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Phylogenetic conservatism and antiquity of a tropical specialization: Army-ant-following in the typical antbirds (Thamnophilidae)

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Abstract

One of the most novel foraging strategies in Neotropical birds is army-ant-following, in which birds prey upon arthropods and small vertebrates flushed from the forest floor by swarm raids of the army-ant *Eciton burchellii*. This specialization is most developed in the typical antbirds (Thamnophilidae) which are divisible into three specialization categories: (1) those that forage at swarms opportunistically as army-ants move through their territories (*occasional* followers), (2) those that follow swarms beyond their territories but also forage independently of swarms (*regular* followers), and (3) those that appear incapable of foraging independently of swarms (*obligate* followers). Although army-ant-following is one of the great spectacles of tropical forests, basic questions about its evolution remain unaddressed. Using a strongly resolved molecular phylogeny of the typical antbirds, we found that army-ant-following is phylogenetically conserved, with *regular* following having evolved only three times, and that the most likely evolutionary progression was from least (*occasional*) to more (*regular*) to most (*obligate*) specialized, with no reversals from the *obligate* state. Despite the dependence of the specialists on a single ant species, molecular dating indicates that army-ant-following has persisted in antbirds since the late Miocene. These results provide the first characterization of army-ant-following as an ancient and phylogenetically conserved specialization.

Keywords: Ancestral character state reconstruction; Army-ant-following; Ecological specialization; *Eciton*; Foraging strategies; Thamnophildae

1. Introduction

Army-ant-following, in which birds attending marauding army-ant swarms prey upon arthropods and small vertebrates flushed from the forest floor (Willis and Oniki, 1978), is one of the most novel foraging strategies of tropical regions. Such specializations have been implicated in increased tropical biodiversity by the simple fact that no ecological counterpart exists for them in temperate regions (Rahbek and Graves, 2001; Terborgh, 1985). Although it represents one of the most amazing tropical spectacles, army-ant-following has received surprisingly little research attention, particularly from an evolutionary perspective, and the bulk of our ecological knowledge of these birds stems almost entirely from the impressive collection of studies by Edwin O. Willis (e.g. Willis, 1968a,b,1969) and a recently published monograph (Willson, 2004).

One species of diurnal, swarm-raiding ant, *Eciton burchelli*, is the primary dependable resource for ant-following birds, frogs (*Bufo marinus*), and teid lizards (*Ameiva,*

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Kentropyx) that forage on escaping prey, for tachinid and stylopid flies that lay eggs on flushed arthropods (Rettenmeyer, 1963; Schneirla, 1971; Willis and Oniki, 1978), and for ant-butterflies that forage on the scat of army-ant-following birds (Ray and Andrews, 1980). A recent coextinction study (Koh et al., 2004) characterized *E. burchellii* as a "keystone mutualist" because of its widespread Neotropical distribution (lowland forests more or less continuously from southern Mexico to southern Peru and Brazil) (Watkins, 1976) and the dependence of such a taxonomically diverse assemblage of organisms on it. Swarms of a second widespread army-ant species, *Labidus praedator*, are also followed regularly, but are a less dependable resource because they usually only swarm above ground after heavy rains (Willis and Oniki, 1978).

The army-ant-following specialization in birds can be classified more specifically as a dependence on catching prey that has been flushed by another organism (Willson, 2004). Army-ant-following woodcreepers (Dendrocolaptinae), for example, are known to also follow peccary (Tayassuidae) herds through the forest (Willis, 1966). The peccaries perform the same function for the birds as army-ants—beating prey from the forest floor. Army-ant-following is most developed as a foraging specialization in the typical antbirds (Passeriformes: Thamnophilidae), a monophyletic (Irestedt et al., 2004), Neotropical radiation of 208 insectivorous, socially monogamous species, 94 of which attend army-ant swarms to some extent (Remsen et al., 2007; Zimmer and Isler, 2003). The specialization in antbirds has been characterized as parasitism on the army-ants, because the birds significantly reduce the rate at which the ants capture prey (Wrege et al., 2005). Antbirds that parasitize army-ant swarms compose three classes of specialization: (1) species that only forage at swarms opportunistically as army-ants move through their territory (*occasional* followers; 70 species), (2) species that regularly attend swarms beyond their territories, but are also often found foraging independently of swarms (*regular* followers; 8 species), and (3) *obligate* followers (16 species) that appear incapable of foraging independently of swarms or other beaters of prey (Skutch, 1996; Willis and Oniki, 1978; Willson, 2004; Zimmer and Isler, 2003). Although *occasional* and *regular* army-ant-following is also exhibited by some species in other avian families (e.g. Furnariidae, Thraupidae), *obligate* army-ant-following is limited to the typical antbirds (Thamnophilidae) (Pierpont, 1986; Willson, 2004).

Other than what can be inferred from the current taxonomy and a recently published phylogeny of the Thamnophilidae with taxon sampling too sparse to address the evolution of army-ant-following (Irestedt et al., 2004), nothing is known about the evolution of this remarkable specialization. Even the most basic questions concerning how army-ant-following evolved in the typical antbirds remain unanswered: Did army-ant-following evolve many times or is it phylogenetically conserved? Did its evolution progress from a less specialized to a more specialized state? Did reversals from the most specialized state occur? Foraging substrate specialists such as army-ant-followers are often characterized as being more vulnerable to extinction, because of their dependence on a subset of the resources utilized by competing taxa (Koh et al., 2004). Assuming extinction rates are higher than rates of adaptation, army-ant-following, like any heritable adaptation to the environment, is expected to be phylogenetically conservative (Peterson et al., 1999). An important question in this regard is how long army-ant-following has persisted as a foraging strategy. Here, we present a well-supported, densely sampled phylogeny of the Thamnophilidae, which is used in conjunction with GIS analyses of species distributions to gain insights into the evolution, temporal persistence, and biogeography of this remarkable foraging strategy in antbirds.

