

It is possible that the number of interactions could be affected by larval competition, mainly due to subcutaneous *Philornis* larval habits. In a system ruled by competition, one can assume that parasites do not share hosts and its structure follows a chequerboard pattern (Gotelli & Ellison 2002). However, nestedness and chequerboard are mutually exclusive matrix patterns because a nested structure intrinsically assumes host sharing, whereas chequerboards depends on the number of species pairs that never co-occur in any host.

In addition, the C-Score, which is the average of all possible chequerboard pairs calculated for species that occur at least once in the matrix, was acquired and tested against a null model-derived probability of 5000 runs in EcoSim 7.0 software under fixed-fixed (FF) and fixed-equiprobable (FE) algorithms (http://homepages.together.net/∼gentsmin/ecosim.htm). The possible corroboration of a co-parasite pattern was assumed as nestedness strength.

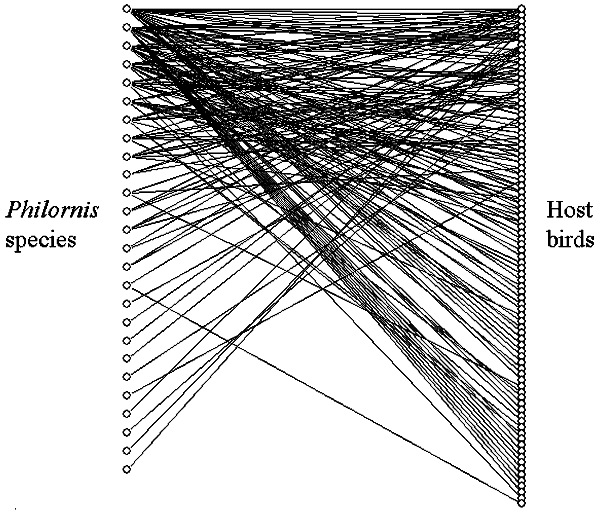

Figure 1. Network diagram of the *Philornis*-bird system ordered by decreasing number of interactions. The matrix was constructed based on the following studies: Amat *et al.* (2007), Couri *et al.* (2005), Fessl *et al.* (2001), Higgins *et al.* (2005), Mendonça & Couri (1999), Nores (1995), Spalding *et al.* (2002) and Teixeira (1999). The matrix is comprised of 26 species of *Philornis* and 85 species of neotropical bird.

Visual analysis of the network (Figure 1) was consistent with a nested pattern: (1) On the top of the network it was possible to observe that some flies parasitize many bird species and many bird species are hosts of many fly species. (2) Diagonal lines link flies with fewer interactions to the most common hosts, and the birds that host fewer species are linked to those flies which parasitize many hosts. (3) The absence of parallel lines linking species with fewer interactions show that the structure was not based on specific–specific interactions (Guimarães *et al.* 2007).

Nestedness was statistically corroborated by matrix temperatures. Temperatures calculated in NTC ($T = 6.69°$) and Nestedness ($T = 8.07°$) were low and differed from simulated temperatures of randomized matrices (NTC, $T_{sim} = 19.2°$, $SD_{sim} = 2.1°$, $P(T < 6.69°) = 10^{-8}$) and (Nestedness, $T_{FF} = 10.5°$, $SD_{TFF} = 1.04°$, $CI_{95\%} = 8.73–12.7°$, $T_{FE} = 22.7°$, $SD_{TFE} = 1.50°$, $CI_{95\%} = 20.1–25.8°$). The analysis performed in Nestedness and FF algorithm generated a temperature value closed to the lower confidence limit and may not be significant. Although FF is considered the most conservative algorithm, it may not always detect nestedness when it is present (Ulrich & Gotelli 2007). Under this assumption, matrix nestedness was considered statistically corroborated.

Additionally, the co-occurrence analysis (C-score) supported a pattern of co-parasitism. In a competitively structured community, the C-score should be significantly larger than expected by chance (http://homepages.together.net/~gentsmin/ecosim.htm). In the current analysis, observed C-score ($C_{obs} = 7.57$) was lower than mean simulated indices under both algorithms ($C_{simFF} = 8.01$, $P(obs < sim)_{FF} = 0.0798$, $C_{simFE} = 9.51$, $P(obs < sim)_{FE} = 0.012$). This result did not necessarily support nestedness, yet it refuted a chequerboard pattern that is incongruent with nestedness (Almeida-Neto *et al.* 2007).

In the present study, the nested pattern was assumed as evidence of generalist and specialist co-existence. Under this conjecture, *Philornis* cannot be considered a strict generalist based on high number of host species, but a genus that includes both generalists and specialists in a nested way.

