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Patterns of host specificity and transmission among parasites of wild primates

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Abstract

Multihost parasites have been implicated in the emergence of new diseases in humans and wildlife, yet little is known about factors that influence the host range of parasites in natural populations. We used a comprehensive data set of 415 micro- and macroparasites reported from 119 wild primate hosts to investigate broad patterns of host specificity. The majority (68%) of primate parasites were reported to infect multiple host species, including animals from multiple families or orders. This pattern corresponds to previous studies of parasites found in humans and domesticated animals. Within three parasite groups (viruses, protozoans and helminths), we examined parasite taxonomy and transmission strategy in relation to measures of host specificity. Relative to other parasite groups, helminths were associated with the greatest levels of host specificity, whereas most viruses were reported to infect hosts from multiple families or orders. Highly significant associations between the degree of host specificity and transmission strategy arose within each parasite group, but not always in the same direction, suggesting that unique constraints influence the host range of parasites within each taxonomic group. Finally characteristics of over 100 parasite species shared between wild primates and humans, including those recognised as emerging in humans, revealed that most of these shared parasites were reported from multiple host orders. Furthermore, nearly all viruses that were reported to infect both humans and non-human primates were classified as emerging in humans.

Keywords: Infectious disease; Multihost pathogen; Transmission strategy; Zoonosis; Wildlife; Emerging pathogens

1. Introduction

The majority of parasites examined to date, including over 60% of human pathogens and 80% of those infecting domesticated animals, are capable of infecting multiple host species (Cleaveland et al., 2001; Taylor et al., 2001; Woolhouse et al., 2001). Recent emerging diseases in humans, including those caused by Ebola, Influenza A, Nipah, and SARS viruses, are associated with multihost pathogens maintained in non-human animal populations (Murphy, 1998; Hahn et al., 2000; Dobson and Foufopoulos, 2001; Taylor et al., 2001; Williams et al., 2002). Multihost pathogens also pose problems for wildlife conservation, and have caused population declines or high mortality among African carnivores, harbor seals, sea otters, black-footed ferrets, and African apes (Roelke-Parker et al., 1996; Harvell et al., 1999; Daszak et al., 2000; Jensen et al., 2002; Miller et al., 2002; Walsh et al., 2003). Despite their threats to global health and conservation, factors that influence the evolution and ecology of multihost parasites and their distributions in wild animal populations are not well understood (Desdevises et al., 2002), in part because conventional studies have focused most commonly on single host-pathogen systems (Anderson and May, 1991;

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Bull, 1994; Day, 2001) or on domesticated animals and humans (Cleaveland et al., 2001; Taylor et al., 2001).

A variety of ecological and evolutionary factors may influence patterns of parasite specificity. Here we focus on two key variables. First, transmission strategies that increase encounters with new hosts, such as transmission by biting arthropods or through contaminated soil or water, are predicted to increase the range of hosts that a pathogen can infect (Woolhouse et al., 2001). Second, greater genetic variability and more rapid generation times might allow certain pathogens to readily exploit new host species. For instance, parasites with high antigenic variation should have an increased ability to recognise host proteins or evade host immune defenses (Bitter et al., 1998; Simon et al., 1998).

In this study, we assembled a comprehensive database of infectious diseases reported from wild primate populations to investigate the frequency and characteristics of multihost pathogens. Indeed, several recent papers have highlighted that a majority of parasites reported to infect humans and domesticated animals can in fact infect more than one host species (Cleaveland et al., 2001; Taylor et al., 2001). This is not necessarily surprising because both humans and domesticated animals have cosmopolitan distributions, exist in large dense populations, and can be exposed to a wide diversity of pathogens from wildlife sources. In contrast to these earlier papers, our study focused on parasites reported from wild populations of non-human primates, in part because they represent a diverse group of mammals that have been threatened by infectious diseases (Wallis and Lee, 1999; Walsh et al., 2003; Leroy et al., 2004), and they have been identified as wild reservoirs or ancestral hosts for a growing number of human pathogens (Wolfe et al., 1998, 2004).

Using a similar database of host-pathogen records, Nunn et al. (2003) tested a suite of socioecological factors predicted to influence parasite species richness in wild primates, and demonstrated that host population density and geographic range size were positively associated with parasite species richness in wild primates. In this paper, we focused on traits of the parasites themselves by examining the association between host specificity and transmission strategy within and among multiple parasite taxonomic groups. We predicted that parasites transmitted by direct contact would be relatively more host specific than parasites with greater opportunities for among-host dispersal. We also predicted that viruses, owing to their short generation times and high mutation rates, would have broader host ranges. Finally we investigated the transmission and specificity of parasites reported from both humans and wild non-human primates to ascertain the risks that these shared parasites pose in relation to human emerging diseases.

2. Materials and methods

2.1. Parasite records from wild primates

A database of disease-causing organisms reported from wild primate populations was compiled from 258 published references, including scientific papers and book sections. We searched for reports using primate species' Latin binomials as keywords in major online reference databases (Biological Abstracts, AGRICOLA, Medline, Web of Science). We also searched by primate genus name, following the taxonomic scheme of Corbet and Hill (1991), as well as by common taxonomic variants (based on Rowe, 1996; Groves, 2001). The vast majority of papers and reports used in our data set were published between 1970 and 1999, with the total time frame spanning 1940–2002. For each parasite species reported from a wild primate population, we recorded information on hosts, parasites and sampling locality. We defined parasites broadly to include viruses, protozoa, fungi, arthropods, helminths and bacteria. Our original data set included 2173 cumulative lines of data, where each line was a record of a parasite species reported from a wild primate population. Nomenclature for viruses followed the International Committee on the Taxonomy of Viruses database (ITCVdb) available online (http://www.ncbi.nlm.nih.gov/ICTVdb/Ictv/), and nomenclature for other parasite species followed the guidelines published by the National Center for Biotechnology Information (NCBI). Additional details about the database are described in Nunn et al. (2003), Nunn and Altizer (2005), and are available on the Global Mammal Parasite Database website (www.mammalparasites.org). From our original host-parasite database, we generated a list of parasite species reported from free-living primate populations. To this initial list of parasite species, we recorded whether or not the parasite has been reported to infect humans based on records from Ashford and Crewe (1998) and Taylor et al. (2001), and also recorded information on transmission and specificity described below.

2.2. Scoring parasite specificity

For all parasite species, information on the taxonomic range of primates and other species reported as hosts was compiled by searching for published records of vertebrate animals infected under natural conditions using two online databases (BIOSIS and Web of Science). To assess virus specificity, we searched the PubMed online database (in addition to Web of Science) using ICTV virus names. We assigned a score from 1 to 5 to each parasite based on the taxonomic affiliation of affected hosts as follows: 1 = species specific; 2 = genus specific; 3 = family specific; 4 = order specific; and 5 = vertebrate specific (i.e. can infect multiple host orders). For host groupings at the level of primate families, we followed the taxonomy of Corbet and Hill (1991). We based specificity scores on recorded