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Phylogenetic signals in host–parasite associations for Neotropical bats and Nearctic desert rodents

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Hosts and their parasites have strong ecological and evolutionary relationships, with hosts representing habitats and resources for parasites. In the present study, we use approaches developed to evaluate the statistical dependence of species trait values on phylogenetic relationships to determine whether host–parasite relationships (i.e. parasite infections) are contingent on host phylogeny. If host–parasite relationships are contingent on the ability of hosts to provide habitat or resources to parasites, and if host phylogeny is an effective surrogate for among-host variation in habitat and resource quality, host–parasite relationships should evince phylogenetic signals (i.e. be contingent on host phylogeny). Because the strength of ecological relationships between parasites and their hosts may affect the likelihood of phylogenetic signals occurring in host–parasite relationships, we hypothesized that (1) host specificity would be positively correlated with the strength of phylogenetic signals and (2) the strength of phylogenetic signals will be greater for parasites that rely more on their host throughout their life cycle. Analyses were conducted for ectoparasites from tropical bats and for ectoparasites, helminths, and coccidians from desert rodents. Phylogenetic signals were evaluated for parasite presence and for parasite prevalence. The frequency of phylogenetic signal occurrence was similar for parasite presence and prevalence, with a signal detected in 24–27% of cases at the species level and in 67% and 15% of cases at the genus level for parasites of bats and rodents, respectively. No differences in signal strength or the likelihood of detecting a signal existed between groups of parasites. Phylogenetic signal strength was correlated with host specificity, suggesting that mechanisms increasing host specificity also increase the likelihood of a phylogenetic signal in host use by parasites. Differences in the transmission mode did not affect signal strength or the likelihood of detecting a signal, indicating that variation in host switching opportunities associated with the transmission mode does not affect signal strength. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **116**, 312–327.

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INTRODUCTION

Hosts and their parasites form coevolutionary relationships or exhibit co-adaptation (Kim, 1985; Poulin, 2011). As such, host–parasite interactions result in complex evolutionary systems in which phylogenetic signals (i.e. ecological similarity among species that is related to phylogenetic relationships) may manifest for parasite traits, for host traits or for properties of the coevolved association (Poulin, Krasnov & Moulliot, 2011a). The inclusion of host phylogenetic information has advanced the understanding of variation in parasite community composition among host species (Morand & Harvey, 2000; Krasnov *et al.*, 2004, 2010), with parasite communities being molded by combinations of geographical, phylogenetic, ecological, and developmental characteristics of their hosts (Locke, McLaughlin & Marcogliese, 2013). As in other systems, variation exists in the relative contribution of these sets of host characteristics to parasite community composition.

Strong coevolutionary relationships often lead to high host specificity, the degree to which parasites are restricted to particular species of hosts (Dick &

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Patterson, 2007; Poulin *et al.*, 2011b). However, host specificity is not necessarily coupled with cospeciation because parasites may exhibit host switching, leading to a lack of congruence between the phylogeny of the hosts and that of their parasites (Poulin, 2011). Nonetheless, patterns of host specificity (Dick & Patterson, 2007; Poulin *et al.*, 2011b) and host susceptibility (Woolhouse *et al.*, 2002) that are associated with phylogenetic relationships of hosts document the potential for host–parasite associations to evince phylogenetic signals. If aspects of host–parasite relationships, such as parasite prevalence or density, are contingent on the ability of the parasite to effectively use the habitats or resources provided by the host, and if similarity among hosts in the habitats and resources they provide is associated with host phylogenetic relationships, then phylogenetic signals in aspects of host–parasite relationships will reflect the degree to which phylogenetically conserved host traits mold patterns of host use by parasites.

Host phylogenetic information has been increasingly incorporated into comparative studies of parasites, although this has generally focused on evaluations of distance–decay relationships (Krasnov *et al.*, 2010; Poulin, 2010a), network analysis (Poulin, 2010b; Krasnov *et al.*, 2012) or metacommunity structure (Dallas & Presley, 2014). Distance–decay relationships determine how differences in parasite community composition relate to phylogenetic distances between hosts. However, this approach does not explicitly evaluate the extent to which variation in host–parasite associations is dependent on host phylogenetic relationships (i.e. the strength of phylogenetic signals in host–parasite associations). Because parasites represent a large proportion of species and biodiversity in any ecosystem (Dobson *et al.*, 2008), and because hosts provide habitat and resources for their parasite faunas, evaluating the phylogenetic signals of such symbiotic associations may have important implications for understanding biodiversity dynamics in space and time.

The previous two decades have seen a proliferation of studies that incorporate evolutionary perspectives to understand ecological phenomena (Losos, 2008; Cavender-Bares *et al.*, 2009; HilleRisLambers *et al.*, 2012). The focus of much of this work has evaluated associations between phylogenetic relationships and ecological traits of species (Losos *et al.*, 2003; Revell, Harmon & Collar, 2008; Graham *et al.*, 2012; Díaz *et al.*, 2013; Pearman *et al.*, 2014). These relationships can be grouped into four commonly occurring patterns: (1) niche conservatism, closely-related species are more ecologically similar than expected based on phylogenetic relationships; (2) phylogenetic signals, ecological similarity that is related to phylogenetic relationship (i.e. the expected outcome of a Brownian motion model); (3) random patterns, no relationship between ecological similarity and phylogenetic relationship; and (4) convergent evolution, ecologically similar species are more distantly related than expected based on phylogenetic relationships.

According to a Brownian motion model, the state of a trait can change during each instant in time, with the magnitude and direction of change being independent of the current state of the trait, with a net expected change through time of zero (Felsenstein, 1988; O'Meara *et al.*, 2006). When evolution occurs as a result of Brownian motion (or phylogenetic inertia), trait differences between species are proportional to the phylogenetic branch lengths that separate them (Felsenstein, 1985, 2004). This relationship represents a phylogenetic signal or phylogenetic effect (Freckleton, Harvey & Pagel, 2002; Revell *et al.*, 2008). Mechanisms that cause systematic deviations from the assumptions of a Brownian model, such as convergent evolution, stabilizing selection or a high rate of change in selection pressures or evolutionary constraints, will suppress the occurrence of a phylogenetic signal (Losos, 2011). A phylogenetic signal for host–parasite associations would be indicative of the suitability of hosts for a parasite being proportional to the phylogenetic distances between host species.

Phylogenetic signals for host–parasite associations may be pervasive, rare or contingent on host group, parasite group or environmental context. We measured phylogenetic signal strength for parasite presence and prevalence separately for each species of parasite, and determined the pervasiveness of these signals for two groups of host (Neotropical bats and Nearctic desert rodents) and for three groups of parasites (arthropod ectoparasites, helminths, and coccidians). In addition, we addressed two hypotheses to determine whether the strength of ecological relationships between parasites and their hosts affect the likelihood of evincing a phylogenetic signal. First, because closely-related hosts should provide similar habitats and resources for parasites, and because host specificity effectively is a measure of resource specialization, we predict that phylogenetic signal strength should be correlated positively with host specificity. Second, the transmission mode may determine the likelihood of host switching (Poulin, 2011), which would affect the strength or occurrence of a phylogenetic signal in host–parasite associations. Helminths have relatively complex life cycles that include intermediate hosts, whereas coccidians produce sporulated oocysts that can survive in the environment for years without a host. The use of intermediate hosts and oocysts are life cycle stages that are disassociated from the mammalian host, which provide opportunities to encounter different mammalian species that

represent potential hosts. Consequently, helminths and coccidians have greater potential for host switching at evolutionary time scales compared to the life histories of arthropod ectoparasites on rodents. The ectoparasite fauna of bats can be divided into two groups: those that have reduced life cycles that are completed entirely on the host (i.e. polyctenid bat bugs, spinturnicid wing mites, chirodiscid mites, and myobiid mites) and those that become disassociated from the hosts during at least one stage in the life cycle. We predict that opportunities for host switching associated with mode of parasite transmission have a negative effect on the strength or occurrence of a phylogenetic signal (i.e. phylogenetic signals will be stronger and more common for parasite groups with few opportunities for host switching compared to parasite groups with transmission modes that facilitate host switching).