2. Materials and methods

2.1. Taxon sampling

We sampled 70 thamnophilid species (Table 1), including individuals from all but one genus of *obligate* and *regular* army-ant-following antbird (Willis, 1968b). Taxonomy follows the checklist of the South American Classification Committee (Remsen et al., 2007) except for *Myrmotherula haematonota*, which we place in the new genus *Epinecrophylla* (Isler et al., 2006), and *Sakesphorus bernardi*, which we place in the genus *Thamnophilus* (Brumfield and Edwards, 2007). We included representatives of 40 of the 46 thamnophilid genera, and one recently rediscovered *obligate* ant-follower (*Pithys castaneus*) (Lane et al., 2006). Five of the unsampled genera do not attend ant-swarms and their likely phylogenetic relationships would not affect the analysis (Zimmer and Isler, 2003). The unsampled monotypic genus (*Skutchia borbae*) represents an *obligate* ant-follower whose likely phylogenetic placement is with *Phlegopsis*. *Skutchia borbae* was placed in the genus *Phlegopsis* formerly, but was elevated to generic status based on plumage differences (Willis, 1968b). Because all members of this clade are *obligate* army-ant-followers, excluding *Skutchia* will not affect the ancestral state reconstructions. Trees were rooted using four outgroup taxa (*Chamaeza campanisoma, Hylopezus berlepschi, Liosceles thoracicus,* and *Pipra mentalis*).

2.2. Data collection

Data for seven species were downloaded from Genbank (Brumfield and Edwards, 2007; Tello and Bates, 2007): *Thamnomanes caesius* (EF030197, EF030259, EF030288, EF030320), *Cymbilaimus lineatus* (EF030221, EF030254, EF030283, EF030315), *Frederickena unduligera* (EF030222, EF030255, EF030284, EF030316), *Sakesphorus luctuosus*, (EF030225, EF030258, EF030287, EF030319), *Thamnophilus doliatus* (EF030234, EF030267, EF030296,

Table 1
Ingroup taxa used in this study with collector and frozen tissue collection voucher number (Louisiana State University Museum of Zoology, LSUMZ; Field Museum of Natural History, FMNH; Burke Museum of Natural History, UWBM; United States National Museum, USNM; University of Alaska Museum (UAM))

Species	Tissue number[a]	Locality	Collector/Preparator
*Cymbilaimus lineatus**	B18168 (LSUMZ)	Bolivia: depto. Santa Cruz; Velasco; Parque Nacional Noel Kempff Mercado	A. W. Kratter
Hypoedaleus guttatus	DHB1805 (UWBM)	Argentina: prov. Misiones; Posadas	D. H. Baepler
Batara cinerea	RTB520 (UWBM)	Bolivia: depto. Santa Cruz; San Lorenzo	R. T. Brumfield
Mackenziaena leachii	B5986 (USNM)	Argentina: prov. Misiones; 45 km N Posadas	B. K. Schmidt
Frederickena viridis	B9259 (USNM)	Guyana: Northwest District; Baramita	R. T. Brumfield
*Frederickena unduligera**	B4281 (LSUMZ)	Peru: depto. Loreto; lower Napo region, E. bank Río Yanayacu, ca. 90 km N Iquitos	D. L. Dittmann
Taraba major	321773 (FMNH)	Peru: depto. Madre de Dios; Hacienda Amazonia	S. M. Lanyon
*Sakesphorus luctuosus**	B7012 (USNM)	Brazil: Para; 52 km SSW Altamira	G. R. Graves
*Thamnophilus doliatus**	RTB390 (UWBM)	Bolivia: depto. Santa Cruz; prov. Cordillera, 10.6 km E Abapó	R. T. Brumfield
Thamnophilus [*Sakesphorus*] *bernardi**	B5136 (LSUMZ)	Peru: depto. Lambayeque; Las Pampas, km 885 Pan-American Hwy, 11 road km from Olmos	D. L. Dittmann
Thamnophilus aethiops	399223 (FMNH)	Brazil: Alagoas; Ibateouara, Engenho Coimbra, Usina Serra Grande	J. G. Tello
Megastictus margaritatus	B6836 (LSUMZ)	Peru: depto. Loreto; 5 km N Amazonas, 85 km NE Iquitos	G. H. Rosenberg
Neoctantes niger	321806 (FMNH)	Peru: depto. Cuzco; Tono	D. F. Stotz
Thamnistes anabatinus	B5467 (LSUMZ)	Peru: depto. San Martin; 20 km by road NE Tarapoto	T. J. Davis
Dysithamnus mentalis	392443 (FMNH)	Brazil: Pernambuco; Serra do Espelho	S. Roda, M.F. Silva
Dysithamnus plumbeus	B33684 (LSUMZ)	Peru: depto. Cajamarca; Nuevo Peru; 16 km NE junction Ríos Tabuconas and Chinchipe	A. T. Urbay
Thamnomanes saturninus	389947 (FMNH)	Brazil: Rondônia; Cachoeira Nazare, W bank Río Jiparana	T. S. Schulenberg
*Thamnomanes caesius**	B9482 (USNM)	Guyana: Northwest District; Baramita	R. T. Brumfield
Pygiptila stellaris	389931 (FMNH)	Brazil: Rondônia; Cachoeira Nazare, W bank Río Jiparana	A. T. Peterson
Epinecrophylla [*Myrmotherula*] *haematonota*	B2509 (LSUMZ)	Peru: depto. Loreto; 1 km N Río Napo, 157 km by river NNE Iquitos	G. H. Rosenberg
Myrmotherula brachyura	B4722 (LSUMZ)	Peru: depto. Loreto; S Río Amazonas, ca 10 km SSW mouth Río Napo on E. bank Quebrada Vainilla	T. J. Davis
Myrmotherula longicauda	B39036 (LSUMZ)	Bolivia: depto. Cochabamba; San Onofre	D. C. Schmitt
Myrmotherula axillaris	392444 (FMNH)	Brazil: Pernambuco; Serra do Espelho	S. Roda, M.F. Silva
Dichrozona cincta	391144 (FMNH)	Bolivia: depto. La Paz; T.C.O Campamento Araona, "Palmasola", Rio Manupari	J. M. Bates
Myrmorchilus strigilatus	392862 (FMNH)	Brazil: Sergipe; Caninde do Sao Francisco, Curituba, Fazenda Miramar	M. F. Silva, M. Silva, G. Coelho
Herpsilochmus rufimarginatus	339650 (FMNH)	Venezuela: Bolivar; Tumaremo, 23 km S	S. M. Lanyon
Microrhopias quixensis	321993 (FMNH)	Peru: depto. Madre de Dios; Hacienda Amazonia	S. M. Lanyon
Formicivora rufa	391399 (FMNH)	Brazil: Amapa; Amapa, Fazenda Itapoa	J. M. C. Silva
Drymophila genei	432972 (FMNH)	Brazil: Minas Gerais; Parque Nacional Caparao	J. M. Goerck
Terenura humeralis	389942 (FMNH)	Brazil: Rondônia; Cachoeira Nazare, W bank Río Jiparana	T. S. Schulenberg

