

Invited Review

# Against all odds: Explaining high host specificity in dispersal-prone parasites

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## Abstract

Host specificity gauges the degree to which a parasite occurs in association with a single host species. The measure is indicative of properties of the host and parasite, as well as their ecological and co-evolutionary relationships. Host specificity is influenced by the behavior and ecology of both parasite and host. Where parasites are active, vagile and coupled with hosts whose behavior and ecology brings the parasite into contact with many potential hosts, the likelihood of host switching is increased, usually leading to lowered specificity. Bat flies are specialized, blood-feeding ectoparasites of bats worldwide. In the bat fly – bat system, numerous properties interrupt the linkage of parasite to host and should decrease specificity. For bat flies these include high levels of activity, proclivity to abandon a disturbed host, the ability to fly, and a life-history strategy that includes a pupal stage decoupled from the host. For bats these include rapid, frequent and wide-ranging flight, high species richness encouraging inter-specific encounters during foraging, roosting and reproductive events, the utilization of large, durable roosting structures that are often shared with other bat species, and utilization of common entrance/exit flyways. The biological and ecological characteristics of bats and flies should together facilitate interspecific host transfers and, over time, lead to non-specific host-parasite associations. Large surveys of Neotropical mammals and parasites, designed to eliminate artifactual host-to-host parasite transfers, unequivocally demonstrate the high host specificity of bat flies. High degrees of specificity are remarkable in light of myriad host and parasite characteristics that ought to break down such specificity. Although host-specific parasites often have limited dispersal capability, this is not the case for some groups, including active, mobile bat flies. Host specificity in parasites with high dispersal capability is likely related to adaptive constraints. Among these may be a reproductive filter selecting for specificity based on mate availability, and co-evolved immunocompatibility where parasites use the same or similar immune-signaling molecules as their hosts to avoid immunological surveillance and response.

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## 1. Introduction

Host specificity is a phenomenon produced by parasite–host couplings. It is indicative of intrinsic biological properties of both host and parasite, as well as emergent properties of their ecological and evolutionary relationships. The degree of host specificity is the product of historical associations of parasite and host lineages (Brooks and McLennan, 1993; Page, 2003). Ecological determinants of host specificity are difficult to isolate, and may include local

environmental conditions, the geographic range of utilized hosts, or host body mass (Krasnov et al., 2004a, 2005, 2006). Physical and biological characteristics shaping host specificity invite elucidation while the properties of host specificity drive theoretical predictions. Nonetheless, the degree of host specificity among arthropod ectoparasites, and even methodologies employed to assess specificity, remain contentious (Poulin, 2007).

Bat flies (Diptera: Streblidae and Nycteribiidae) are little-known, yet are the most conspicuous ectoparasites of bats worldwide (Mammalia: Chiroptera). Highly specialized blood-feeders, they only parasitize bats, living in their fur, on their flight membranes or (in one genus), under

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their skin (Dick and Patterson, 2006; Fig. 1). With nearly a million described insect species on earth (Grimaldi and Engel, 2005) and the diversity of vertebrates infested by parasites, it is surprising that true ectoparasitism – blood-feeders spending most of their life-span on the host – has evolved in only four insectan orders: Diptera, Hemiptera, Phthiraptera and Siphonaptera. All but the Phthiraptera contain groups restricted to bats. The diversification of about 570 nominal bat fly species has far surpassed that of the 122 bat flea (Ischnopsyllidae) and 32 bat bug (Polycetenidae) species.

Long, intimate associations between bats and bat flies have facilitated adaptations of a variety not observed in other ectoparasite groups, including features of the eyes, wings, ctenidia, setae, body shape, leg length and orientation, and reproductive strategy. The Streblidae in particular have radiated widely in the Western Hemisphere, where 156 species (nearly 70% of the world's total) are obligately associated with eight of the nine families of bats (Dick and Patterson, 2006). Many morphological and reproductive features of bat flies are clearly adaptive to an obligate association with host bats and this article focuses on how characteristics of both parasites and hosts might affect host specificity. A general rule holds across a wide range of parasite taxa: where a parasite's mode of transmission is coupled with host behavior that exposes the parasite to a variety of hosts, selection tends to favor host switching, which leads to a decrease in host specificity (Poulin, 2007). Here, using bat flies and their host bats as a

model system, we focus on characteristics of parasites and hosts that ought to reduce the degree of host specificity.