MATERIAL AND METHODS

Paraguayan bats and their ectoparasites

Bats and their ectoparasites were collected from 28 sites throughout Paraguay from 1995 to 1998 (Presley & Willig, 2008). Protocols for collection and processing were designed to minimize the likelihood of contamination (i.e. assignment of ectoparasites to the wrong host individual). Research involving live animals conformed to the guidelines of the American Society of Mammalogists (Sikes, Gannon & Animal Care and Use Committee of the American Society of Mammalogists, 2011) and was approved by the Animal Care and Use Committee of Texas Tech University. Details about collection, identification, and deposition of specimens are available elsewhere (Willig *et al.*, 2000; Presley, 2004; Presley & Willig, 2008).

A total of 2908 bats, representing 41 species and four families (Phyllostomidae, 14 species; Noctilionidae, two species; Molossidae, 14 species; and Vespertilionidae, 11 species) were inspected for ectoparasites. Collections resulted in 17 536 individuals and 95 species of arthropod ectoparasite (Presley, 2004), including bat flies (Nycteribiidae, Streblidae), bat bugs (Polyctenidae), fleas (Ischnopsyllidae), ticks (Argasidae, Ixodidae), and mites (Chirodiscidae, Macronyssidae, Myobiidae, Spinturnicidae, Trombiculidae). In South America, these arthropod groups differ in their level of host specificity and in the number of host families with which they are associated. Most bat flies, bat bugs, and fleas are highly host specific, typically occurring on a single host species or genus (Presley, 2004; Dick & Gettinger, 2005; Graciolli, Dick & Gettinger, 2006; Dick, 2007; Dick & Patterson, 2007). By contrast, host specificity of mites and ticks from bats is more variable than that of their insect counterparts (Presley, 2004).

Sevilleta rodents and their parasites

Rodent and parasite data (http://sev.lternet.edu/data/sev-13) were collected as part of the Sevilleta Long-Term Ecological Research project, located in central New Mexico. Data are from 1992 to 1997, and represent 2547 individuals, 15 species, and three families (Cricetidae, Heteromyidae, and Sciuridae) of host that were parasitized by 26 species of coccidians, 26 species of helminths, and 28 species of ectoparasites. Endo- and ectoparasites were examined by necropsy (Duszynski & Wilber, 1997), including host coat, stomach, intestines, body cavity, and faeces. Parasites included coccidians (Eucoccidiorida), acanthocephalans (Moniliformida), tapeworms (Cyclophyllidea), nematodes (Ascaridida, Oxyurida, Rhabditida, Spirurida, Strongylida, and Trichurida), and arthropods (Siphonaptera, Phthiraptera, and Diptera). At Sevilleta, arthropod ectoparasites exhibited host specificity (occurring on one species or genus of host) more often than did coccidians or helminths; however, each group comprised species that were associated primarily with cricetids, primarily with heteromyids or were broadly distributed among all families of rodents (Dallas & Presley, 2014).

Mammalian phylogeny

A species-level supertree for mammals (Bininda-Emonds *et al.*, 2007) was the basis for estimating phylogenetic relationships for each host group. Two bat species (*Lasiurus blossevillii* and *Eumops patagonicus*) from Paraguay were not represented in the supertree; each of their positions in the phylogeny was estimated by a closely-related congener that was not already present in the study area (*Lasiurus egregius* and *Eumops hansae*, respectively). The effects of these substitutions on the detection of phylogenetic signals are probably small because the lengths of terminal branches for congeners are generally the same or differ little within the context of tree height (i.e. distance from root to tips), resulting in highly similar pairwise distances between congeners and all other species in a phylogeny.

Analysis of phylogenetic signals

Phylogenetic signals of host–parasite associations were evaluated separately based on parasite presence (binary data) or prevalence (continuous data). If a parasite species was recorded from any individual of a host species, the parasite was considered to

have an association with that host species. However, nonprimary host–parasite associations, transient associations or contamination could potentially bias results as a single occurrence is indistinguishable from a primary association based on binary data. In addition, the likelihoods of detecting transients or contamination are correlated positively with the number of hosts inspected for parasites. Prevalence is the number of host individuals of a particular species that are infected with one or more individuals of a particular parasite taxon, divided by the number of host individuals examined for parasites (Bush *et al.*, 1997). As such, prevalence is less susceptible to biases associated with transients or contamination or with differences in number of host individuals that have been inspected for parasites.

Phylogenetic signals are difficult to detect for parasites that occur on only one host species (i.e. monoxenous parasites) because the value for the host–parasite association is the same for all but one species (i.e. 0). Many parasites of Paraguayan bats (41 of 95) or of Sevilleta rodents (33 of 80) were recorded from a single host species. Often, congeners that are highly host specific occur on closely-related host species. Consequently, phylogenetic signals for host–parasite associations may manifest at the level of parasite genus rather than parasite species. We evaluated the strength of phylogenetic signals for the presence and prevalence of each parasite species and of each parasite genus that was represented by multiple species.

Detailed assessments of the strengths and weaknesses of metrics that estimate the strength of phylogenetic signals (i.e. a measure of the statistical dependence of values on phylogenetic relationships; Revell *et al.*, 2008) revealed that Pagel's λ (Pagel, 1999; Freckleton *et al.*, 2002) performed well under a Brownian motion model, provided reliable effect size measures, and performed better than alternative metrics (e.g. Blomberg's *K*; Blomberg, Garland & Ives, 2003) in discriminating between complex models of trait evolution (Münkemüller *et al.*, 2012). We used Pagel's λ to evaluate phylogenetic signals based on parasite prevalence. The *D*-statistic estimates phylogenetic signals in binary traits (Fritz & Purvis, 2010) and was used to evaluate signals based on parasite presence. Each approach compares an empirical trait distribution on a phylogenetic tree to simulated distributions based on a Brownian motion model (Felsenstein, 1985, 1988).

A maximum likelihood approach was used to estimate Pagel's λ based on the distribution of values (i.e. parasite prevalence) with respect to the corresponding phylogeny. If $\lambda = 0$, the distributions of values is independent of phylogeny (i.e. exhibit no phylogenetic signal). If $\lambda = 1$, the distribution of values is consistent with an evolutionary model of Brownian motion. A maximum likelihood ratio test was used to determine whether estimated values of λ differed significantly from 0, indicating the existence of a phylogenetic signal in parasite prevalence that is consistent with a Brownian motion model (Freckleton *et al.*, 2002).

The *D*-statistic provides an estimate of the strength of a phylogenetic signal in binary values that can be compared with a random rearrangement of values at the tips of a phylogeny and with a Brownian threshold model (Fritz & Purvis, 2010). If $D = 1$, values are randomly distributed at the tips of the phylogeny. If $D = 0$, the distribution of values correspond to a Brownian motion model of evolution. Significance was estimated by comparing estimates of *D* for the host associations of each parasite species with simulated distributions based on 1000 permutations of randomly shuffled values across the tips of the tree. Tests of phylogenetic signal were executed with the R packages *caper* (Orme *et al.*, 2013) and *phytools* (Revell, 2014). We considered a significant phylogenetic signal to be present for values of λ significantly > 0 and values of *D* significantly < 1.