(*continued on next page*)

Table 1 (*continued*)

Species	Tissue number[a]	Locality	Collector/Preparator
Terenura sharpei	B39086 (LSUMZ)	Bolivia: depto. Cochabamba; San Onofre, ca 43 km W Villa Tunari	R. T. Brumfield
Cercomacra tyrannina	B2273 (LSUMZ)	Panama: prov. Darién; Cana on E slope Cerro Pirré	D. Braun
Cercomacra serva	B27609 (LSUMZ)	Peru: depto. Loreto; sa 77 km WNW Contamana, 7 degrees, 05'S, 75 degrees, 39'W	A. P. Capparella
Pyriglena leuconota	334469 (FMNH)	Bolivia: depto. Santa Cruz; Chiquitos: San Jose-San Ignacio Rd., Km 69	D. E. Willard
Myrmoborus myotherinus	391406 (FMNH)	Brazil: Pará; Serra dos Carajas	J. M. C. Silva
Hypocnemis cantator	391136 (FMNH)	Bolivia: depto. El Beni; Hacienda Los Angeles, 10 km E Riberalta	J. G. Tello
Hypocnemoides maculicauda	391414 (FMNH)	Brazil: Pará; Caxiuanã	J. M. C. Silva
Myrmochanes hemileucus	B3649 (LSUMZ)	Peru: depto. Loreto; S end of Isla de Iquitos	M. B. Robbins
Gymnocichla nudiceps	B2228 (LSUMZ)	Panama: prov. Darien; Cana, on E slope Cerro Pirre	M. B. Robbins
Sclateria naevia	391418 (FMNH)	Brazil: Amapá; Tartarugalzinho, Fazenda Caiena	J. M. C. Silva
Percnostola rufifrons	B7011 (LSUMZ)	Peru: depto. Loreto; 5 km N Amazonas, 85 km NE Iquitos	G. H. Rosenberg
Percnostola lophotes	433492 (FMNH)	Peru: depto. Madre de Dios; Moskitania, 13.4 km NNW Atalaya, l bank Alto Madre de Dios	B. J. O'Shea
Schistocichla schistacea	B4686 (LSUMZ)	Peru: depto. Loreto; S Rio Amazonas, ca 10 km SSW mouth Río Napo on E. bank Quebrada Vainilla	S. W. Cardiff
Myrmeciza exsul	20240 (UAM)	Panama: prov. Panama	M. J. Miller
Myrmeciza berlepschi	B12026 (LSUMZ)	Ecuador: prov. Esmeraldas; El Placer	J. Kennard
Myrmeciza pelzelni	B7523 (LSUMZ)	Venezuela: terr. Amazonas; Cerro de la Neblina	J. P. O'Neill
Myrmeciza hemimelaena	20237 (UAM)	Peru: depto. Ucayali	M. J. Miller
Myrmeciza atrothorax	322209 (FMNH)	Peru: depto. Madre de Dios; Hacienda Amazonia	S. M. Lanyon
Myrmeciza melanoceps	B43013 (LSUMZ)	Peru: depto. Loreto; ca. 54 km NNW mouth Río Morona on west bank	J. Alvarez
Myrmeciza goeldii	B9293 (LSUMZ)	Bolivia: depto. Pando; Nicolás Suarez, 12 km by road S of Cobija, 8 km W on road to Mucden	J. V. Remsen
Myrmeciza hyperythra	B7342 (LSUMZ)	Peru: depto. Loreto; N. bank Río Amazonas, 5 km ENE Oran, 85 km NE Iquitos	T. C. Maxwell
Myrmeciza fortis	20533 (UAM)	Peru: depto. Ucayali	M. J. Miller
Myrmeciza immaculata	20534 (UAM)	Panama: prov. Bocas del Toro	M. J. Miller
Myrmornis torquata	389880 (FMNH)	Brazil: Rondônia; Cachoeira Nazare, W bank Río Jiparana	T. S. Schulenberg
Pithys albifrons	391430 (FMNH)	Brazil: Amapá; Tartarugalzinho, Fazenda Caiena	J. M. C. Silva
Pithys castaneus	B42817 (LSUMZ)	Peru: depto. Loreto; ca 54 km NNW mouth Río Morona	K. Eckhardt
Gymnopithys leucaspis	B4136 (LSUMZ)	Peru: depto. Loreto; Lower Río Napo region, E. bank Río Yanayacu	S. W. Cardiff
Gymnopithys bicolor	B2096 (LSUMZ)	Panama: prov. Darién; about 6 km NW Cana	S. M. Lanyon
Gymnopithys rufigula	B7512 (LSUMZ)	Venezuela: terr. Amazonas; Cerro de la Neblina camp VII	D. E. Willard
Gymnopithys salvini	391147 (FMNH)	Bolivia: depto. La Paz; Puerto Araona, Rio Manupari	J. M. Bates
Gymnopithys lunulatus	B27384 (LSUMZ)	Peru: depto. Loreto; NE bank Río Cushabatay, 8 km WNW Contamana	A. W. Kratter
Rhegmatorhina hoffmannsi	389933 (FMNH)	Brazil: Rondônia; Cachoeira Nazare, W bank Río Jiparana	D. E. Willard
Rhegmatorhina gymnops	B35298 (LSUMZ)	Brazil: Pará; 126 km NW Alta Floresta, S. bank of Río Sao Benedito	A. Aleixo
Rhegmatorhina melanosticta	B4248 (LSUMZ)	Peru: depto. Loreto; Lower Río Napo region, E. bank Río Yanayacu	S. W. Cardiff

Table 1 (*continued*)

Species	Tissue number[a]	Locality	Collector/Preparator
Hylophylax naevioides	B2230 (LSUMZ)	Panama: prov. Darien; 5 km N Amazonas, 85 km NE Iquitos	G. H. Rosenberg
Hylophylax punctulatus	B18327 (LSUMZ)	Bolivia: depto. Santa Cruz; Velasco; Parque Nacional Noel Kempff Mercado, 86 km ESE Florida	M. D. Cardeño
Hylophylax poecilinotus	391148 (FMNH)	Bolivia: La Paz; T.C.O. Campamento Araona, "Palmasola", Rio Manupari	J. M. Bates
Phlegopsis nigromaculata	389842 (FMNH)	Brazil: Rondônia; Cachoeira Nazare, W bank Río Jiparana	D. E. Willard
Phlegopsis erythroptera	B9617 (LSUMZ)	Bolivia: depto. Pando; Nicolás Suarez, 12 km by road S of Cobija, 8 km W on road to Mucden	D. C. Schmitt
Phaenostictus mcleannani	B2135 (LSUMZ)	Panama: prov. Darien; ca 6 km NW Cana	M. B. Robbins

Sequences for species denoted with an asterisk downloaded from Genbank. The phylogenetic tree was rooted using the following outgroup taxa: *Chamaeza campanisona* (Formicariidae: KGB14 [UWBM]), *Hylopezus berlepschi* (Formicariidae: 322345 [FMNH]), *Liosceles thoracicus* (Rhinocryptidae: 390080 [FMNH]), *Pipra mentalis** (Pipridae: B18078 [LSUMZ]).