## 2. Flies as parasites – bats as hosts

Host specificity of ectoparasites is influenced by the behavior and ecology of both parasite and host (Wenzel et al., 1966; Kunz, 1982; Marshall, 1981, 1982; Brooks and McLennan, 1993; Krasnov et al., 2004b; Kunz and Lumsden, 2003; ter Hofstede and Fenton, 2005; Poulin, 2007). Bats and bat flies comprise a system in which both hosts and parasites exhibit characteristics that potentially and actually interrupt the linkage of host and parasite, which should decrease host specificity.

Although wing reduction (Fig. 1a and b) and loss has occurred in several bat fly lineages (Dittmar et al., 2006), the majority (79%) of New World species are volant (Whitaker et al., in press; Fig. 1c). Their ability to fly, coupled with the flies' excitable tendency to leave the host when disturbed (Wenzel et al., 1966; our unpublished observations), should lead to frequent movements from host to host. Moreover, an unending disruption of the linkage of parasite and host stems from the reproductive strategy of bat flies, adenotrophic viviparity. Females produce a single larva which is retained within their bodies through the third instar; every 10 days, females leave the host to larviposit onto the roost substrate, where the larva immediately pupates (Overall, 1980; Fritz, 1983). Following about 3 weeks' development, the adult emerges from the puparium and must locate and colonize a host individual, often having to choose among multiple potential host species (Fig. 2). Bat flies can only survive for a brief time without a host (Overall, 1980; C.W. Dick, unpublished observations), intensifying pressure to find a suitable host. The de-coupling of the parasite and host during the pupal stasis (equal to one third of the entire adult life span) ought to reduce the host specificity of bat flies.

Bats present unique opportunities and challenges to parasites. They are wide-ranging, volant animals that can move rapidly and frequently, potentially interacting with many other bat species during foraging, roosting and reproductive endeavors. One tropical humid forest in Guyana (Iwokrama) supports at least 86 species of bats, all potentially within cruising range of each other (Lim and Engstrom, 2001). Bats also vary tremendously in the roosting structures they utilize (Kunz, 1982). Although different species occupy roosts as different as foliage and leaf tents to mines and caves, most Neotropical bats roost in natural cavities such as hollow trees, logs and caves (Patterson et al., 2007). Larger, longer-lived roost structures may be utilized simultaneously by several bat species (Goodwin and Greenhall, 1961), often resting in close proximity (Kunz, 1982; Fig. 2). When a newly eclosed fly crawls or flies to a host, it could easily encounter a species other than that of its parents. Finally, bats often exhibit distinct roost preferences, some roosting in "twilight zones" near entrances and others deep inside the cavity. Nevertheless,

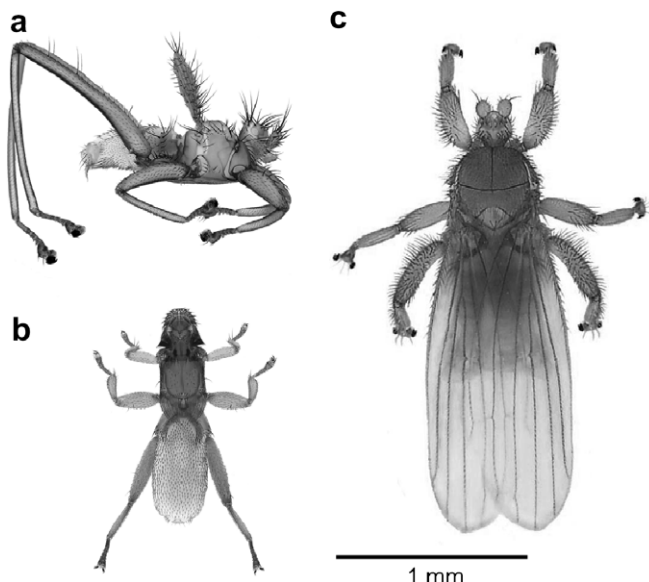


Fig. 1. Representative bat flies (Diptera: Streblidae). (a) *Megistopoda aranea*. This species infests furred regions of its host and is characterized by lateral body compression, vestigial wings (stenoptery), and greatly elongated hind legs. (b) *Metelasmus pseudoopterus*. This species infests furred regions of its host and is characterized by dorsoventral body compression, vestigial wings (brachyptery), and a cephalic ctenidium. (c) *Trichobius corynorhini*. This species infests flight membranes of its host; its body is not compressed and it possesses fully functional wings (macroptery) and legs of relatively equal length.