We used Spearman rank correlations to determine whether phylogenetic signals based on presence and prevalence were independent, and to determine whether phylogenetic signals were associated with host specificity (S_{TD}*). S_{TD}* combines phylogenetic and ecological information to calculate host specificity for each ectoparasite species within the context of the entire host assemblage. S_{TD}* measures 'the average taxonomic distinctness of all host species used by a parasite species' (Poulin & Mouillot, 2005). Monoxenous parasites have an S_{TD}* of 0; oligoxenous parasites occur on multiple species of the same genus and have an S_{TD}* of 1.0; and parasites that are less host specific have values > 1.0. We used an analysis of variance to determine whether phylogenetic signals (*D* and λ) were different between groups of parasites that differ in transmission modes. In addition, we used a chi-squared contingency test to determine whether the likelihood of a significant signal was contingent on parasite group. For Paraguayan bats, ectoparasites were grouped into species for which all life-history stages occur on the host vs. species for which some life-history stages occur off host. For Sevilleta rodents, parasites were grouped into coccidians, helminths, and arthropod ectoparasites. All analyses were conducted in R, version 3.0.1.

RESULTS

Parasite presence

For Paraguayan bats, ectoparasite presence exhibited a phylogenetic signal in 26 of 95 (27%) cases at the species level and in 14 of 21 (67%) cases at the

genus level (Fig. 1A, Table 1). Only two genera of ectoparasite did not evince a phylogenetic signal when such a signal was present for at least one species of that genus (macronyssid mites of the genus *Steatonyssus* and myobiid mites of genus *Ewingana*). By contrast, three genera of streblid bat fly (*Noctiliostrebla*, *Paradyschiria*, and *Strebla*) exhibited a phylogenetic signal when no signal occurred for a species within the genus.

For Sevilleta rodents, parasite presence exhibited a phylogenetic signal in 20 of 80 (25%) cases at the species level and in two of 13 (15%) cases at the genus level (Fig. 2A, Table 2). *Eimeria* occurred in every rodent species; such invariance cannot be evaluated for signal strength. Three parasite genera did not evince a phylogenetic signal despite a signal manifesting for at least one species from each of those genera: the coccidian genus *Eimeria*, the flea genus *Meringis*, and the louse genus *Neohaematopinus*. Only the tapeworm genus *Catenotaenia* exhibited a phylogenetic signal without a signal occurring for any constituent species.

Parasite prevalence

Ectoparasites from Paraguayan bats exhibited a phylogenetic signal for prevalence in 25 of 95 (26%) cases at the species level, and in 14 of 21 (67%) cases at the genus level (Fig. 1B, Table 1). Three species of *Trichobius* exhibited a signal for prevalence that did not manifest at the genus level. Six genera (three streblids, one nycteribiid, and two macronyssids) evinced a phylogenetic signal for prevalence when no species exhibited a signal within those genera.

Parasites of Sevilleta rodents exhibited a phylogenetic signal for prevalence in 19 of 80 (24%) cases at

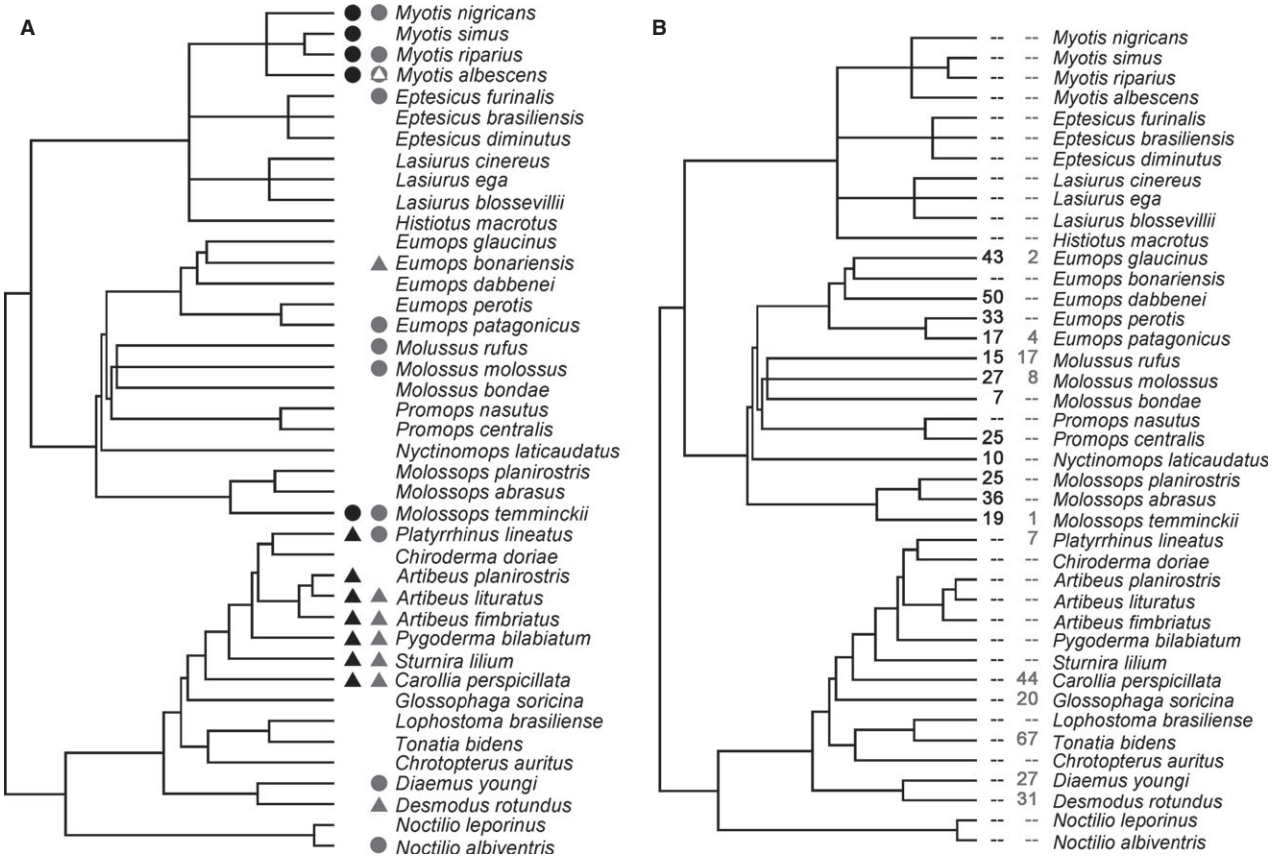

Figure 1. Phylogenetic trees for bats from Paraguay showing examples of phylogenetic signals for (A) parasite presence and for (B) prevalence. Black symbols (● or ▲) represent significant phylogenetic signals for a spinturnicid mite (*Spinturnix americanus*) and a macronyssid mite (*Macronyssoides kochi*), respectively. Grey symbols (● and ▲) represent random associations with phylogeny for the macronyssid mites *Macronyssus crosbyi* and *Parichoronyssus euthysternum*, respectively. Both *M. crosbyi* and *P. euthysternum* occurred on *Myotis albescens*, as indicated by △. Black numbers represent significant phylogenetic signals in prevalence for bat bugs of the genus *Hesperoctenes*, and grey numbers represent random associations with phylogeny for bat flies of the genus *Trichobius*. Prevalence was rounded to the nearest percentile, with two dashes (--) indicating hosts on which the parasite did not occur.

