Original Contribution

Correlates of Viral Richness in Bats (Order Chiroptera)

Amy S. Turmelle[1,3] and Kevin J. Olival[2,4]

[1]*Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996*
[2]*Sackler Institute for Comparative Genomics, American Museum of Natural History, New York, NY 10024*
[3]*Division of Viral and Rickettsial Diseases, Centers for Disease Control and Prevention, 1600 Clifton Rd. NE, Mailstop G-33, Atlanta, GA 30333*
[4]*Wildlife Trust, New York, NY 10001*

Abstract: Historic and contemporary host ecology and evolutionary dynamics have profound impacts on viral diversity, virulence, and associated disease emergence. Bats have been recognized as reservoirs for several emerging viral pathogens, and are unique among mammals in their vagility, potential for long-distance dispersal, and often very large, colonial populations. We investigate the relative influences of host ecology and population genetic structure for predictions of viral richness in relevant reservoir species. We test the hypothesis that host geographic range area, distribution, population genetic structure, migratory behavior, International Union for Conservation of Nature and Natural Resources (IUCN) threat status, body mass, and colony size, are associated with known viral richness in bats. We analyze host traits and viral richness in a generalized linear regression model framework, and include a correction for sampling effort and phylogeny. We find evidence that sampling effort, IUCN status, and population genetic structure correlate with observed viral species richness in bats, and that these associations are independent of phylogeny. This study is an important first step in understanding the mechanisms that promote viral richness in reservoir species, and may aid in predicting the emergence of viral zoonoses from bats.

Keywords: Chiroptera, emerging infectious disease, IUCN, population structure, sampling effort, viral richness

INTRODUCTION

Emerging infectious diseases (EIDs) are mostly viral and zoonotic in origin (Taylor et al., 2001; Wolfe et al., 2007) and a growing number are discovered each year (Woolhouse et al., 2008). Several studies have undertaken large-scale analyses to determine risk factors associated with EIDs (Taylor et al., 2001; Jones et al., 2008), and have identified host range, as well as pathogen taxonomy and molecular

characteristics as the most important (Cleaveland et al., 2001; Woolhouse and Gowtage-Sequeria, 2005; Holmes and Drummond, 2007; Pulliam and Dushoff, 2009). Molecular characteristics of viruses that likely contribute to emergence in novel hosts include physical or biochemical features, e.g., the ability to replicate in the cytoplasm (Pulliam and Dushoff, 2009), and evolutionary potential, e.g., rapid mutation rates and processes such as recombination or reassortment (Holmes and Drummond, 2007). Additionally, viruses that utilize highly conserved cell receptors (e.g., rabies virus) may have higher probabilities of successful cross-species transmission and emergence (Holmes and Drummond, 2007).

Despite the importance of intrinsic pathogen characteristics, host life history, ecology, and spatial structure also contribute to the emergence, persistence, and intensity of zoonotic outbreaks (Bolzoni et al., 2007; Webb et al., 2007; Plowright et al., 2008).

As viruses may be relatively unstable outside their hosts, the dynamics and frequency of intra- or interspecific host interactions will largely affect encounter probabilities related to disease emergence (Pulliam, 2008). The structure of wildlife populations across the landscape also has strong implications for infectious disease dynamics and emergence (Real and Biek, 2007). Major developments have been made in theoretical (Rand et al., 1995; Boots and Sasaki, 1999, 2000; Haraguchi and Sasaki, 2000; Boots et al., 2004; Cross et al., 2005; Webb et al., 2007) and experimental (Bull et al., 1991; Messenger et al., 1999; Kerr et al., 2006; Boots and Mealor, 2007) studies linking population structure, disease dynamics, and pathogen evolution, with particular advances in our understanding of how contact networks regulate pathogen persistence and virulence. Evidence from natural systems has validated the ecological theories on spatial infection processes (Ewald, 1991; Herre, 1993; de Roode et al., 2008), and recent studies have highlighted the importance of contact and transmission heterogeneities in modeling disease prevalence and control strategies (Barlow, 1996; Lloyd-Smith et al., 2005; Donnelly et al., 2006; May, 2006; Bolzoni et al., 2007; Bohm et al., 2009).

Another key factor in predicting the emergence of zoonoses is the number of viruses, or viral richness, found in natural reservoir species (Wolfe et al., 2005). This largely unknown, natural diversity of pathogens in wildlife hosts has been termed the "zoonotic pool" (Morse, 1993). The fields of phylogenetics, population genetics, and biogeography have led to key advancements in our understanding of host–pathogen coevolution in relation to pathogen diversity (Pybus et al., 2000; Grenfell et al., 2004), and numerous studies have documented coevolution between pathogens and their hosts (Smith, 1996; Asikainen et al., 2000; Gaunt et al., 2001; Nieberding et al., 2004; Criscione et al., 2005; Biek et al., 2006; Dragoo et al., 2006; Criscione and Blouin, 2007; Liu et al., 2008). However, we know little about which factors are most important in creating and sustaining pathogen richness within reservoir hosts. Comparative approaches are needed that test for patterns of pathogen richness across multiple factors for groups of potential reservoir host species.

Few studies have simultaneously examined phylogenetic and socioecological factors affecting parasite richness, and the majority have focused on primates. Davies and Pedersen (2008) found that host geographic range overlap was a significant determinant of viral communities in primates, although phylogenetic relatedness was also an important predictor of richness for other taxonomic groups of parasites in their analysis. A separate study found a significant correlation between viral species richness, host geographic range area, and population density across primates when corrections for phylogeny and sampling effort were included (Nunn et al., 2003). A similar study also found a correlation between viral richness, host phylogenetic diversity, and host geographic range overlap (Nunn et al., 2004). In a more recent study, threatened primates harbored lower parasite species richness compared to nonthreatened hosts, although this effect was not significant for viruses when other host socioecological traits were included (Altizer et al., 2007). Ezenwa (2004) found that group size and social behavior were important correlates with parasite diversity in African bovids. Gregory (1990) found positive correlations between helminth richness and geographic range, but no associations with host socioecological traits, in Holarctic waterfowl. Across studies, host population density, geographic range area, and phylogeny emerge as consistent predictors of parasite richness. All of these studies also report highly significant positive correlations between parasite richness and sampling effort, which suggests that parasite richness has been largely underestimated for many vertebrate hosts.