EF030327), *Thamnophilus bernardi* (EF030223, EF030256, EF030285, EF030317), and *Pipra mentalis* (DQ294404, DQ294491, DQ294535, DQ294448). From all other individuals, we sequenced portions of three mitochondrial protein-coding genes (ND2, ND3, cyt *b*) and one nuclear intron (β-fibrinogen intron 5). DNA was extracted from 25 mg of pectoral muscle using DNeasy kits (Qiagen Inc., Valencia, CA). In a 25 μl total volume, PCR amplifications contained approximately 50 ng of genomic template DNA, 1.5 mM $MgCl_2$, 200 mM dNTPs, and 0.1 U Promega *Taq* or AmpliTaq (Applied Biosystems, Inc., Foster City, CA). Thermocycling consisted of an initial denaturation step (94 °C for 2 min) followed by 35 cycles of 94 °C for 1 min, a 30 s annealing step (ND2, ND3, cyt *b*: 45 °C, β-fibrinogen intron 5: 50 °C), and a 72 °C extension for 1 min. To facilitate cloning of PCR products through addition of an adenine to all amplicons, a 7 min extension at 72 °C was performed as the final step. PCR primers and internal sequencing primers are presented in Table 2. Amplicons were purified using PEG precipitation, eluted in 12.5 μl of diH_2O, and sequenced directly with an ABI Prism cycle sequencing kit (Applied Biosystems Inc.) and an ABI 3100 Genetic Analyzer. Sequencing reactions were purified with AutoSeq G-50 spin columns (Amersham Biosciences, Piscataway, NJ). Both strands were sequenced.

2.3. Phylogenetic analysis

Sequences were aligned manually using Sequencher 4.1.2 (Gene Codes Corporation, Ann Arbor, MI). Protein-coding mitochondrial sequences were translated into amino acids to verify the absence of stop codons or other anomalous residues. Maximum-likelihood and Bayesian methods were the primary methods of phylogenetic analysis. The optimal maximum-likelihood model for each gene and the combined data set was chosen using the program ModelTest (Posada and Crandall, 1998) to perform hierarchical likelihood ratio tests on a series of nested models (Swofford et al., 1996). Likelihood scores to use in these tests were calculated for each model on a neighbor-joining tree (Saitou and Nei, 1987) reconstructed from the raw percent sequence divergence distance matrix using PAUP* (Swofford, 2003). With the optimal maximum-likelihood model, the most-likely tree for each gene and the combined data set was reconstructed with the program PAUP* using heuristic searches with 10 random-addition replicates and TBR branch-swapping. A parsimony analysis of the concatenated data was also performed with all sites weighted equally and the same heuristic search parameters as in the likelihood analysis, except 100 random-addition replicates were used.

Table 2
List of primers used in PCR amplification and cycle sequencing

Gene	Primer	Sequence (5′ ⇒ 3′)	Location
cyt *b*	L14990	CCA TCC AAC ATC TCA GCA TGA TGA AA	L14990 (cyt *b*)
cyt *b*	H16065	AAC TGC AGT CAT CTC CGG TTT ACA AGA C	H16065 ($tRNA_{Thr}$)
cyt *b*	cytb.intf	CAC GAR ACY GGR TCY AAY AAY CC	L15496 (internal)
cyt *b*	cytb.intr	GGR TTR TTR GAY CCR GTY TCG TG	H15496 (internal)
ND2	L5215	TAT CGG GCC CAT ACC CCG AAA AT	L5193 ($tRNA_{Met}$)
ND2	H6313	CTC TTA TTT AAG GCT TTG AAG GC	H6313 ($tRNA_{Trp}$)
ND2	L5758	GGN GGN TGR RBH GGN YTD AAY CAR AC	L5733 (internal)
ND2	H5766	DGA DGA RAA DGC YAR RAY YTT DCG	H5766 (internal)
ND3	L10755	GAC TTC CAA TCT TTA AAA TCT GG	L10733 ($tRNA_{Gly}$)
ND3	H11151	GAT TTG TTG AGC CGA AAT CAA C	H11154 ($tRNA_{Arg}$)
βf5	FIB5L	CGC CAT ACA GAG TAT ACT GTG ACA T	S713
βf5	FIB5H	GCC ATC CTG GCG ATC TGA A	AS767

The mitochondrial primers are numbered according to location in the *Gallus* genome (Desjardins and Morais, 1990) and the β-fibrinogen external primers with regard to a *Gallus* cDNA sequence (Weissbach et al., 1991).

Fig. 1. Maximum-likelihood (a) and most parsimonious (b) trees from heuristic searches of the concatenated data matrix. Bayesian (before slash) and bootstrap (after slash) support values presented for the maximum-likelihood tree. Bootrap support values presented for the parsimony tree. Trees rooted using four outgroup taxa (not pictured).

To assess nodal support in the phylogeny, the optimal maximum-likelihood models for each data set (cytochrome *b*, ND2, ND3: GTR + G+ I; b-fibrinogen intron 5: HKY + G) were used in a site-partitioned Bayesian analysis (Table 3). Uniform interval priors were assumed for the parameters, except for base frequencies, which were assigned a Dirichlet prior (Huelsenbeck and Ronquist, 2001). Four heated chains were run for 5.0×10^6 generations, and sampled every 1000. Trees from the first 5.0×10^5 generations were discarded as "burn-in", with the remaining 4501 trees from the stationary distribution used to estimate posterior probabilities of tree topology and other maximum-likelihood parameters, including transition rates between army-ant-following behaviors (see ancestral character state reconstruction section below). Three independent runs with different random seeds were performed to insure the posterior probabilities were stable. We also assessed nodal support using 100 maximum-likelihood and parsimony non-parameteric bootstrap replicates using the same heuristic search options described above.