Table 1. Results for analyses of phylogenetic signals for associations of arthropod ectoparasites with bat hosts based on parasite presence or prevalence

		Presence		Prevalence	
Ectoparasite taxon	Hosts	*D*	Pr(*D* = 1)	λ	Pr(λ = 0)
Streblidae					
Aspidoptera	5	−0.94	**0.001**	0.13	0.251
Aspidoptera falcata	4	0.15	0.075	0.00	1.000
Aspidoptera phyllostomatis	3	−2.29	**0.001**	0.08	0.490
Mastoptera minuta	1	−12.99	0.720	0.00	1.000
Megistopoda	6	−0.89	< **0.001**	0.16	0.182
Megistopoda aranea	4	−1.41	**0.001**	0.07	0.529
Megistopoda proxima	5	−0.03	**0.031**	0.00	1.000
Metelasmus	4	−1.23	**0.002**	0.02	0.857
Metelasmus pseudopterus	3	−2.17	**0.002**	0.01	0.933
Metelasmus paucisetus	1	−9.09	0.363	0.00	1.000
Noctiliostrebla	3	−1.63	**0.001**	0.95	< **0.001**
Noctiliostrebla aitkeni	2	0.19	0.164	0.13	0.796
Noctiliostrebla dubia	1	−42.99	0.059	0.13	0.797
Noctiliostrebla maai	1	−5.37	0.061	0.13	0.797
Paradyschiria	2	−4.19	< **0.001**	1.00	< **0.001**
Paradyschiria fusca	1	−188.95	0.078	0.13	0.797
Paradyschiria parvula	1	−20.23	0.069	0.13	0.797
Paratrichobius longicrus	3	0.94	0.420	0.00	1.000
Speiseria ambigua	1	38.04	0.144	1.06	< **0.001**
Strebla	7	−0.03	**0.013**	1.06	< **0.001**
Strebla chrotopteri	1	−11.86	0.229	0.00	1.000
Strebla diaemi	2	0.53	0.218	0.00	1.000
Strebla guajiro	3	0.15	0.083	0.00	1.000
Strebla weidemanni	1	−7.75	0.146	0.00	1.000
Trichobius	12	0.74	0.184	0.35	0.103
Trichobius angulatus	1	22.04	0.866	0.00	1.000
Trichobius diaemi	1	−16.65	0.153	0.00	1.000
Trichobius dugesii	1	−99.32	0.109	1.06	< **0.001**
Trichobius joblingi	2	0.30	0.199	0.02	0.848
Trichobius jubatus	5	0.30	0.097	1.06	< **0.001**
Trichobius parasiticus	1	−16.81	0.132	0.00	1.000
Trichobius uniformis	1	−58.51	0.139	1.06	< **0.001**
Xenotrichobius noctilionis	1	−10.04	0.071	0.13	0.797
Polyctenidae					
Hesperoctenes	12	−1.07	< **0.001**	1.06	< **0.001**
Hesperoctenes angustatus	1	−0.31	0.464	0.00	1.000
Hesperoctenes cartus	1	−1.75	0.357	0.00	1.000
Hesperoctenes fumarius	3	−1.42	**0.003**	1.06	< **0.001**
Hesperoctenes longiceps	1	−5.45	0.310	0.00	1.000
Hesperoctenes minor	1	−1.27	0.354	0.00	1.000
Hesperoctenes parvulus	1	−14.16	**0.027**	0.00	1.000
Hesperoctenes setosus	1	−22.24	< **0.001**	1.06	< **0.001**
Hesperoctenes sp1	2	−0.64	0.052	1.06	< **0.001**
Hesperoctenes sp2	1	−5.82	0.290	0.00	1.000
Hesperoctenes sp3	2	0.44	0.195	1.06	< **0.001**
Nycteribiidae					
Basilia	8	−0.68	< **0.001**	0.54	< **0.001**
Basilia bequaerti	2	2.09	0.855	0.00	1.000
Basilia carteri	4	−0.59	**0.007**	0.35	0.056

Table 1. *Continued*

Ectoparasite taxon	Hosts	Presence		Prevalence	
		D	Pr(*D*) = 1	λ	Pr(λ) = 0
Basilia juquiensis	1	97.75	0.731	0.00	1.000
Basilia plaumanni	3	−1.05	**0.010**	0.11	0.427
Basilia speiseri	2	−1.72	**0.024**	0.04	0.769
Ischnopsyllidae					
Hormopsylla fosteri	1	−27.41	< **0.001**	1.06	< **0.001**
Myodopsylla wolffsohni	2	−1.51	**0.017**	0.00	1.000
Rothschildopsylla noctilionis	1	−18.59	< **0.001**	1.06	< **0.001**
Spinturnicidae					
Periglischrus	17	0.24	**0.005**	0.67	< **0.001**
Periglischrus caligus	1	−12.45	0.110	1.06	< **0.001**
Periglischrus herrerai	3	0.65	0.246	0.00	1.000
Periglischrus iheringi	11	−0.41	< **0.001**	1.06	< **0.001**
Periglischrus ojasti	7	0.17	**0.033**	0.00	1.000
Periglischrus tonatii	1	4.26	0.670	0.00	1.000
Spinturnix	7	−0.27	**0.002**	0.14	0.285
Spinturnix americanus	5	−1.69	< **0.001**	0.10	0.480
Spinturnix banksi	1	−5.44	0.413	0.00	1.000
Spinturnix orri	2	2.45	0.941	0.00	1.000
Spinturnix surinamensis	1	−0.17	0.502	0.00	1.000
Macronyssidae					
Chiroptonyssus	28	0.17	**0.004**	1.06	< **0.001**
Chiroptonyssus haematophagus	23	0.50	**0.040**	1.04	< **0.001**
Chiroptonyssus robustipes	6	0.94	0.405	1.01	< **0.001**
Chiroptonyssus venezolanus	11	0.49	0.054	1.06	< **0.001**
Chiroptonyssus sp1	12	1.61	0.740	0.00	1.000
Macronyssoides	8	−0.52	< **0.001**	0.71	< **0.001**
Macronyssoides conciliatus	3	1.88	0.960	0.00	1.000
Macronyssoides kochi	7	−1.15	< **0.001**	0.85	**0.002**
Macronyssoides sp1	1	−16.92	0.195	0.00	1.000
Macronyssus	14	0.88	0.306	0.78	< **0.001**
Macronyssus crosbyi	11	1.08	0.561	0.18	0.304
Macronyssus meridionalis	4	0.32	0.106	0.04	0.674
Macronyssus sp2	1	−121.66	0.430	0.00	1.000
Macronyssus sp3	3	1.25	0.617	0.00	1.000
Parichoronyssus	12	0.58	0.099	1.06	< **0.001**
Parichoronyssus crassipes	4	0.58	0.189	0.00	1.000
Parichoronyssus cyrtosternum	1	1.19	0.535	0.00	1.000
Parichoronyssus euthysternum	8	0.71	0.211	0.00	1.000
Parichoronyssus sclerus	2	0.60	0.269	0.00	1.000
Radfordiella	2	−4.07	< **0.001**	1.06	< **0.001**
Radfordiella desmodi	2	0.44	< **0.001**	1.06	< **0.001**
Radfordiella oudemansi	1	−30.02	0.132	0.00	1.000
Steatonyssus	18	0.55	0.071	0.96	< **0.001**
Steatonyssus furmani	6	1.08	0.535	0.16	0.424
Steatonyssus joaquimi	14	0.62	0.099	1.06	< **0.001**
Steatonyssus sp1	2	−5.10	< **0.001**	0.38	0.083
Steatonyssus sp2	3	−0.28	**0.042**	0.00	1.000
Argasidae					
Ornithodoros hasei	20	0.33	**0.011**	0.84	< **0.001**
Ixodidae					
Amblyomma sp1	2	−1.48	**0.017**	1.06	< **0.001**