A definitive test of the above-mentioned hypotheses of *Philornis* generalism require more information and field experimentation. Nevertheless, it is possible to speculate on its occurrence. The biological mechanisms underlying *Philornis* host selection are unclear regarding nest shape or kind. All shapes (cup, dome, cavity, hanging basket, stick platform) provide conditions for *Philornis* survival: they allow adult flies and larvae to access the nestlings and provide substrate for larvae pupation. Nevertheless, it is possible that different constitution of the nest substrate may be a factor of preference. This was observed for coprophagous species. They interact with birds that dig their nests into hard substrate, such as in cliffs (*Galbula ruficauda* host of *P. aitkeni* and *P. rufoscutellaris*), in the ground, sandy soil and termite tree domes (*Trogon surrucura, Momotus momota* and *Chelidoptera tenebrosa* hosts for *Philornis* spp.; Teixeira *et al.* 1990). Nests on hard substrate support organic accumulation. In the case of subcutaneous larvae, substrates may have a different effect. Different substrate composition may affect conditions of *Philornis* pupation phase (temperature, humidity, hardness, pH, etc).

Short larval period or the fact that many birds breed for a few months per year does not necessarily support the idea that flies must parasitize many birds with complementary breeding seasons to survive. Even though *Philornis* life cycle depends on birds, it is possible that *Philornis* species persist by parasitizing adult birds (Arendt 1985) or in diapause at the pupal stage (Dodge 1971).

It is evident that the system is poorly understood and more information is needed on the hosts' and parasites' natural histories. Nevertheless, the results obtained in the present study are a fundamental step towards the clarification of the structure of the *Philornis*-bird interactions, mainly in relation to the *Philornis* generalist paradigm that permeated earlier studies. This alternative perspective may foster further studies on the dynamics and mechanisms that underlie this interaction system.

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Appendix 1. Species used to construct the interaction networks and their respective number of interactions (k), trophic habit for *Philornis* and families for birds.

Philornis species	k	Habit
P. angustifrons (Loew, 1861)	28	Subcutaneous
P. downsi Dodge & Aitken, 1968	27	Subcutaneous/Free-living haem
P. pici (Macquart, 1854)	17	Subcutaneous
P. trinitensis Dodge & Aitken, 1968	14	Subcutaneous
P. glaucinis Dodge & Aitken, 1968	13	Subcutaneous
P. deceptivus Dodge & Aitken, 1968	10	Subcutaneous
P. seguyi Garcia, 1952	8	Subcutaneous
P. torquans (Nielsen, 1913)	7	Subcutaneous
P. gagnei Couri, 1983	5	Unknown
P. diminutus Couri, 1984	3	Subcutaneous
P. falsificus Dodge & Aitken, 1968	3	Free-living haematophagous
P. obscurus (Wulp, 1896)	3	Unknown
P. sanguinis Dodge & Aitken, 1968	3	Subcutaneous
P. mansoni Couri, 1986	2	Subcutaneous
P. porteri Dodge, 1955	2	Subcutaneous
P. vulgaris Couri, 1984	2	Subcutaneous
P. aitkeni Dodge, 1963	1	Free-living coprophagous
P. carinatus Dodge, 1968	1	Subcutaneous
P. frontalis Couri, 1984	1	Subcutaneous
P. medianus Couri, 1984	1	Subcutaneous
P. mimicola Dodge, 1968	1	Unknown
P. nielseni Dodge, 1968	1	Unknown
P. niger Dodge & Aitken, 1968	1	Subcutaneous
P. querulus Dodge & Aitken, 1968	1	Subcutaneous
P. rufuscutellaris Couri, 1983	1	Free-living coprophagous
P. spermophilae Townsend, 1895	1	Subcutaneous
Host bird species	k	Family
Molothrus bonariensis (Gmelin, 1789)	9	Icteridae
Pitangus sulphuratus (Linneaus, 1766)	7	Tyrannidae
Mimus gilvus (Vieillot, 1808)	5	Mimidae
Troglodytes aedon Vieillot, 1809	5	Troglodytidae
Cacicus cela (Linnaeus, 1758)	4	Icteridae
Mimus polyglottos (Linnaeus, 1758)	4	Mimidae

Appendix 1. Continued.