Bats (Order Chiroptera), which comprise nearly 1200 species, have been linked as natural reservoir hosts to a rapidly growing number of EIDs (Calisher et al., 2006). This includes several viruses that cause severe disease in humans: Ebola (Leroy et al., 2005) and Marburg (Swanepoel et al., 2007) filoviruses, SARS and related coronaviruses (Li et al., 2005; Dominguez et al., 2007; Muller et al., 2007; Carrington et al., 2008; Gloza-Rausch et al., 2008; Tong et al., 2009), as well as Nipah (Johara et al., 2001), Hendra (Halpin et al., 2000) and related paramyxoviruses (Drexler et al., 2009). It has recently been suggested that two human cases of acute respiratory illness in Malaysia may be linked to reoviruses of bat origin (Chua et al., 2007; Chua et al., 2008). Furthermore, evidence supports the association of bats with lyssavirus infection in humans globally (Lumio et al., 1986; Allworth et al., 1996; Warner et al., 1999; Favi et al., 2002; Messenger et al., 2002; Fooks et al., 2003; da Rosa et al., 2006; van Thiel et al., 2008). The importance of bat-borne zoonoses has only recently been appreciated, and no studies to date have examined factors

that may explain the large diversity of viruses in the Order Chiroptera. Bats exhibit a wide range of morphological, ecological, and behavioral characteristics, and similarly, are characterized by highly variable patterns of genetic population structure (Nowak, 1999; Burland and Worthington-Wilmer, 2001). These features make the Order Chiroptera ideal for testing hypotheses regarding patterns of host–pathogen coevolution and viral richness.

Many hypotheses have been suggested for the association of bats and EIDs, some of which include high species diversity, long life spans, capacity for long-distance dispersal, dense roosting aggregations (colony size) for many species, the use of torpor and hibernation, unique immunology, and spatial population structure (Messenger et al., 2003a; Calisher et al., 2006). While all of these factors are likely to be important, we investigate the significance of colony size, migratory ability, population genetic structure, geographic range area and distribution (continental vs. island), International Union for Conservation of Nature and Natural Resources (IUCN) threatened status, and body mass in generalized linear models of viral richness across Chiroptera, while accounting for sampling effort and phylogeny. We hypothesize that larger colony sizes will be positively correlated with viral richness, as a larger number of susceptible individuals in a population will permit greater viral establishment and persistence (Anderson and May, 1986). We also hypothesize that stronger population structure will be positively associated with viral richness, due to coevolutionary forces as a driver of within-lineage pathogen diversity and the importance of metapopulation structure in invasion and enzootic infection processes (Webb et al., 2007). As island taxa tend to have more restricted geographic ranges, and may be more prone to extinction, we predict that species with an island distribution will have fewer viruses than bats with a continental range distribution. Threatened bat species may have fewer viruses than nonthreatened taxa because parasites may be more likely to go extinct in smaller fragmented host populations (May and Anderson, 1979). However, threatened species may be more susceptible to multihost pathogens, potentially as a result of reduced immunological diversity, stress, and poor nutritional status of hosts across fragmented landscapes (Lyles and Dobson, 1993; Messenger et al., 2003a). Migratory species are expected to harbor more viruses than nonmigratory species as they sample more diverse habitats and may be subject to greater interspecific contact. Larger hosts with greater body mass may

harbor greater viral richness, as has been suggested from studies in primates (Nunn et al., 2003). Although we explore associations of life history, genetics, and ecology with viral infection in bats, these factors may predict infection but not disease in bats. It has been suggested that bats may not develop clinical disease from infection with certain viral pathogens, such as filoviruses, henipaviruses, and coronaviruses; however, clinical signs of disease are observed following infection with other viral pathogens such as lyssaviruses. This is, to our knowledge, the first meta-analyses to quantitatively investigate the effect of these explanatory variables on viral richness in bats.

METHODS

Data Collection

Population genetic structure data were gathered from published literature by searching Science Citation Index Expanded and ISI Zoological Record for the years 1985–2009 with various combinations of keywords: population, structure, genetic*, bat*, mammal*, and Chiroptera. Additional references not identified during keyword searches were collected from published reviews (Burland and Worthington-Wilmer, 2001), literature cited, and the Digital Dissertation Database. Population genetic data for 54 species of bats were compiled. Representative nuclear allelic F_{ST} (Wright, 1951) or mitochondrial haplotypic φ_{ST} (Excoffier et al., 1992) estimates of population structure from each species were calculated separately as the mean of all pairwise F_{ST} or φ_{ST} values in a study, and taken across multiple studies for the same species when available. A global mean value was also obtained by averaging F_{ST} and φ_{ST} when available. Thus, the global F_{ST} value for each bat species summarizes data from single or multiple, mitochondrial and nuclear, empirical estimates. The advantage of F_{ST} over direct measures of genetic diversity such as nucleotide diversity is that, as a ratio that describes the proportion of population genetic subdivision, it is largely independent from the mutation process so that data from different molecular markers can be easily compared (Pannell and Charlesworth, 2000). This comparability, along with its common use, makes F_{ST} the most appropriate statistic for comparative analyses of population structure across studies using different molecular markers. As previous studies have suggested potential correlations between population structure indices and geographic sampling distance (Burland and Worthington-Wilmer, 2001),

the average geographic sampling distance (km) between populations was calculated from empirical studies to test for this bias.