2.4. Ancestral character state reconstruction

To reconstruct the evolutionary history of army-ant-following, we coded each species as (1) a non-follower or *occasional* follower (these are operationally the same because nearly all understory insectivores will follow a swarm if it moves through their territory), (2) a *regular* follower, or (3) an *obligate* follower. Ancestral character state reconstructions for this multi-state character were performed using both parsimony (Maddison and Maddison, 2000; Maddison, 1990) as well as maximum-likelihood and Bayesian Markov Chain Monte Carlo (MCMC) methods that incorporate a statistical model of trait evolution (Mooers and Schluter, 1999; Ronquist, 2004). Bayesian methods have the advantage of building into the analysis uncertainty about both the process of character change and the phylogeny (Huelsenbeck et al., 2003; Pagel et al., 2004). Bayesian MCMC ancestral state reconstructions and character transition rate estimations were performed using the program BayesMS (Buschbom and Barker, 2006; Pagel et al., 2004). The set of trees used in the Bayesian character analysis were the same 4501 trees generated by MrBayes (Huelsenbeck and Ronquist, 2001) to estimate nodal confidence in the phylogeny. On each tree in the set, the maximum-likelihood rates of character change were estimated using a uniform prior. Phylogenetic uncertainty was accounted for by averaging the estimates across the set of 4501 trees. Ancestral state probabilities for a given node were estimated by multiplying the mean ancestral probability at that node across all trees by the proportion of the trees in which the node was found as determined by the Bayesian phylogenetic analysis (see Phylogenetic analysis section above) (Pagel et al., 2004). Parsimony reconstructions were performed using MacClade (Maddison and Maddison, 2000), and assumed equal transition rates between all character states.

Table 3
Summary of model parameters and tree scores for maximum-likelihood and Bayesian analyses for all taxa

	ND2	ND3	cyt *b*	βf5	Combined
# Trees	1	2	1	1	1
-ln(*L*)	22542.1	6891.7	19292.3	4514.7	54484.5
r_{AC}	0.283	0.469	0.285	1.486	0.409
r_{AG}	13.797	7.212	9.473	4.081	7.616
r_{AT}	0.458	0.333	0.785	0.747	0.529
r_{CG}	0.385	0.208	0.179	1.558	0.335
r_{CT}	7.326	7.212	9.473	4.081	7.616
α	0.669	0.829	0.768	2.247	0.703
p_{iv}	0.341	0.401	0.488	NA	0.372
freq(A)	0.378	0.360	0.355	0.307	0.360
freq(C)	0.361	0.357	0.390	0.159	0.345
freq(G)	0.049	0.067	0.055	0.206	0.073
freq(T)	0.212	0.216	0.200	0.328	0.223

The maximum-likelihood parameters were used in bootstrap analyses of the data. NA indicates parameters that were not estimated.

2.5. Dating ancestral nodes

Two molecular clock calibrations available for mitochondrial variation in birds equate 1.6% (Fleischer et al., 1998) or 2.0% sequence divergence (Shields and Wilson, 1987) with one million years of evolution. The 1.6% calibration is based on cyt *b* variation in Hawaiian oscine passerines and may be more applicable to suboscine passerine antbirds than the 2.0% rate, which was derived from mitochondrial RFLP variation in geese. To date relevant ancestral nodes in the antbird phylogeny, we first reduced the dataset to just the cyt *b* sequences and used a parametric likelihood ratio test to examine whether the genetic variation was consistent with a molecular clock. On a tree composed of the species in Fig. 1 and with the same topology, parameters in the GTR + G + INV substitution model were estimated with and without a clock constraint and the likelihood calculated. The test statistic is two times the absolute difference in log likelihood scores. To generate a null distribution, we used the program Seq-Gen (Rambaut and Grassly, 1997) to evolve 100, 1045-bp long sequences along the topology according to the substitution model parameters that had been optimized on the unconstrained tree (rate matrix = 2.3492 21.3981 2.1128 0.3466 36.4922; base frequencies = 0.3003 0.3512 0.1154; shape parameter = 1.4852; proportion of invariant sites = 0.5282). On each simulated data set, the model parameters were optimized with and without a clock constraint and the likelihoods calculated. Statistical significance at a level of $\alpha = 0.95$ would occur if the test statistic fell into the top 5% of values in the simulated distribution.

2.6. GIS analyses

To examine the geographical context of army-ant-following in light of the phylogeny, we constructed antbird