Table 1. *Continued*

Ectoparasite taxon	Hosts	Presence		Prevalence	
		D	Pr(*D*) = 1	λ	Pr(λ) = 0
Rhipicephalus sp1	2	0.86	0.416	0.00	1.000
Trombiculidae					
Beamerella acutascuta	7	1.35	0.813	0.00	1.000
Euschoengastia megastyrax	1	−15.78	0.800	0.00	1.000
Eutrombicula sp1	1	−19.34	0.348	0.00	1.000
Hooperella vesperuginus	2	2.05	0.844	1.06	< **0.001**
Trombicula	7	1.03	0.494	0.00	1.000
Trombicula dicrura	3	1.35	0.693	0.00	1.000
Trombicula sp1	1	−305.45	0.225	0.00	1.000
Trombicula sp2	6	0.97	0.424	0.00	1.000
Chirodyssidae					
Labidocarpus sp1	2	2.10	0.829	0.00	1.000
Lawrenceocarpus sp1	2	1.38	0.689	0.12	0.873
Perisopalla precaria	1	−3.92	0.345	0.00	1.000
Parkosa	9	0.78	0.234	0.97	**0.002**
Parkosa maxima	5	0.55	0.142	1.02	< **0.001**
Parkosa tadarida	7	0.61	0.165	0.92	**0.022**
Pseudolabidocarpus sp1	2	−0.89	**0.030**	1.06	< **0.001**
Myobiidae					
Eudusbabekia	5	−1.20	**0.001**	0.22	0.098
Eudusbabekia lepidoseta	1	−4.56	0.343	0.00	1.000
Eudusbabekia viguerasi	3	−2.12	**0.002**	0.16	0.263
Eudusbabekia sp1	1	−27.22	0.198	0.00	1.000
Ewingana	2	−0.61	0.081	1.06	< **0.001**
Ewingana sp1	1	−8.06	0.298	0.00	1.000
Ewingana sp2	1	−55.69	< **0.001**	1.06	< **0.001**

Parasite presence: a parasite occurs on at least one individual of a host species or it does not. Parasite prevalence: the percentage of individuals of each host species on which a parasite occurs. Analyses were conducted for each ectoparasite species and for each ectoparasite genus represented by multiple species. Hosts: number of bat species with which an ectoparasite species or genus was associated. *D* is an estimate of phylogenetic signal based on presence data; *D* = 1 corresponds to a random pattern; *D* = 0 corresponds to a Brownian model. Pr(*D*) = 1 is probability that the signal is random for ectoparasite presences. λ estimates the phylogenetic signal based on prevalence data; λ = 0 corresponds to a random pattern; λ = 1 corresponds to a Brownian model. Pr(λ) = 0 is probability that the signal is random for ectoparasite prevalences. Significant ($P \leq 0.05$) deviations from randomness are bold. Ectoparasite taxa that occur on a single host species (Hosts = 1) often have little power to detect a phylogenetic signal.

the species level and in two of 13 cases (15%) at the genus level (Fig. 2B, Table 2). Nine parasite species exhibited a phylogenetic signal for prevalence that did not manifest for the corresponding genera, including six coccidians (congeners of *Eimeria*), two fleas (*Meringis nidi* and *Oropsylla idahoensis*), and one louse (*Neohaematopinus spilosomae*). Each parasite genus that exhibited a phylogenetic signal for prevalence also contained species that exhibited a signal.

Comparison of signals for presence and prevalence

For bat ectoparasites, 56 of 95 (59%) species did not exhibit a phylogenetic signal regardless of approach and only 12 (13%) species exhibited a phylogenetic signal via both approaches. For the majority of species (72%), no difference in the ability to detect a phylogenetic signal existed based on data type (i.e. binary vs. continuous). Of the remaining 27 species, 14 only exhibited a phylogenetic signal for parasite presence and 13 only exhibited a phylogenetic signal for prevalence (Table 1). By contrast, only two of 21 genera did not exhibit a phylogenetic signal regardless of approach, nine genera exhibited a signal for both approaches, five genera exhibited a signal only for presence, and five genera exhibited a signal only for prevalence.

For rodent parasites, 49 of 80 (61%) species did not exhibit a significant a phylogenetic signal regardless

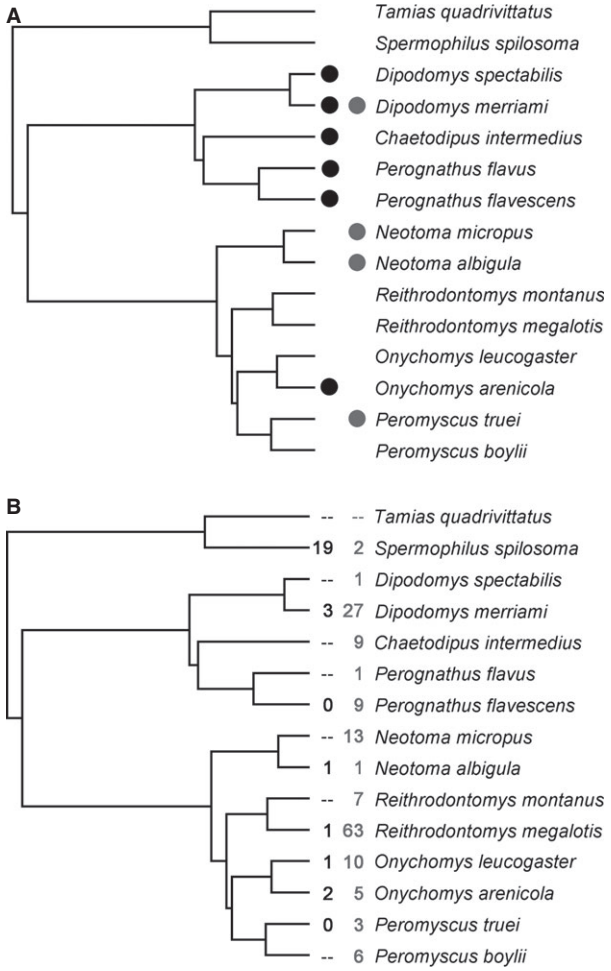

Figure 2. Phylogenetic trees for rodents from the Sevilleta Long-Term Ecological Research site in New Mexico showing examples of phylogenetic signals for (A) parasite presence and for (B) parasite prevalence. Black symbols (●) and numbers represent significant phylogenetic signals or a louse (*Fahrenholzia pinnata*) and a nematode (*Physaloptera massino*), respectively. Grey symbols (●) and numbers represent random associations with phylogeny for a flea (*Anomiopsyllus novomexicanesis*) and nematode (*Mastophoros dipodomis*), respectively. Prevalence was rounded to the nearest percentile, with two dashes (--) indicating hosts on which the parasite did not occur and 0 indicating hosts with a prevalence between 0.0 and 0.5.

of approach and eight species exhibited a signal via both approaches, indicating that, for most species (71%), the ability to detect a phylogenetic signal was not contingent on approach. Of the remaining 23 species, 11 only exhibited a phylogenetic signal for parasite presence and 12 only exhibited a phylogenetic signal for prevalence (Table 2). By contrast, nine of 13 (69%) genera did not exhibit a phylogenetic signal regardless of approach, no genus exhibited a signal via both approaches, two genera exhibited a signal only for presence, and two genera exhibited a signal only for prevalence.