Bat species were assigned as being migratory or non-migratory based on definitions presented in Fleming and Eby (2003) and data from previous ecological studies (including capture-mark-recapture data) or published reviews (McCracken, 1987; Burland and Worthington-Wilmer, 2001; Fleming and Eby, 2003). If a species had populations that were both migratory and nonmigratory, e.g., *Tadarida brasiliensis* (McCracken and Gassel, 1997), then the species was coded as migratory. Average colony size was recorded from the Mammalian Species account for a species when available, or the IUCN Red List database, or reconciled from both sources. The distribution of a species was coded from geographic range data presented in the IUCN Red List database (IUCN, 2009), and was either "continental" or "island." If a species distribution included continental and island areas, assignment reflects the majority of the geographic range. IUCN Red List status was obtained directly from the database (IUCN, 2009). Body mass data were gathered from Norberg and Rayner (1987), and we used geographic range area estimates from Jones et al. (2003).

We then searched the literature and compiled records for all known viruses occurring in the 54 bat species with available population structure data. Viral information was available for 33 of 54 (61%) species for which we also had population structure estimates. The majority of the viral associations were obtained from previously published reviews (Messenger et al., 2003a; Calisher et al., 2006; Wong et al., 2007), but additional literature searches on PubMed and Web of Science were conducted to identify recent events. When possible, we also recorded the method of viral detection from the original papers cited. Typical methods of detection included mouse inoculation or cell culture for viral isolation, although alternate methods included the fluorescent antibody test (FAT) or polymerase chain reaction (PCR) to detect viral antigen from organs or tissues of bats. One exclusion criterion was employed in our database, and this was for records of arbovirus detection through serology only. As bats are likely to be incidental hosts to most arboviruses, and positive serological results may be nonspecific in differentiating viruses with noted cross-reactivity (e.g., genus *Flavivirus*), serological detection of arbovirus antibodies was not considered as evidence of a viral association. All viral records were considered unique for subsequent analysis with the exception of bat gammaherpesviruses (BatGHV), where BatGHV-1, 2, 4, 6, and 7 were considered one viral species, and the phylogenetically distant BatGHV-3 was considered to be a separate unique virus (Wibbelt et al., 2007).

Previous studies have demonstrated that sampling effort is likely to be uneven across species, and can confound interpretations with other biological variables of interest. To account for variation in sampling effort across species, we searched the ISI Zoological Record from 1945 to 2009 for each bat species. The number of citations per species was recorded, and used as an index of sampling effort (Gregory, 1990; Nunn et al., 2004, 2005; Altizer et al., 2007). Only bat species with one or more known viral associations were included in our dataset ($n = 33$), as we found that sampling effort was a highly significant predictor of the presence or absence of viral records across all taxa ($n = 54$; $r^2 = 0.56$; $P < 0.0001$).

Statistical Analysis

In the full dataset for bats with population structure and viral information ($n = 33$), the global F_{ST} statistic averaged nuclear and mitochondrial indices ($n = 8$), or represented a single nuclear ($n = 17$) or mitochondrial ($n = 8$) statistic. Generalized linear models of the viral richness data included migration, distribution, and IUCN status as binomial categorical predictors, and colony size, population genetic structure, body mass, geographic range area, and sampling effort as covariates. Covariates were log-transformed to satisfy normality criteria. There were no significant covariate interactions in our analyses, and our limited sample sizes precluded us from testing across multiple levels for all categorical interactions. A mixed stepwise variable selection procedure was employed in JMP v.7.0.1 (SAS Institute, Inc., Cary, NC) to identify optimal models, with the cutoff value for variables to enter and leave set at $\alpha = 0.20$. As we had incomplete information for the geographic range area of all taxa (28 of 33), the stepwise procedure was run with and without this variable included for optimal model selection. The Egyptian fruit bat (*Rousettus aegyptiacus*) had the most viral records ($n = 8$), was identified as an outlier in the generalized linear model testing (Studentized residual > 3), and was omitted from subsequent analyses. The best model and subsets identified from the stepwise procedure were then analyzed in the generalized linear framework using a normal distribution and identity link function. For categorical levels, means and standard deviation of viral richness estimates are presented.

Phylogenetic Correction

The best model and subsets were reanalyzed to test for phylogenetic dependence, as traits among related species may be more similar due to common ancestry and should not be considered independent in comparative analyses (Felsenstein, 1985; Harvey and Pagel, 1991). A generalized least squares (GLS) framework (Grafen, 1989; Martins and Hansen, 1997; Garland and Ives, 2000), using the APE package (Paradis et al., 2004) in R (The R Foundation for Statistical Computing, http://www.R-project.org) and supplementary code (Duncan et al., 2007), was used to estimate λ, a parameter that tests whether the evolution of phenotypic traits are independent of phylogenetic relationships among taxa. As comparative sequence data were not available for all of the bats with viral information, a mammalian supertree with branch length information was used as a source tree for the phylogenetic correlation matrix (Bininda-Emonds et al., 2007). After excluding one outlier, 29 of the 32 taxa of interest were represented in the mammalian supertree, and a pruned phylogeny with branch lengths was extracted (Fig. 1a). The remaining (three) taxa not found in the supertree were manually added to the pruned phylogeny in a way that minimized assumptions of relationships (i.e., branch length = 0) (Fig. 1b). A correlation matrix was computed from the expected variances and covariances of shared branch lengths between taxa, assuming a model of Brownian motion (Martins and Hansen, 1997; Garland and Ives, 2000). The PGLS function (Duncan et al., 2007) was used to find the maximum likelihood estimate of λ, as well as estimated coefficients and confidence intervals on regression predictor variables. The parameter λ varies between 0 and 1, with zero values indicating independent phenotypic trait evolution with respect to phylogeny, and values close to one indicating dependence between trait evolution and phylogeny (Pagel, 1999; Freckleton et al., 2002). A null distribution of λ was also created, through 1000 randomizations of the model and data, to evaluate the significance of the observed estimate. Akaike information criterion scores corrected for small sample sizes (AICc) were used to identify the best model among subsets (Burnham and Anderson, 2002).