Host bird species	k	Family
Myiozetetes cayanensis (Linnaeus, 1766)	4	Tyrannidae
Thamnophilus murinus Sclater & Salvin, 1868	4	Thamnophilidae
Crotophaga ani Linnaeus, 1758	3	Cuculidae
Galbula ruficauda Cuvier, 1816	3	Galbulidae
Leptotila verreauxi Bonaparte, 1855	3	Columbidae
Mimus saturninus (Lichtenstein, 1823)	3	Mimidae
Molothrus rufoaxillaris Cassin, 1866	3	Icteridae
Phacellodomus striaticollis (Orbigny & Lafresnaye, 1838)	3	Furnariidae
Pseudoseisura lophotes (Reichenbach, 1853)	3	Furnariidae
Ramphocelus carbo (Pallas, 1764)	3	Thraupidae
Zonotrichia capensis (Statius Müller, 1776)	3	Emberizidae
Leptotila rufaxilla (Richard & Bernard, 1792)	2	Columbidae
Anumbius annumbi (Vieillot, 1817)	2	Furnariidae
Cacicus haemorrhous (Linnaeus, 1766)	2	Icteridae
Glaucis hirsuta (Gmelin, 1788)	2	Trochilidae
Icterus nigrogularis (Hahn, 1819)	2	Icteridae
Legatus leucophaius (Vieillot, 1818)	2	Tyrannidae
Leptasthenura platensis Reichenbach, 1853	2	Furnariidae
Margarops fuscatus (Vieillot, 1808)	2	Mimidae
Myiarchus tyrannulus (Statius Müller, 1776)	2	Tyrannidae
Megascops choliba (Vieillot, 1817)	2	Strigidae
Molothrus oryzivora (Gmelin, 1788)	2	Icteridae
Suiriri affinis (Burmeister, 1856)	2	Tyrannidae
Suiriri islerorum Zimmer, Whittaker & Oren, 2001	2	Tyrannidae
Sporophila lineola (Linnaeus, 1758)	2	Emberizidae
Sporophila nigricollis (Vieillot, 1823)	2	Emberizidae
Thraupis episcopus (Linnaeus, 1766)	2	Thraupidae
Turdus fumigatus Lichtenstein, 1823	2	Turdidae
Tyrannus melancholicus Vieillot, 1819	2	Tyrannidae
Volatinia jacarina (Linnaeus, 1766)	2	Emberizidae
Xiphocolaptes albicollis (Vieillot, 1818)	2	Dendrocolaptidae
Chrysomus thilius (Molina, 1782)	1	Icteridae
Amazona amazonica (Linnaeus, 1766)	1	Psittacidae
Amazona vittata (Boddaert, 1783)	1	Psittacidae
Camarhynchus pallidus (Sclater & Salvin, 1870)	1	Emberizidae
Camarhynchus parvulus (Gould, 1837)	1	Emberizidae
Camarhynchus psittacula Gould, 1837	1	Emberizidae
Certhidea olivacea Gould, 1837	1	Emberizidae
Coccyzus melacoryphus Vieillot, 1817	1	Cuculidae
Coereba flaveola (Linnaeus, 1758)	1	Coerebidae
Patagioenas leucocephala (Linnaeus, 1758)	1	Columbidae
Columbina talpacoti (Temminck, 1810)	1	Columbidae
Dendroica petechia (Linnaeus, 1766)	1	Parulidae
Dulus dominicus (Linnaeus, 1766)	1	Dulidae
Estrilda astrild (Linnaeus, 1758)	1	Estrildidae
Furnarius rufus (Gmelin, 1788)	1	Furnariidae
Gallus gallus (Linnaeus, 1758)	1	Phasianidae
Geospiza fortis Gould, 1837	1	Emberizidae
Geospiza fuliginosa Gould, 1837	1	Emberizidae
Gymnomystax mexicanus (Linnaeus, 1766)	1	Icteridae
Icterus cayanensis (Linnaeus, 1766)	1	Icteridae
Icterus dominicensis (Linnaeus, 1766)	1	Icteridae
Icterus icterus (Linnaeus, 1766)	1	Icteridae
Manacus manacus (Linnaeus, 1766)	1	Pipridae
Melanerpes striatus (Statius Muller, 1776)	1	Picidae
Nesomimus parvulus (Gould, 1837)	1	Mimidae
Oryzoborus angolensis (Linnaeus, 1766)	1	Emberizidae
Paroaria dominicana (Linnaeus, 1758)	1	Emberizidae
Passer domesticus (Linnaeus, 1758)	1	Passeridae
Piculus rubiginosus (Swainson, 1820)	1	Picidae
Mionectes macconnelli (Chubb, 1919)	1	Tyrannidae

Appendix 1. Continued.

Host bird species	k	Family
Progne chalybea (Gmelin, 1789)	1	Hirundinidae
Psarocolius decumanus (Pallas, 1769)	1	Icteridae
Pyrocephalus rubinus (Boddaert, 1783)	1	Tyrannidae
Quiscalus lugubris Swainson, 1838	1	Icteridae
Satrapa icterophrys (Vieillot, 1818)	1	Tyrannidae
Schistochlamys melanopis (Latham, 1790)	1	Thraupidae
Sialia sialis (Linnaeus, 1758)	1	Turdidae
Sicalis flaveola (Linnaeus, 1766)	1	Emberizidae
Sporophila bouvreuil (Statius Müller, 1776)	1	Emberizidae
Sporophila caerulescens (Vieillot, 1823)	1	Emberizidae
Sporophila intermedia Cabanis, 1851	1	Emberizidae
Tachyphonus rufus (Boddaert, 1783)	1	Thraupidae
Thamnophilus palliatus (Lichtenstein, 1823)	1	Thamnophilidae
Thamnophilus ruficapillus Vieillot, 1816	1	Thamnophilidae
Thraupis palmarum (Wied, 1821)	1	Thraupidae
Turdus nudigenis Lafresnaye, 1848	1	Turdidae
Zenaida macroura (Linnaeus, 1758)	1	Columbidae