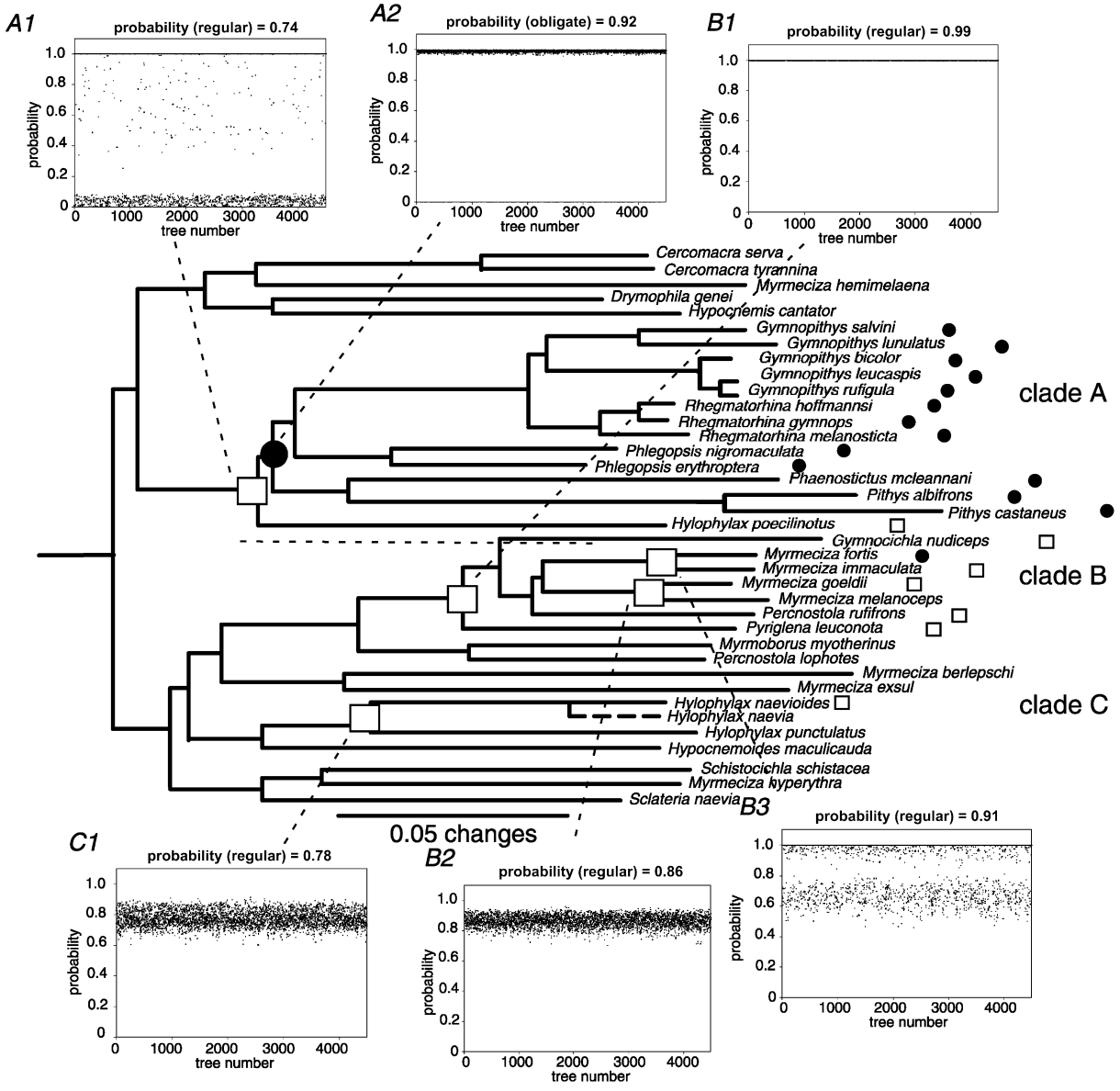

Fig. 2. Bayesian posterior probabilities of army-ant-following (circle: *obligate*, square: *regular,* all other taxa are *occasional/non-followers*), mapped onto relevant ancestral nodes of a maximum-likelihood phylogeny of the Thamnophilidae. To improve the visibility of ancestral node reconstructions only the portion of the tree containing army-ant-following taxa is depicted. Graphs show maximum-likelihood reconstructed node at each of 4501 MCMC-trees sampled from the posterior probability distribution. Independent origin of army-ant-following highlighted in clades A, B, and C. Nodal support is presented above branches (Bayesian posterior probabilities before forward slash, maximum-likelihood bootstrap after forward slash) except for those nodes having less than 0.5 Bayesian posterior probability and less than 50% bootstrap value.

species density maps for each of the three foraging categories as well as for the species in the sister clades to clades A, B, and C (see Online Supplementary Material). ArcView shape files containing distribution maps (Ridgely et al., 2003) of thamnophilid and furnariid species were downloaded from InfoNatura (2005). To construct species density maps, we created a 50×50 km grid that encompassed the entire Neotropical region (9380 cells) using ArcView GIS 3.3 (ESRI 2003) with the Area Tools extension. We determined the grid cells that each species occurred in by overlaying species distributions onto the grid in ArcView. Species distributions were converted to 50×50 km grids by selecting those cells that intersected the species distributions. The number of species that occurred in each grid cell was then tallied and mapped. Because *regular* army-ant-following furnariids (ovenbirds) compete with antbirds and are part of the dominance hierarchy (Willson, 2004), we performed a second analysis that included the *regular* furnariid army-ant-followers (Willis and Oniki, 1978).

3. Results

3.1. Sequence variation and phylogenetic analyses

All data from this study were deposited into TreeBASE (Accession No. S1805). Sequences of cyt *b* (1045 bp,