RESULTS

One hundred unique viral records were obtained for 33 bat species (Table 1). The majority of the viral records, 31% (31 of 100), were from the Family Rhabdoviridae and most of these were lyssaviruses (i.e., rabies and related viruses). Viruses from the Flaviviridae and Paramyxoviridae were the second and third most frequent, accounting for 13% (13 of 100) and 12% (12 of 100) of associations, respectively. Each bat species was associated with 1–8 viruses, and the mean number of viral records per bat
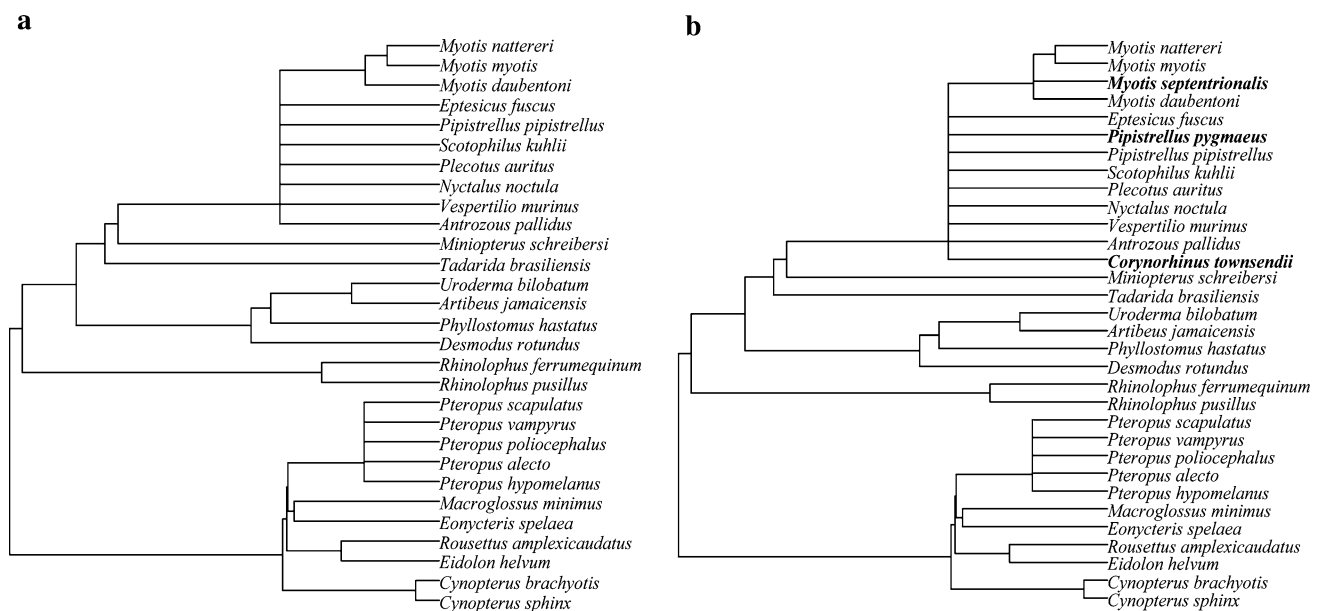

Figure 1. **a** The phylogeny extracted from the mammalian supertree (*with branch lengths*) for 29 of 32 taxa (Bininda-Emonds et al., 2007). **b** The phylogeny in which three additional taxa were added (*highlighted in bold*).

Table 1. Bats with Available Population Genetic Structure and Viral Richness Data

Family	Genus	Species	IUCN[a]	Migratory	Range[b]	Colony size	Global F_{ST}	No. of publications	No. of viruses	F_{ST} references	Virus references
Vespertilionidae	Antrozous	pallidus	LC	Y	C	60	0.244	175	1	(Weyandt and Van Den Bussche, 2007)	(Burns et al., 1956)
Phyllostomidae	Artibeus	jamaicensis	LC	N	I	10	0.013	271	4	(Ortega et al., 2003; Carstens et al., 2004)	(Downs et al., 1963; Calisher et al., 1971; Price and Everard, 1977; Aguilar-Setien et al., 2008)
Vespertilionidae	Corynorhinus	townsendii	LC	N	C	50	0.081	50	1	(Piaggio and Perkins, 2005), [Piaggio, personal communication]	(Blanton et al., 2007)
Pteropodidae	Cynopterus	brachyotis	LC	N	I	8	0.074	105	5	(Peterson and Heaney, 1993; Heaney et al., 2005; Campbell et al., 2006)	(Salaun et al., 1974; Johara et al., 2001; Calisher et al., 2006)
Pteropodidae	Cynopterus	sphinx	LC	N	C	36	0.164	180	3	(Storz et al., 2001; Campbell et al. 2006)	(Pavri and Singh, 1968; Kelkar et al., 1981; Reynes et al., 2004)
Phyllostomidae	Desmodus	rotundus	LC	N	C	60	0.468	400	2	(Wilkinson, 1985, Martins et al., 2007)	(Burns et al., 1956; Correa-Giron et al., 1972; Seymour et al., 1978)
Pteropodidae	Eidolon	helvum	NT	Y	C	500,000	0.153	142	5	(Juste et al., 2000)	(Kemp et al., 1988; Hayman et al., 2008; Kuzmin et al., 2008; Markotter et al., 2008; Razafindratsimandresy et al., 2009; Tong et al., 2009)
Pteropodidae	Eonycteris	spelaea	LC	N	I	5000	0.120	71	4	(Maharadatunkamsi et al. 2003)	(Johara et al., 2001; Lumlertdacha et al., 2005; Calisher et al., 2006)
Vespertilionidae	Eptesicus	fuscus	LC	N	C	50	0.464	841	5	(Turmelle, 2002), [Turmelle, personal communication]	(Constantine, 1970; Trimarchi and Debbie, 1977; CDC, 2000; Dominguez et al., 2007)
Pteropodidae	Macroglossus	minimus	LC	N	I	1	0.105	36	1	(Heaney et al., 2005)	(Calisher et al., 2006)