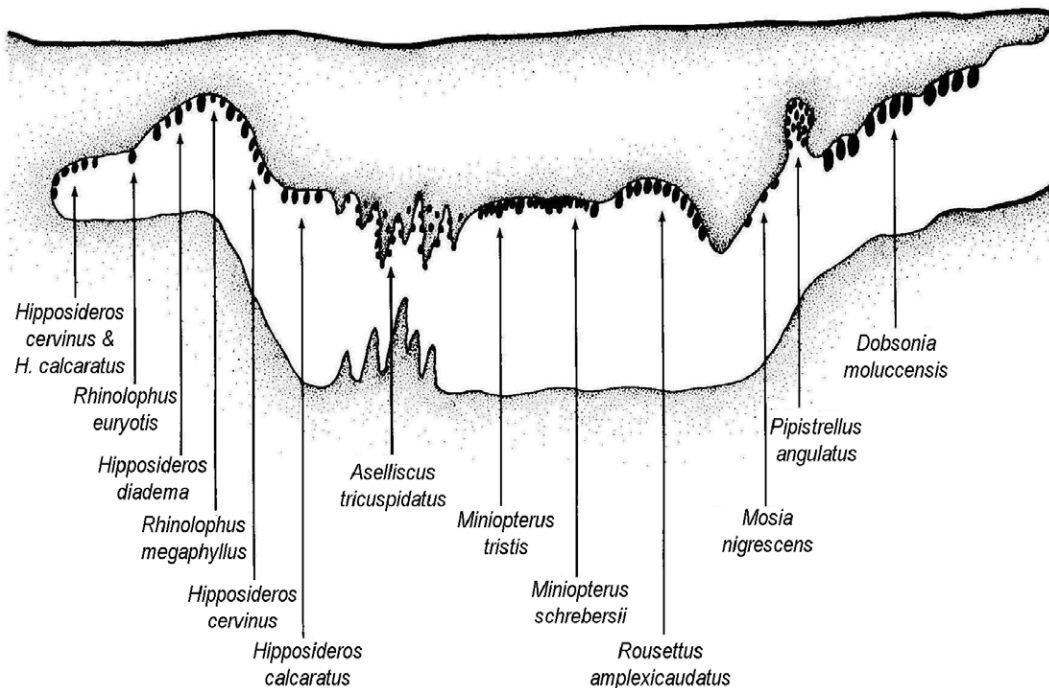


Fig. 2. Diagrammatic view of a cave in New Ireland, in the Bismarck Archipelago, showing the spatial roosting arrangement of 12 species of bats (Reprinted with permission. Hill, J.E., Smith, J.D. *Bats: A Natural History*. British Museum (Natural History), London. Copyright 1984; taxonomy as per Simmons, 2005). Not only do their flies larviposit in the vicinity of several neighboring species, but nightly emergence and return of the bats brings up to a dozen species of bats into proximity to newly eclosed bat flies inside the cave entrance.

bats frequently use common passages to enter and exit (Fig. 2), often in congested throngs at twilight, where they can potentially exchange flies. The roosting biology of bats correlates with the number of parasite species present on a host species as well as the prevalence and intensity of infestation (Patterson et al., 2007).

In concert, the biological and ecological characteristics of bat hosts and fly parasites provide many chances for intra- and inter-specific transfers of ectoparasites. Over evolutionary time, this should lead to non-specific host-parasite associations.