Host specificity and transmission mode

Phylogenetic signals based on presence (D) and prevalence (λ) were not correlated for parasites of bats ($\rho = -0.046$, $P = 0.627$) or rodents ($\rho = -0.091$, $P = 0.386$), indicating that each approach measured independent aspects of host–parasite associations. A phylogenetic signal based on presence was correlated positively with host specificity (S_{TD}*) for bats ($\rho = 0.705$, $P < 0.001$) and for rodents ($\rho = 0.315$, $P = 0.002$); however, a phylogenetic signal based on prevalence was not correlated with host specificity for either host group (bats, $\rho = 0.108$, $P = 0.229$; rodents, $\rho = 0.142$, $P = 0.173$). Ectoparasites that spend their entire life cycle on their bat hosts and those that have developmental stages off host did not evince differences in phylogenetic signal strength based on presence ($P = 0.420$) or prevalence ($P = 0.442$). In addition, the likelihood of a significant phylogenetic signal was not contingent on all life-history stages occurring on the host (presence, $\chi^2 = 0.04$, $P = 0.840$; prevalence, $\chi^2 = 0.58$, $P = 0.447$). Similarly, coccidian, helminth, and arthropod parasites from Sevilleta rodents did not exhibit differences in phylogenetic signal strength based on presence ($P = 0.412$) or prevalence ($P = 0.948$) and the likelihood of a significant signal was not contingent on group membership (presence, $\chi^2 = 2.38$, $P = 0.305$; prevalence, $\chi^2 = 0.24$, $P = 0.888$).

DISCUSSION

Hosts and their parasites often have strong ecological and evolutionary relationships that manifest via cospeciation, with phylogenetic relationships among parasites often mirroring those of their hosts (Hafner *et al.*, 1994, 2003). However, the congruence of host and parasite phylogenies is not universal; indeed, parasite phylogenies may show little concordance with those of their hosts (Caira & Jensen, 2001; Johnson, Adams & Clayton, 2002). The present study is the first to determine whether variation in aspects of host–parasite associations is contingent on host evolutionary relationships.

The presence of a phylogenetic signal was contingent on the aspect of the association (presence vs. prevalence). Of the 70 species and 23 genera of parasites that exhibited phylogenetic signals, 50 species and 14 genera only exhibited signals for one of the two approaches, with similar numbers of taxa

Table 2. Results for analyses of phylogenetic signals for associations of coccidian (Eucoccidiorida), helminth (Moniliformida, Cyclophyllidea, Ascaridida, Oxyurida, Rhabditida, Spirurida, Strongylida, and Trichurida), and arthropod (Siphonaptera, Phthiraptera, and Diptera) parasites with rodent hosts based on parasite presence or parasite prevalence

		Presence		Prevalence	
Parasite taxon	Hosts	D	Pr(D) = 1	λ	Pr(λ) = 0
Eucoccidiorida					
*Eimeria**	15	–	–	0.44	0.270
Eimeria albigulae	2	−1.80	**0.005**	1.09	< **0.001**
Eimeria arizonensis	3	−0.26	0.129	0.00	0.994
Eimeria balphai	3	−0.55	**0.050**	0.00	1.000
Eimeria callospermophili	2	0.63	0.167	0.98	0.149
Eimeria chaetodipi	1	0.79	0.404	1.09	< **0.001**
Eimeria chihuahuaensis	1	−1.27	0.257	0.00	1.000
Eimeria chobotari	10	0.44	0.145	0.00	1.000
Eimeria dipodomysis	2	0.12	0.070	0.09	0.717
Eimeria eremici	1	4.95	0.861	0.00	1.000
Eimeria hispidensis	1	0.48	0.392	1.09	< **0.001**
Eimeria knoxjonesi	1	5.62	0.881	0.00	1.000
Eimeria lachrymalis	1	4.71	0.848	0.00	1.000
Eimeria ladronensis	2	−2.06	**0.006**	0.00	1.000
Eimeria langebarteli	3	0.13	0.168	0.00	1.000
Eimeria leucopi	1	5.48	0.870	0.00	1.000
Eimeria liomysis	2	−2.06	**0.018**	0.00	1.000
Eimeria merriami	2	0.08	0.054	0.18	0.620
Eimeria mohavensis	1	−1.08	0.266	0.00	1.000
Eimeria onychomysis	2	−1.08	**0.029**	0.00	1.000
Eimeria perognathi	1	0.79	0.408	1.09	< **0.001**
Eimeria peromysci	4	−1.34	< **0.001**	0.03	0.929
Eimeria reedi	5	0.10	0.089	1.08	**0.004**
Eimeria scholtysecki	2	−2.08	**0.020**	0.00	1.000
Eimeria sevilletensis	2	−0.95	**0.038**	0.00	1.000
Eimeria tamiasciurus	1	−6.45	< **0.001**	1.09	< **0.001**
Isospora peromysci	1	5.98	0.862	0.00	1.000
Moniliformida					
Moniliformis clarki	8	0.94	0.428	0.00	1.000
Cyclophyllidea					
Catenotaenia	4	−0.53	**0.021**	0.00	1.000
Catenotaenia californica	1	−0.99	0.255	0.00	1.000
Catenotaenia peromysci	3	0.16	0.183	0.00	1.000
Hymenolepis citelli	2	0.67	0.167	0.98	0.149
Mathovetaenia dipodomi	2	−2.23	**0.019**	0.95	**0.019**
Oochoristica deserti	1	−1.34	0.270	0.00	1.000
Raillietina	2	0.82	0.231	0.00	1.000
Raillietina loeweni	1	−1.12	0.119	0.00	1.000
Raillietina retactalis	1	−0.94	0.251	0.00	1.000
Raillietina salmoni	1	−0.96	0.282	0.00	1.000
Raillietina selfi	1	−1.75	0.132	0.00	1.000
Taenia krabbei	1	−1.96	0.128	0.00	1.000
Ascaridida					
Aspicularis ackerti	3	−0.31	0.113	0.00	1.000
Oxyurida					
Citellina triradiata	1	−5.46	< **0.001**	1.09	< **0.001**
Heteroxynema cucullatum	2	1.32	0.678	1.09	< **0.001**
Heteromyoxyuris deserti	9	0.62	0.240	0.29	0.379