Table 1. continued

Family	Genus	Species	IUCN[a]	Migratory	Range[b]	Colony size	Global F_{ST}	No. of publications	No. of viruses	F_{ST} references	Virus references
Vespertilionidae	Miniopterus	schreibersii	NT	Y	C	5000	0.620	251	6	(Miller-Butterworth et al., 2003)	(Sulkin et al., 1970; Serra-Cobo et al., 2002; Botvinkin et al., 2003; Poon et al., 2005; Konstantinov et al., 2006; Markotter et al., 2008)
Vespertilionidae	Myotis	daubentonii	LC	N	C	100	0.017	306	2	(Ngamprasertwong et al., 2008)	(Whitby et al., 2000; Gloza-Rausch et al., 2008)
Vespertilionidae	Myotis	myotis	LC	N	C	5000	0.310	753	3	(Castella et al., 2000, 2001; Ruedi and Castella, 2003; Ruedi et al., 2008)	(Serra-Cobo et al., 2002; Amengual et al., 2007; Wibbelt et al., 2007)
Vespertilionidae	Myotis	nattereri	LC	N	C	275	0.017	367	4	(Rivers et al., 2005)	(Serra-Cobo et al., 2002; Wibbelt et al., 2007)
Vespertilionidae	Myotis	septentrionalis	LC	N	C	30	0.002	129	1	(Arnold, 2007)	(Blanton et al., 2007)
Vespertilionidae	Nyctalus	noctula	LC	Y	C	100	0.020	574	5	(Petit and Mayer, 1999)	(L'vov et al., 1973, 1979; Muller et al., 2004; Wibbelt et al., 2007)
Phyllostomidae	Phyllostomus	hastatus	LC	N	C	55	0.031	131	1	(McCracken and Bradbury, 1981)	(Constantine, 1970)
Vespertilionidae	Pipistrellus	pipistrellus	LC	Y	C	50	0.044	715	5	(Racey et al., 2007)	(Muller et al., 2004; Calisher et al., 2006; Cui et al., 2007; Wibbelt et al., 2007)
Vespertilionidae	Pipistrellus	pygmaeus	LC	Y	I	250	0.024	130	1	(Racey et al., 2007)	(Gloza-Rausch et al., 2008)
Vespertilionidae	Plecotus	auritus	LC	N	C	50	0.019	568	2	(Burland et al., 1999)	(Muller et al., 2004; Wibbelt et al., 2007)
Pteropodidae	Pteropus	alecto	LC	Y	C	5000	0.023	86	4	(Webb and Tidemann, 1996)	(Fraser et al., 1996; Halpin et al., 1996; Speare et al., 1997; Philbey et al., 1998; Halpin et al., 2000, 2007)
Pteropodidae	Pteropus	hypomelanus	LC	N	I	250	0.882	48	4	(Olival, 2008)	(Chua et al., 2001, 2002; Johara et al., 2001; Arguin et al., 2002; Pritchard et al., 2006)

Table 1. continued

Family	Genus	Species	IUCN[a]	Migratory	Range[b]	Colony size	Global F_ST	No. of publications	No. of viruses	F_ST references	Virus references
Pteropodidae	Pteropus	poliocephalus	NT*	Y	C	25,000	0.014	175	4	(Webb and Tidemann, 1996)	(Gard and Marshall, 1973; Halpin et al., 1996, 2000; Philbey et al., 1998; Barrett et al., 2005)
Pteropodidae	Pteropus	scapulatus	LC	Y	C	200,000	0.028	92	2	(Sinclair et al., 1996)	(Halpin et al., 1996; Speare et al., 1997)
Pteropodidae	Pteropus	vampyrus	NT	Y	I	5000	−0.006	58	1	(Olival, 2008)	(Johara et al., 2001)
Rhinolophidae	Rhinolophus	ferrumequinum	LC	N	C	125	0.102	735	4	(Rossiter et al., 2000)	(Kim et al., 1994; Serra-Cobo et al., 2002; Li et al., 2005; Calisher et al., 2006; Cui et al., 2007; Shi and Hu, 2008)
Rhinolophidae	Rhinolophus	pusillus	LC	N	C	1000	0.088	110	2	(Yoshino et al., 2008)	(Sulkin et al., 1970; Iwasaki et al., 2004)
Pteropodidae	Rousettus	aegyptiacus	LC	N	C	5000	0.493	249	8	(Juste et al., 1996)	(Kalunda et al., 1986; Wellenberg et al., 2002; Calisher et al., 2006; McKnight et al., 2006; Rector et al., 2006; Muller et al., 2007; Swanepoel et al., 2007; Towner et al., 2007; Markotter et al., 2008)
Pteropodidae	Rousettus	amplexicaudatus	LC	N	I	2000	0.100	47	1	(Heaney et al., 2005)	(Arguin et al., 2002)
Vespertilionidae	Scotophilus	kuhlii	LC	N	I	500	0.070	23	4	(Hisheh et al., 2004)	(Johara et al., 2001; Arguin et al., 2002; Reynes et al., 2004; Calisher et al., 2006; Cui et al., 2007)
Molossidae	Tadarida	brasiliensis	LC	Y	C	500,000	0.070	412	3	(McCracken and Gassel, 1997; Russell et al., 2005)	(Enright et al., 1955; Burns et al., 1956; Burns and Farinacci 1956; Constantine and Woodall, 1964; Sulkin et al., 1966)
Phyllostomidae	Uroderma	bilobatum	LC	N	C	30	0.010	47	1	(Meyer et al., 2009)	(Seymour et al., 1978)
Vespertilionidae	Vespertilio	murinus	LC	Y	C	100	0.071	229	1	(Safi et al., 2007)	(Hutson, 2004)