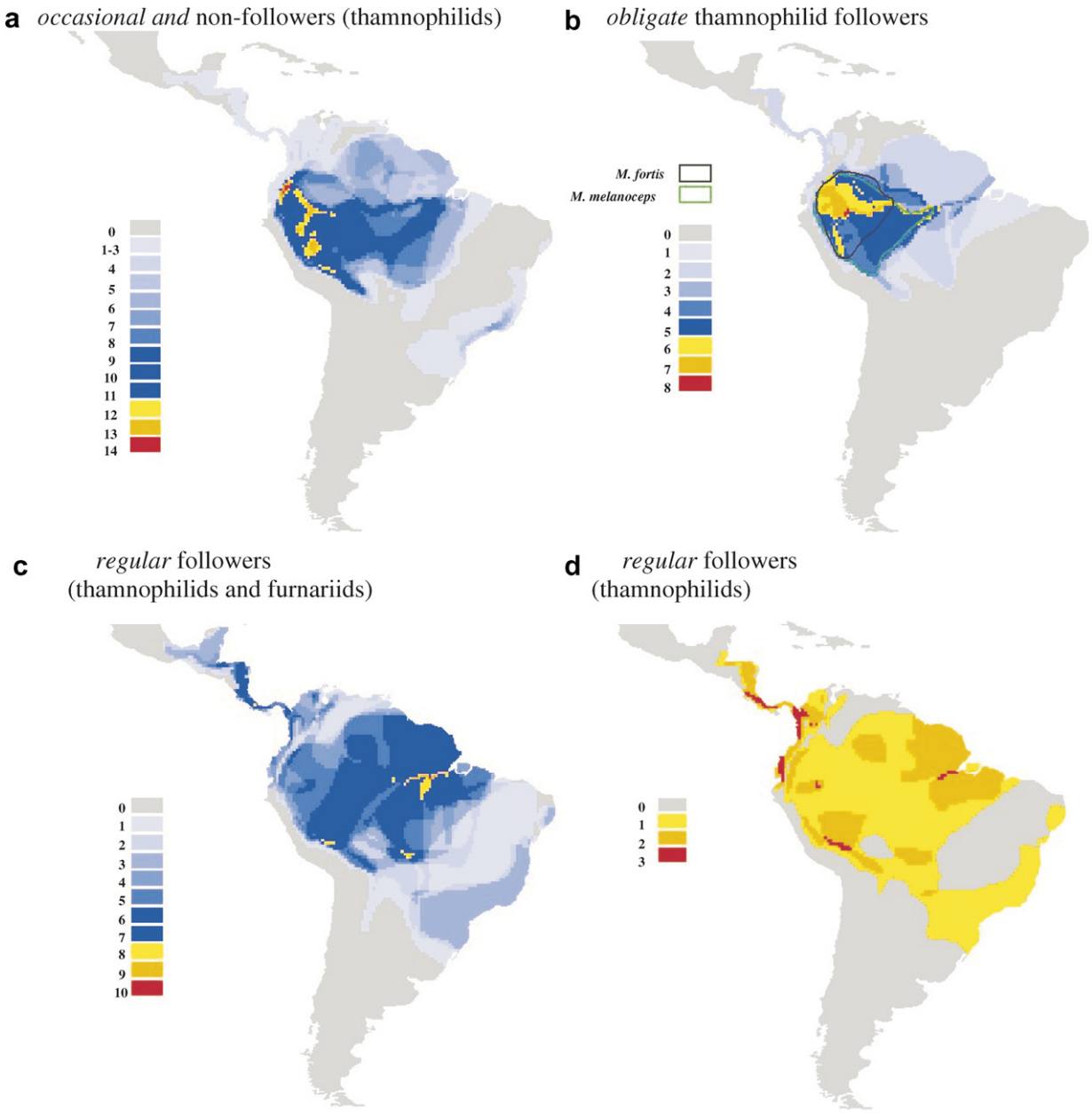

Fig. 3. Species-richness maps of (a) *occasionallnon-following* species that are sister to ant-following clades A, B, and C (Fig. 1); (b) *obligate* army-ant-followers, with distributions of *Myrmeciza fortis* (*obligate*) and *M. melanoceps* (*occasional*) outlined; (c) *regular* army-ant-followers (pooling thamnophilid and furnariid species); (d) *regular* thamnophilid army-ant-followers.

corresponding to bases 14,991–16,035 of the chicken mitochondrial genome), ND2 (1041 bp, corresponding to bases 5220–6280), ND3 (351 bp, corresponding to bases 10,776–11,126), and βf5 (571 bp) were obtained for most taxa (Genbank Accession Nos. EF639874–EF640139), creating a total data set of 2977 bp. Missing from the data set were βf5 for *Myrmeciza berlepschi* and *Myrmotherula brachyura*. Thirty-one base-pairs of difficult-to-align βf5 sequence were excluded from all analyses. No stop codons or other anomalous amino acid residues were detected in the mitochondrial protein-coding sequences. Homogeneity of base frequencies across all taxa was not rejected for any of the data sets ($P > 0.05$).

A partition homogeneity test found no significant differences ($P > 0.05$) in phylogenetic signal among the trees reconstructed from the individual genes. In addition, Shimodaira–Hasegawa tests (Shimodaira and Hasegawa, 1999) found no significant disagreement in the topologies of phylogenies reconstructed from the individual genes. Phylogenetic analysis of the combined data set resulted in a single most-likely tree ($-\ln L = 54484.5$), with the majority of nodes supported by high (>70%) non-parametric bootstraps and posterior probabilities greater than 0.95 (Fig. 1a). The parsimony analysis resulted in a single most parsimonious tree (12,865 steps), but the strongly supported nodes were found only near the tips of the tree

(Fig. 1b). Other weighting schemes that could have produced a more strongly supported parsimony tree were not explored.

3.2. Ancestral character state reconstruction

To address the evolutionary progression of army-ant-following and whether reversals from army-ant-following were observed, we estimated ancestral character states using parsimony and Bayesian methods. Most posterior probabilities of the ancestral states fell below the statistically significant 0.95 level, reflecting the uncertainty inherent in ancestral character state reconstruction. Both parsimony and Bayesian ancestral state reconstructions indicated that *regular* army-ant-following evolved independently three times in the typical antbirds from *occasional* army-ant-following ancestors (see clades A, B, and C in Fig. 2), with two of these lineages (clades A and B) leading eventually to *obligate* army-ant-following. Army-ant-following represents a derived state in the typical antbirds that is phylogenetically conserved.

Ancestral nodes at the base of the *obligate* clades A and B (Fig. 2) had ambiguous character states based on parsimony reconstructions, but Bayesian reconstructions suggest the evolution of army-ant-following was progressive, following a chronological specialization sequence from *occasional* to *regular* to *obligate*. In clade A, the common ancestor of *Hylophylax poecilinotus* (a *regular* follower) and its large sister clade of *obligate* followers was a *regular* follower with 0.74 posterior probability (Fig. 2). Similarly, the common ancestor of *Myrmeciza fortis* (an *obligate* follower) and *M. immaculata* (a *regular* follower) was a *regular* follower with a posterior probability of 0.91.

We did not observe evolutionary reversals from the most specialized *obligate* state, but did detect one reversal from *regular* following ancestors. *Myrmeciza melanoceps*, an *occasional* follower, is embedded within a clade of *regular* and *obligate* followers and the ancestral reconstruction suggests its most recent common ancestor was a *regular* follower (posterior probability = 0.86) (Fig. 2).

3.3. Dating ancestral nodes

A parametric likelihood ratio test did not reject ($P = 0.18$) clock-like evolution of the thamnophilid cyt *b* sequences. Using an estimate of 1.6% cyt *b* sequence divergence per million years derived from a study of Hawaiian honeycreepers (Fleischer et al., 1998), we made a very rough estimate that the common ancestor of "*obligate/regular*" ant-following clade A (Fig. 2) existed approximately 6.4 Mya (late Miocene), and the common ancestor of the largely *regular* ant-following clade B occurred approximately 4.2 Mya (early Pliocene).

3.4. GIS analyses

We were interested in examining whether the only reversal we observed, a shift from *regular* to *occasional* following in *M. melanoceps*, occurred in a region of the Neotropics with a relatively high number of co-occurring army-ant-following antbirds. Assuming competition would be most intense in such a region, this could suggest a role for competition in the reversal. We were also interested in whether *M. fortis,* the only *obligate* follower in clade B, occurred in the same region. Willson's (2004) community ecology study of army-ant-following birds in southeastern Peru found that *M. fortis* preferred following swarms of *L. praedator*. Intense competition at *E. burchellii* swarms could influence the evolution of such a preference. Our GIS analysis revealed that the number of co-occurring *obligate* army-ant-following species is highest in western Amazonia (Fig. 3b), the region in which both *M. melanoceps* and *M. fortis* occur. In contrast, the densities of *regular* followers were highest around the periphery of the Amazon basin (Fig. 3d).