Table 2. *Continued*

Parasite taxon	Hosts	Presence		Prevalence	
		D	Pr(*D*) = 1	λ	Pr(λ) = 0
Syphacia	5	0.41	0.132	1.09	< **0.001**
Syphacia eutamii	3	1.33	0.611	1.09	< **0.001**
Syphacia peromysci	3	1.07	0.345	0.00	1.000
Rhabditida					
Heligmosomum polygyrum	6	1.25	0.632	0.00	1.000
Spirurida					
Gonglyonema peromysci	1	7.25	0.865	0.00	1.000
Mastophorus dipodomis	14	−6.44	< **0.001**	0.00	1.000
Physaloptera massino	8	1.93	0.959	1.05	**0.050**
Protospirura ascaroidea	8	1.04	0.510	0.00	1.000
Strongylida					
Nematodirus neotoma	1	−1.30	0.121	0.00	1.000
Pterygodermatites dipodomis	4	1.75	0.877	0.00	1.000
Trichurida					
Trichuris	2	−1.787	**0.017**	0.18	0.633
Trichuris dipodomis	2	−1.965	**0.026**	0.62	0.250
Trichuris elatoris	2	−1.918	**0.019**	0.00	1.000
Siphonaptera					
Amaradix euphorbi	1	5.88	0.874	0.00	1.000
Anomiopsyllus	4	0.52	0.296	0.00	1.000
Anomiopsyllus novomexicanensis	4	0.57	0.313	0.00	1.000
Anomiopsyllus nudatus mexicanus	1	−1.63	0.133	0.00	1.000
Echidnophaga gallinacea	7	−0.05	**0.032**	0.00	1.000
Malaraeus sinomus	3	−0.20	0.116	0.00	1.000
Meringis	3	0.29	0.090	0.00	1.000
Meringis altipectin	1	6.06	0.582	0.00	1.000
Meringis arachis	7	0.27	0.084	0.00	1.000
Meringis nidi	2	–0.83	**0.041**	1.09	**0.002**
Meringis parkeri	1	−1.09	0.243	0.00	1.000
Opisodasys robustus robustus	1	−1.24	0.150	0.00	1.000
Orchopeas	5	0.74	0.323	0.00	1.000
Orchopeas sexdentatus agilis	3	−0.24	0.100	0.00	1.000
Orchopeas caedens	2	0.77	0.190	0.00	1.000
Orchopeas leucopus	3	1.19	0.422	0.00	1.000
Oropsylla	4	1.76	0.857	0.00	1.000
Oropsylla idahoensis	3	1.03	0.333	1.08	**0.003**
Oropsylla montana	2	1.47	0.772	0.00	1.000
Thrassis	4	1.35	0.586	1.08	**0.004**
Thrassis aridis campestris	2	0.65	0.156	1.06	**0.021**
Thrassis bacchi consimilis	2	0.62	0.090	1.09	< **0.001**
Thrassis bacchi pansus	2	1.13	0.443	1.09	< **0.001**
Phthiraptera					
Enderleinellus suturalis	1	−5.82	< **0.001**	1.09	< **0.001**
Fahrenholzia pinnata	6	−0.70	**0.005**	0.96	**0.002**
Hoplopleura	4	0.99	0.432	0.00	1.000
Hoplopleura hesperomydis	1	5.37	0.864	0.00	1.000
Hoplopleura onychomydis	1	5.44	0.608	0.00	1.000
Hoplopleura reithrodontomydis	2	0.88	0.309	0.00	1.000
Neohaematopinus	2	0.63	0.123	0.00	1.000
Neohaematopinus neotomae	1	−1.45	0.130	0.00	1.000
Neohaematopinus spilosomae	1	−9.83	< **0.001**	1.09	< **0.001**

Table 2. *Continued*

Parasite taxon	Hosts	Presence		Prevalence	
		D	$Pr(D) = 1$	λ	$Pr(\lambda) = 0$
Polyplax auricularis	2	−0.86	**0.024**	0.00	1.000
Cuterebra	2	1.29	0.736	0.00	1.000
Cuterebra austeni	1	−1.57	0.141	0.00	1.000
Cuterebra neomexicana	1	5.38	0.856	0.00	1.000

Parasite presence: a parasite occurs on at least one individual of a host species or it does not. Parasite prevalence: the percentage of individuals of each host species on which a parasite occurs. Analyses were conducted for each ectoparasite species and for each ectoparasite genus represented by multiple species. Hosts: number of rodent species with which an ectoparasite species or genus was associated. D is an estimate of phylogenetic signal based on presence data; $D = 1$ corresponds to a random pattern; $D = 0$ corresponds to a Brownian model. $Pr(D) = 1$ is probability that the signal is random for ectoparasite presences. λ estimates the phylogenetic signal based on prevalence data; $\lambda = 0$ corresponds to a random pattern; $\lambda = 1$ corresponds to a Brownian model. $Pr(\lambda) = 0$ is probability that the signal is random for ectoparasite prevalences. Significant ($P \leq 0.05$) deviations from randomness are bold. Ectoparasite taxa that occur on a single host species (Hosts = 1) often have little power to detect a phylogenetic signal.
*Eimeria occurred on all rodents from Sevilleta. Invariant presence data will not return a result in the R package *caper*.

exhibiting signals only for parasite presence (26 species and seven genera) or only for prevalence (24 species and seven genera). Parasites could exhibit signals for presence but not prevalence if they occurred only on closely-related hosts, although variation in prevalence was not associated with host phylogeny. This situation typically arises when parasites have a high prevalence for one or more host species, with a low prevalence for congeners or confamilials of those primary hosts. In such cases, the likelihood of transient associations (i.e. positive presence but low prevalence) is related to host phylogeny. By contrast, parasites could exhibit signals for prevalence but not for presence. This situation typically arises if a high prevalence characterizes a group of closely-related host species, although transient associations are not related to host phylogeny, with the parasite having low prevalence on a random selection of distantly-related host species.

The transmission mode can affect the opportunity, frequency or ability of a parasite to switch hosts. Parasites with life-history stages that are not associated with the host or parasites with complex life cycles that include intermediate hosts have more opportunities to switch hosts. This may decrease phylogenetic congruence between hosts and their parasites, and reduce the likelihood that phylogenetic signals arise (Losos, 2011). Nonetheless, there was no difference in phylogenetic signal strength, or in the likelihood of a phylogenetic signal, between groups of parasites that differ in life-cycle characteristics that may affect the transmission mode and host switching potential. This may be expected because bats and their ectoparasites are remarkably host-specific despite opportunities to encounter new hosts (Dick, 2007; Dick & Patterson, 2007). For rodent parasites, 33 of 80 taxa occurred on one host species and 66 parasites occurred on three or fewer host species, despite five to 10 (mean of 7.75) species of host being recorded from each site. This indicates that local sympatry of host species has little effect on the number of infected hosts. In addition, metacommunity dynamics for the parasites of Sevilleta rodents are primarily driven by variation in host traits that define the environment for parasites and not by host phylogeny or transmission opportunities afforded by the host (Dallas & Presley, 2014). Consequently, environmental filters associated with the host may result in unsuccessful transmission regardless of the potential for ecological characteristics of parasites or of host sympatry to facilitate transmission.

Phylogenetic signals by host or parasite group

Phylogenetic signals of host–parasite relationships occurred for each family of Paraguayan bat (i.e. phylogenetic signals arose because of associations restricted to particular host families). Moreover, the number of signals associated with each host family was positively related to the species richness of the family: 30 signals were associated with 16 phyllostomids, 22 signals with 14 molossids, 10 signals with 11 vespertilionids, and three signals with two noctilionids. Similarly, phylogenetic signals of host–parasite relationships occurred for each family of rodent; however, signals were more common for families of rodents that were species poor, with 17 signals associated with two sciurids, 15 signals associated with

five heteromyids, and only seven signals associated with eight cricetids. Nonetheless, in each case, the parasites of the most basal clade of hosts (i.e. phyllostomid bats and sciurids rodents) (Figs 1, 2) exhibited the greatest number of phylogenetic signals, suggesting that the evolutionary age of a clade has a greater effect on phylogenetic signals than does richness of the clade.