[a]IUCN status is least concern (LC) or near-threatened/vulnerable (NT) (*Pteropus poliocephalus is listed as vulnerable)
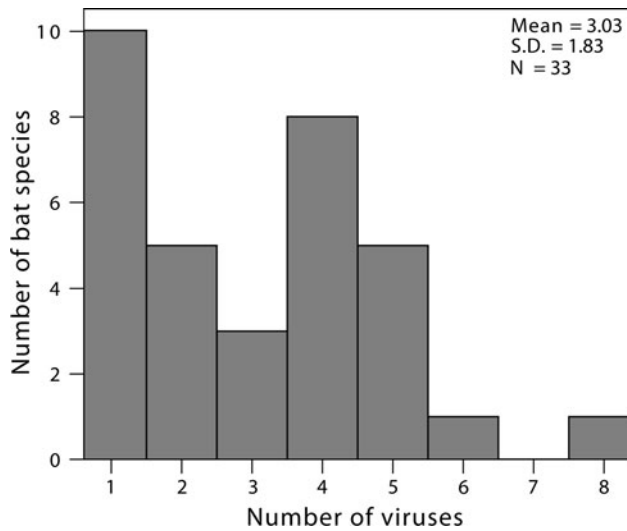[b]Range distribution is continental (C) or island (I)

Figure 2. The number of viruses associated with bats, for species with known population structure estimates and at least one viral association ($n = 33$).

species was 3.03 ± 1.83 (Fig. 2). Average sampling distance was a marginal predictor of global F_{ST} in a univariate regression ($n = 31$, $P = 0.06$), and was not included in subsequent analyses.

Correlates of Viral Richness

The mixed stepwise variable selection procedure converged on a model including IUCN status, distribution, log-transformed global F_{ST}, and log-transformed sampling effort as covariates. The stepwise procedure omitted migratory status and log-transformed average colony size as model predictors ($P > 0.2$). The multivariate model explained 37% of the viral richness data (*Likelihood Ratio* $\chi^2_{4,27} = 14.7$, $P = 0.005$). IUCN status was a significant predictor of viral richness among bats ($P = 0.02$), and near-threatened or vulnerable bats had higher mean viral richness (4.00 ± 2.16) compared to bats of least concern (2.71 ± 1.51) (Fig. 3a). Global F_{ST} was positively associated with viral richness ($P = 0.03$) (Fig. 3b), as was sampling effort ($P = 0.007$) (Fig. 3c). Species range distribution (i.e., island vs. continental) was not a significant predictor of viral richness ($P = 0.12$). A reduced multivariate model excluding distribution as a predictor explained 32% of the viral richness data (*Likelihood Ratio* $\chi^2_{3,28} = 12.4$, $P = 0.006$) (Table 2). In the reduced model, all three predictors significantly explained variation in viral richness ($P < 0.03$).
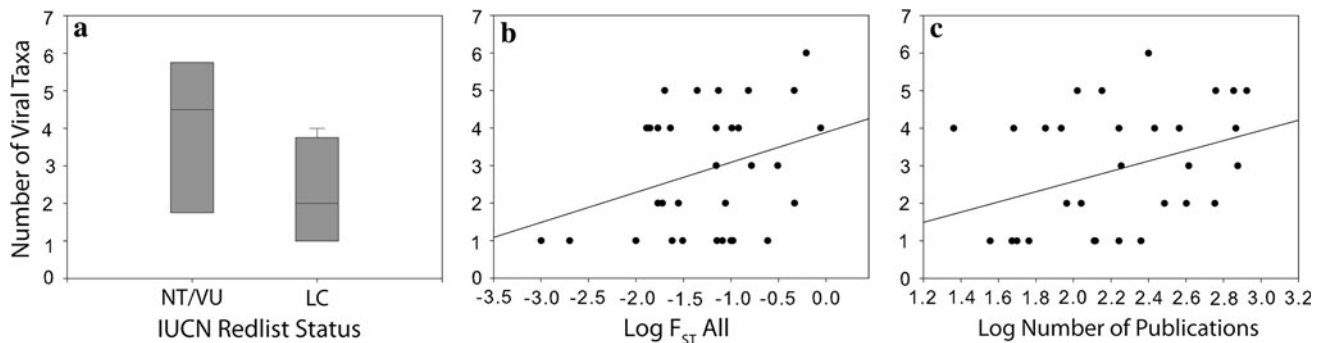

Figure 3. The three significant predictor variables from the best generalized linear model. Panels show the relationship between IUCN threat status (**a**), global F_{ST} (**b**), sampling effort (**c**), and viral richness across bat species ($n = 32$). Each data point represents one bat species in the linear regressions. NT/VU, near-threatened/vulnerable; LC, least concern.