Discussion

This evolutionary analysis of army-ant-following found it to be an ancient and phylogenetically conserved tropical foraging specialization, with a history largely consistent with theoretical expectations of the progression of specializations. What was most surprising was that the evolutionary vulnerability to coextinction hypothesized to accompany specialization was not observed in army-ant-following antbirds. Despite the dependence of army-ant-followers on a single "keystone" army-ant species (Koh et al., 2004), army-ant-following appears to have persisted in thamnophilid antbirds since the late Miocene. This timeframe postdates the advent of diurnal army-ant swarming in *E. burchellii* and *L. praedator* that occurred after these species diverged 20–40 million years ago (Brady, 2003). A recent analysis that examined the tempo of mitochondrial evolution in birds found that the above calibrations likely lead to underestimates of divergence times (Pereira and Baker, 2006), so that the evolution of army-ant-following in the typical antbirds could be even older than 6 million years.

Our results suggest that the evolution of army-ant-following most likely followed a progression from least specialized to most specialized. This result makes intuitive sense in light of the unique behavioral traits associated with some *regular* and most *obligate* followers. In addition to their ant-following behavior, *obligate* and some *regular* army-ant-following antbirds are distinguished by specialized behaviors, such as not defending exclusive territories and "bivouac-checking" (Swartz, 2001; Willson, 2004). If some amount of neurological canalization is associated with these behaviors, reversals to less specialized states may be evolutionarily constrained. Accordingly, we did not observe reversals from *obligate* following in either clade A or B, and we observed only one reversal from *regular* to *occasional* army-ant-following in clade B. Because of the limited number of independent contrasts inherent in this study, phylogenetic studies of army-ant-following in other

bird families will be needed to bolster our conclusions regarding evolutionary reversals from the army-ant-following specialization. Whether such an evolutionary progression is characteristic of other novel avian foraging strategies in the tropics awaits additional comparative studies (Thompson, 1994). The dead-leafing foraging specialization (Greenberg and Gradwohl, 1980) exhibited by other antbird species was recently shown to be phylogenetically conserved in the Thamnophilidae (Hackett and Rosenberg, 1990; Isler et al., 2006).

The GIS analyses of species distributions suggest that competition could have played a role in the evolution and distribution of army-ant-following in antbirds, although we note that other explanations need to be explored. The hierarchical division of swarms into a series of concentric feeding zones, with the largest ant-followers occupying the most productive leading edge of the advancing swarm and the smallest species at the trailing edge (Willis and Oniki, 1978), accommodates the co-existence of army-ant-followers at a single swarm. Interspecific competition among species is intense (Willson, 2004), and the relatively low number of *obligate* thamnophilid species suggests an ecological limit on the resource, perhaps policed through competition. In this regard, the lone *obligate* army-ant-follower of clade B, *M. fortis*, is noteworthy in that the species (1) evolved its *obligate* army-ant-following behavior more recently than *obligate* army-ant-following in clade A, assuming the molecular branch lengths are proportional to time (Fig. 2), and (2) minimizes competition with other *obligate* army-ant-followers by spending a greater proportion of time following *L. praedator* swarms instead of those of *E. burchellii* (Willson, 2004), the premier swarmer attended by clade A species. The distribution of *M. fortis* occurs western Amazonia, a region with the highest number of co-occurring *obligate* army-ant-following species (Fig. 3b). Similarly, the reversal from *regular* to *occasional* army-ant-following observed in *M. melanoceps* (clade B; Fig. 2) could have been induced by competition, because this species also occurs in western Amazonia.

If competition at swarms impacts the distribution of army-ant-followers, we expected to find the evolution of *regular* followers in regions with fewer *obligate* followers. For example, the lone army-ant-follower of clade C (Fig. 2), *Hylophylax naevioides*, occurs as a *regular* army-ant-follower in the forested lowlands west of the Andes, where there are only two *obligate* species (*Gymnopithys bicolor* and *Phaenostictus mcleannani*). Interestingly, the two other species in clade C, *Hylophylax naevia* (not included in this study, but known to be part of this clade; Brumfield, unpublished data) and *Hylophylax punctulata*, occur syntopically with up to five obligate ant-followers east of the Andes. Neither *H. naevia* nor *H. punctulata* follows ants more than occasionally. Could the *regular* army-ant-following behavior of *H. naevioides* have evolved because there were only two *obligate* competitors west of the Andes? The ant-following species density maps illustrate clear differences between *obligate* and *regular* followers. *Obligate* army-ant-followers are found almost exclusively in Amazonia, with increasing densities moving westward towards the Andes. This same pattern was observed in the *occasional/non-follower* map and with patterns found in a meta-analysis of all species of breeding birds in South America (Rahbek and Graves, 2001). In contrast to this general pattern, *regular* followers were most abundant where *obligates* were least prevalent or absent—in the Atlantic coastal forests of Brazil, the Guyanan shield, and the forested lowlands west of the Andes (Fig. 3c and d). This pattern was evident both when thamnophilids were analyzed alone (Fig. 3d) and in concert with furnariids (Fig. 3c). Collectively, these results suggest competition could have played a role in the evolution of army-ant-followers and shaping the distribution of army-ant-following species. Field studies are needed to test this and other possibilities.

Critical caveats to our interpretation of the above distribution patterns are that we did not consider the population densities of the ants across their distributions, nor seasonal variation in ant-swarming. The population densities of *E. burchellii* and *L. praedator* have undoubtedly influenced the distribution and densities of army-ant-following birds. For example, in the Guyanas, where the density of *obligate* followers is relatively low (Fig. 3), population densities of *E. burchellii* also appear to be low (B. J. O'Shea, pers. comm.). Unfortunately, detailed data on the population densities of army-ants across their distributions are unavailable to the best of our knowledge. Higher elevation and drier forests around the periphery of Amazonia experience increased seasonality that could reduce the year-round availability of swarms.

It also remains to be seen if the evolution of army-ant-following had any demonstrable impact on rates of diversification or extinction in the lineages in which it evolved. Too few independent contrasts were available in the current analysis to address these issues with statistical power, so a future test is dependent on the availability of well-supported phylogenies of other bird families containing army-ant-following species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2007.07.019.

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