Phylogenetic signals for parasite presence or prevalence characterized each major group of parasites on bats or rodents, with no differences in signal strength or likelihood between parasite groups. This suggests that symbiotic relationships and co-evolutionary processes necessary to produce phylogenetic signals are of similar importance for each group. In addition, signals for parasite species occurred at similar frequencies for each group of hosts (27% and 26% of analyses for presence and prevalence on bats, respectively, and 25% and 24% of analyses for presence and prevalence on rodents, respectively). By contrast, signals for parasite genera were more frequent for bats (67% of analyses for presence or for prevalence) than for rodents (15% of analyses for presence or for prevalence). This difference indicates that congeneric ectoparasites of bats occur on closely-related hosts in Paraguay more often than do congeneric parasites of rodents in Sevilleta. Importantly, these patterns are only associated with the species pools of the geographical region under consideration for each host group. The results of an analysis of the same parasites for the entire rodent fauna of temperate North America or for the entire bat fauna from the Neotropics may differ for two reasons. First, any change in species pool will change the structure of the tree from which estimates host phylogenetic relationships are derived and therefore the magnitude of the phylogenetic signal for host–parasite associations. Second, parasite species and genera may have relationships with host species that are not included in the current analysis. Consequently, care must be used when extrapolating empirical patterns beyond the study system that is the basis for analysis.

Phylogenetic signals only for parasite presence

The absence of a phylogenetic signal for parasite prevalence when one exists for parasite presence indicates that nonprimary hosts generally are close relatives of primary hosts. This may arise because closely-related hosts have similar physiology or immunology or because they provide similar habitats and resources. These types of similarities between hosts may allow sink populations of parasites to persist on nonprimary hosts. This combination of phylogenetic signals was not unique to a particular group of parasites. It occurred for coccidians, nematodes, tapeworms, lice, and fleas on rodents, and for bat flies, bat bugs, fleas, and three families of mites on bats. Such ubiquity for parasite groups that differ in ecology (e.g. dispersal mode, reproductive rate, location on host, use of intermediate hosts) suggests that similar patterns of presence and prevalence may occur despite difference in the proximal mechanisms affecting the distribution and abundance of ectoparasites, intestinal helminths or intracellular parasites (coccidians). In general, parasite species that only exhibited signals for parasite presence were associated with congeners of bats or congeners of rodents.

An alternative explanation for host–parasite relationships that exhibit a signal for presence but not for prevalence is that a putative species of parasite may actually represent a species complex comprising cryptic species. This requires all but one species in the complex to have low prevalence; otherwise, a signal for prevalence also would occur. Importantly, such parasite taxa represent cryptic species complexes; the results of our species-level analyses would often represent a generic-level analysis for a species complex.

Phylogenetic signals only for prevalence

The absence of a phylogenetic signal for parasite presence, even though a signal existed for prevalence, suggests that nonprimary hosts occur at random with respect to host phylogeny. Consequently, hosts that are closely related to primary hosts are no more susceptible to infection than are distantly-related hosts. Parasites with this combination of results generally exhibited one of four patterns: (1) occurred only on a genus represented by one species at the study site (*Glossophaga soricina*, *Chaetodipus intermedius*); (2) a high prevalence on a genus represented by only one species (*Spermophilus spilosoma*, *Tamias quadrivittatus*), with a low prevalence on distantly-related species; (3) a high prevalence on multiple species of a genus (*Molossus*, *Eumops*), with a low prevalence on other members of the same host family; or (4) a high prevalence on closely-related species from the same subfamily (Phyllostominae) or family (Molossidae, Vespertilionidae, Heteromyidae, Sciuridae), with a low prevalence on more distantly-related hosts. A signal for prevalence but not for presence was not restricted to a particular group of parasites but occurred for coccidians, nematodes, and fleas on rodents, and for bat flies, bat bugs, and five families of mites on bats. Again, similar patterns of parasite distribution and abundance among hosts occurred despite differences in the ecology of

arthropod ectoparasites, intestinal helminths, and intracellular parasites.

Phylogenetic signals for monoxenous parasites

Although phylogenetic signals are difficult to detect for monoxenous parasites, signals did occur for seven monoxenous parasites of Sevilleta rodents and for nine monoxenous parasites of Paraguayan bats (Tables 1, 2). In each case, the time of divergence between the host and its sister taxon in the assemblage was the longest of any host in the species pool. For example, the divergence time to the sister taxon for *Nyctinomops laticaudatus* is the longest of any bat in the Paraguayan assemblage (Fig. 1); the divergence time to the sister taxon of *G. soricina* is the longest for any phyllostomid in the Paraguayan assemblage; and the divergence time to the sister taxon of *C. intermedius* is the longest for any rodent in the Sevilleta assemblage (Fig. 2).

If congeneric monoxenous parasites occur on closely-related hosts, phylogenetic signals may manifest at the generic level for parasites. For example, streblid bat flies are noteworthy for the high proportion of species that are monoxenous (Dick, 2007; Dick & Patterson, 2007). In addition, congeneric streblids often occur on closely-related hosts. Consequently, when congeners are pooled, the congruence between host and parasite phylogenies resulted in a significant phylogenetic signal in parasite presence or prevalence that did not manifest for particular members of each genus (e.g. *Noctiliostrebla*, *Paradyschiria*, *Strebla*) (Table 1). This pattern of parasitic congeners occurring on congeneric hosts suggests cospeciation between hosts and parasites.

Potential evidence for cryptic parasite species

Distributions of parasites across a host phylogeny can provide evidence for cryptic species or for a species complex that has yet to be resolved. For example, the argasid tick *Ornithodoros hasei* was recorded from 20 of 41 bat species in Paraguay, with appreciable prevalence on vespertilionids, molossids, and noctilionids. However, *O. hasei* is now recognized as a species complex (Díaz *et al.*, 2007; Nava *et al.*, 2007). Few reliable diagnostic characters exist for argasids, requiring genetic data to reliably distinguish species (Guglielmone *et al.*, 2010; Dantas-Torres *et al.*, 2012). The distribution and prevalence of *O. hasei* on distantly-related hosts indicate that this species complex probably represents at least three different species (one per host family) in Paraguay. On Sevilleta rodents, the nematode *Heteromyoxyuris deserti* occurred on nine of 15 rodent species, including all three families, with prevalence > 10% on a sciurid (*T. quadrivittatus*) and on three species of heteromyids. This type of distribution suggests that *H. deserti* represents multiple cryptic species. At the time of data collection (1990s), *Heteromyoxyuris* comprised only two species. More recently, a new species was described from *Perognathus flavus* in Mexico, with a prevalence of 56% (García-Prieto *et al.*, 2008). *Heteromyoxyuris deserti* was not recorded from *P. flavus* in Mexico but had a prevalence of 5% on *P. flavus* in Sevilleta. Geographical variation may exist in host-species relationships as a result of spatial variation in the species composition of rodent hosts or of intermediate hosts. However, the phylogenetic pattern of prevalence among hosts suggests that the species of *Heteromyoxyuris* infesting *T. quadrivittatus* may not be the same as the species typically restricted to heteromyids (García-Prieto *et al.*, 2008).

CONCLUSIONS

Host specificity was highly correlated with phylogenetic signal strength based on parasite presence but not with that based on prevalence. This suggests that the ability of parasite to persist on a nonprimary host as a sink population is associated with phylogenetic relationships of the host (i.e. closely-related hosts provide habitats and resources that are similar and are more likely to support populations of nonprimary parasites). However, such nonprimary associations typically are rare, resulting in prevalences that are effectively zero. Differences in the transmission mode of parasites did not affect phylogenetic signal strength or the likelihood of detecting a phylogenetic signal. Rather, variation exists among parasites in the importance of environmental filters for determining host use. Parasites for which filters associated with the host environment are important are more likely to exhibit phylogenetic signals because closely-related hosts provide more similar habitats and resources.

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SHARED DATA

Data deposited in the Dryad digital repository (Presley *et al*., 2015).