Table 2. A Summary of the Models and Scores

Model	Predictors	LogLik	AICc	K	I	Rank	Lambda
2	*iucn, log (fst all), log (no. pubs)*	−54.17	123.7	6	0.0	1	0
1	*iucn, distribution, log (fst all), log (no. pubs)*	−52.99	124.7	7	0.9	2	0
3	*iucn, log (no. pubs)*	−56.42	125.2	5	1.5	3	0
5	*log (fst all), log (no. pubs)*	−56.49	125.3	5	1.6	4	0.02
4	*iucn, log (fst all)*	−56.70	125.7	5	2.0	5	0

The maximum likelihood estimate of phylogenetic signal in the full or reduced models was $\lambda = 0$ (Table 2), indicating that patterns of viral richness are independent from the phylogenetic relationships among bats in this study. Effect tests for parameters in the full or reduced models were similar when compared to the generalized linear models without any phylogenetic correction. The reduced model provided the best explanation of the data (Table 2). The randomization of viral richness trait values across taxa to obtain a null distribution of λ revealed that we cannot reject that our observed value is outside of the null distribution ($P = 0.22$), indicating a lack of power. To test the estimation procedure, a dummy phenotypic data set was created with trait values skewed to match the phylogeny, and an estimate of $\lambda = 1$ was obtained (data not shown).

DISCUSSION

Zoonotic disease emergence is a multipart process which includes: the build-up of risk factors during a ''pre-spillover'' period; a spillover event—when an infected individual from a reservoir population transmits the disease to a new host (Power and Mitchell, 2004); a period of local transmission in the new host that may or may not die out depending on characteristics of the pathogen and host population; and, a potentially self-sustaining transmission period within the new host (Anderson and May, 1986). Risk factors that exist in the ''pre-spillover'' period can be environmental, demographic, or evolutionary; these can be viewed as existing along an eco-evolutionary continuum. Successful cross-species transmission is usually the result of repeated spillover events, i.e., ''viral chatter'' (Wolfe et al., 2005). Standing pathogen diversity in reservoir populations can be critically important for promoting the evolutionary flexibility of pathogens, and likelihood of successful spillover and emergence in a new host (Morse, 1993). Thus, the taxonomic diversity of pathogens in hosts and the genetic diversity of each respective pathogen may both be important predictors of spillover success, or emergence. Mechanisms that promote diversity on either level may increase the likelihood of emergence.

Impact of Genetic Spatial Structure

Population genetic structure and sampling effort were correlated with viral richness in bats. Although a positive linear fit best described the relationship between population genetic structure and viral richness, compared to other polynomial models (data not shown), it is possible that population structure may have a nonlinear impacts on epizootiology and subsequent viral evolution within a host. Modeling, coupled with empirical observations, has shown that the spatial structure of host populations can influence the likelihood of disease establishment (Rodriguez and Torres-Sorando, 2001), rate of pathogen spread (Caraco et al., 2002), duration of epidemics (Park et al., 2002), as well as pathogen virulence (Boots et al., 2004). Extremely low levels of population genetic structure predict a homogeneously mixing population, potentially leading to viral epidemics that rapidly burn out without establishing an enzootic state. This is supported by metapopulation models that have shown an increased extinction probability in cases with increasing migration rates and moderate pathogen virulence (Hess, 1996). In hosts that exhibit extremely high levels of population structure, characterized by little migration between demes and small effective populations, localized disease extinction may preclude viral establishment. However, point estimates of population genetic structure may not capture all migration or fission–fusion dynamics that impact epizootiology, as this one statistic generally describes population substructure that relates to mating probabilities. Furthermore, the duration of incubation and infectious periods has equal importance for predicting the potential reproductive capabilities of a pathogen in any population, structured or not. While we did not examine the genetic diversity within host-specific viral lineages, the epizootiology of lyssaviruses in bats suggests that moderate levels of host population structure can positively influence viral genetic diversity within hosts (Smith, 1996; Messenger et al., 2003b; Davis et al., 2005; Hughes et al., 2005; Franka et al., 2006; Velasco-Villa et al., 2006). Bats with increasing population genetic structure are positively associated with viral richness in this study. However, the current host sampling excludes several families, hundreds of species, and may not be representative for all bats. Furthermore, it will be important to distinguish between pathogens that are directly transmitted or vector-borne, and those that infect single or multiple hosts, as additional data become available. The influence of host population genetic structure may be negligible for vector-borne or multihost viruses, where pathogen distribution and richness may be determined by spatial structure of vectors and all competent hosts. Low sample sizes in the current study precluded partitioned statistical treatment for

all possible transmission strategies. There is also evidence that many other factors, such as host immune response, may promote lineage diversity within pathogens (Grenfell et al., 2004). However, the spatial genetic structure of hosts can serve as a starting point for investigating pathogen distribution, diversification, and spatial control strategies.

Impacts of Host Ecology and Social Behavior

Theoretical modeling of epizootic and enzootic processes predicts that larger populations generally will increase the likelihood of viral establishment (Anderson and May, 1979); however, host colony size was not correlated with viral richness across bats in this study. Bat colony sizes can be extremely variable across species (Kunz, 1982; O'Shea and Bogan, 2003), and are known to be seasonally dynamic in response to variation in prey and habitat resource availability and life history. There is evidence that Brazilian free-tailed bats (*Tadarida brasiliensis*) migrate from Mexico to track seasonal insect abundance in conjunction with formation of large maternity colonies in the southwestern United States (McCracken, 2003). The straw-colored fruit bat (*Eidolon helvum*) also exhibits seasonal fluctuations in colony size correlated with temporal and geographic variation in fruit availability across sub-Saharan Africa (Richter and Cumming, 2006). Colony sizes of the large flying fox (*Pteropus vampyrus*) in Malaysia fluctuate dramatically over time, and dispersal behavior may reflect variation in fruit availability and hunting pressure (Epstein et al., 2009). Although generalized predictions can be made from long-term summary statistics on host aggregation, seasonality also plays a critical role in epizootiological processes and disease emergence (Altizer et al., 2006). In our search of the literature for species-specific colony size estimates, there were frequent references to seasonal and gender variation in gregarious behavior. Seasonal variation in colony size may be more important than typical colony size per se in terms of understanding the importance of contact networks for viral emergence and persistence in bat hosts. Irrespective of potential intra-annual variation, the typical colony sizes of individual host species may also be less important when considering vector-borne and multihost pathogens.

Host geographic range may be an important determinant of pathogen richness, as larger geographic ranges encompass a greater diversity of ecosystems, faunal communities, and may lead to greater spatial population substructure. Geographic range area was not a significant predictor of viral richness among bats in this study, but other studies have highlighted that host geographic range may be an important predictor of parasite richness (Gregory, 1990; Nunn et al., 2003). Smaller geographic ranges have been linked to increased extinction risk across bats (Jones et al., 2003), and may similarly govern parasite dynamics associated with such hosts. However, a study across primates found evidence that host relatedness and the presence of conspecific range overlap were significant predictors of parasite community similarity across taxa (Davies and Pedersen, 2008). Given recent implication of bats in EID spillover events (Halpin et al., 2000; Johara et al., 2001; Leroy et al., 2005; Li et al., 2005; Swanepoel et al., 2007), additional studies on pathogen community similarity that include multiple pathogen taxonomic groups and tests of phylogenetic dependence across bats are needed. Although several socioecological variables were not significant predictors of viral richness across bats in this study, it would be prudent to search more exhaustively among known viral hosts, without limiting the search to species with characterized genetic spatial structure.

IUCN threat status, which combines data on population sizes, distribution, and geographic range area, was a significant predictor of viral richness across bats in this study, whereas individual contributing factors were nonsignificant. In this study, bats that were near-threatened ($n = 3$) or vulnerable ($n = 1$) had higher viral richness compared to bats of least concern ($n = 28$). This result contrasts a previous study in primates (Altizer et al., 2007), where threatened taxa harbored lower parasite richness compared to nonthreatened taxa. Although the categories of threat status under comparison were not identical compared to the Altizer et al. (2007) study, the current study was also much more limited in taxonomic scope for both hosts and parasites under consideration. Although the data suggest that near-threatened or vulnerable bats may be more susceptible to viral infection compared to bats of least concern, the current result warrants caution given the uneven and limited sampling across IUCN threat categories.

Although significant links between phylogeny and parasite richness have been demonstrated in other studies (Nunn et al., 2004), there was no evidence of phylogenetic dependence for patterns of viral richness in this study. Familial monophyly across bats was well supported for the phylogeny used in this study (Bininda-Emonds et al., 2007). However, small sample sizes and the lack of phylogenetic resolution within and among bat genera may have lessened our power to detect dependence between

phylogenetic relatedness and patterns of viral richness, as demonstrated by our inability to reject that our estimate of λ was not nested within the null distribution. It is also possible that viral richness traits may not be evolving under the model of Brownian motion that was employed in our test (Freckleton et al., 2002). Sampling that is more broadly representative of chiropteran diversity may allow for more powerful tests of phylogenetic dependence for trait evolution.

Limitations of a Biogeographic Approach

Although estimates of F_{ST} provide information on historic dispersal and social organization of reservoir species over relatively large geographic or temporal scales, studies of emerging zoonoses and wildlife EIDs would benefit from collecting fine-scale, or real-time spatial data on host movement. Few studies have focused on this, but examples include studies of the reservoir hosts for chronic wasting disease (Conner and Miller, 2004), canine pathogens (Riley et al., 2004), the use of satellite telemetry to quantify migration activity for flying fox reservoirs of Nipah virus (Epstein et al., 2009), and use of contact transmitters on domestic animals and wildlife (Bohm et al., 2009). It is often logistically difficult to collect these data, but the combination of population genetic data with direct measures of host dispersal and contact have the potential to more accurately predict the spatial patterns of host–pathogen dynamics across the landscape (Hess et al., 2004; Real and Biek, 2007; Olival, 2008). Thus, biogeographic inferences can make important macroecological predictions on pathogen richness and epizootiological processes, but control strategies for zoonotic disease will also require attention to multihost interactions, as well as local geographic and temporal scales.

Future Directions

As this study was only able to include a small fraction of bat species (33 of 1200) for which both population genetic and viral richness data were available, it also highlights how little we know about this diverse group of animals that are key players in the health of ecosystems and emergence of infectious diseases globally. Viral richness estimates in this study surely underestimate the real number of viruses associated with bats, in part due to a lack of population structure estimates for the overwhelming majority of bat species and also incomplete disease surveillance. Models fit

to the temporal emergence of viruses suggests that, even for human pathogens, the process of discovery is far from complete (Woolhouse et al., 2008). A number of recently discovered viruses, in addition to many other previously published associations, could not be included in our data set because they were found in species for which we did not have population genetic structure data or other host socioecological variables. This points to a number of considerations for future studies. First, more bat species should be examined using population genetic markers, and efforts should be made to collect samples for genetic work at the same time that animals are captured and handled during viral surveillance or telemetry studies. Second, more standardized methods for detecting viruses in wildlife reservoirs are needed. The majority of studies target limited taxonomic breadth in viral surveillance efforts, and often serology alone can be problematic due to cross-reactivity (Hanlon et al., 2005; Hayman et al., 2008). Novel methods, such as multiplex PCR and DNA microarrays, in addition to diverse collaborative research teams, have the capacity to revolutionize the information gained through viral surveillance efforts and will surely advance our understanding of the processes of pathogen richness, coinfection, and emerging bat zoonoses. Lastly, this study highlights the importance of species-specific evolutionary and life-history characteristics for predicting viral richness in wildlife, and this should be examined for other taxonomic groups. This approach could greatly aid pathogen discovery by focusing sampling efforts to host species with potentially greater viral richness and, hence, greater likelihood of harboring novel zoonotic pathogens.

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