### 3. Host specificity patterns of bat flies

The degree of host specificity among bat flies is known from large coordinated surveys of mammals and their parasites, such as those conducted in Panama (~5000 hosts sampled; Wenzel et al., 1966), Venezuela (>25,000 hosts sampled; Wenzel, 1976), and Paraguay (>6500 hosts sampled; Dick and Gettinger, 2005) (Table 1). These surveys

isolated samples of parasites from each host individual, and were undertaken with progressively more informed and controlled protocols to isolate host mammals during capture and reduce the possibility of host-to-host transfer of parasites during capture and processing. These strict protocols, particularly as employed during the Paraguay survey, have greatly enhanced our ability to accurately discern patterns in host-parasite specificity (Dick, *in press*).

In Panama, Wenzel et al. (1966) documented host distributions of 66 species of streblids, 71% of which were monoxenous (i.e. associated with a single host species). A decade later, Wenzel (1976) treated 116 Venezuelan bat fly species, 75% of which were monoxenous. In Paraguay, where particularly stringent measures were used to control contamination, 87% of the 31 streblid species were monoxenous (Dick and Gettinger, 2005). Parasites not categorized as monoxenous have variously been explained by “strays”, or “accidental transfers”, or deemed “non-primary associations” (Wenzel et al., 1966; ter Hofstede et al., 2004; Whiteman et al., 2004), yet a few bat fly species

Table 1  
Summary of host specificity of Neotropical bat flies based on survey collections of ectoparasites and mammals

Collection	No. flies	Fly species	No. monoxenous	No. oligoxenous	No. polyxenous	% Monoxenous	Reference
Panama	~12,000	66	47	9	10	71.2	Wenzel et al. (1966)
Venezuela	36,663	116	87	19	10	75.0	Wenzel (1976)
Paraguay	2467	31	27	3	1	87.1	Dick and Gettinger (2005)

Monoxenous fly species are those found in strict association with a single host species, oligoxenous fly species parasitize two or more species of a single genus, and polyxenous fly species parasitize species of two or more host genera.

are truly polyxenous, infesting two or more host genera. Almost invariably, non-monoxenous fly species infest closely related hosts, usually congeneric ones. Oligoxenous flies (i.e., associated with two or more congeneric host species) always, and polyxenous flies usually, are restricted to a particular clade of bat taxa. Given the degree of monoxeny and the affinities of non-monoxenous species to particular host clades, host specificity of bat flies is remarkably high in light of numerous characteristics that ought to break down such specificity.

#### 4. Evolution and maintenance of host specificity among bat flies

The evolution of host specificity largely centers on the dynamics of parasite dispersal and adaptation (Timms and Read, 1999). Host-specific parasites often possess limited dispersal capabilities (e.g. lice on solitary fossorial mammals; Hafner et al., 2003) or have become so morphologically, behaviorally, or physiologically adapted to their host that survival on a novel one is untenable (Tompkins and Clayton, 1999). The evolution and maintenance of host specificity among parasites is probably fueled by a selective compromise. On the one hand, additional host species represent additional resources – exploiting them should increase the abundance and overall fitness of the parasite (Poulin, 1998a). Yet broader exploitation strategies expose it to a larger array of potential competitors and impair its ability to tailor its exploitation to the ecology and behavior of any one species. Given the dispersal capabilities of bat flies and the sociality of their bat hosts, specificity in bat flies is likely adaptive rather than being produced by intrinsic dispersal limitations.

##### 4.1. Reproductive filter

Combes (1991) outlined an elegant explanation for the evolution of parasite life cycles and why a particular parasite species might be present or absent on a given host species. His framework has been named the Filter Concept (FC; Poulin, 1998b), and has direct application to the evolution and maintenance of host specificity. Two filters constrain parasite establishment on host species; the Encounter Filter (EF) and the Compatibility Filter (CF) (Combes, 1991). The EF excludes potential hosts the parasite cannot encounter and colonize for behavioral or ecological reasons and is analogous to dispersal limitation (Timms and Read, 1999). The CF excludes all host individuals on which the parasite cannot survive for morphological, physiological, or immunological reasons, and is analogous to adaptive limitation (Timms and Read, 1999). The EF and CF together constrain the host pool of the parasite, such that host specificity will be increased (Combes, 1991).

However, the FC as formulated refers exclusively to host characteristics impinging on the parasite; it does not account for a factor critical to the parasite – the probability of encountering mates. There is distributional evidence for

co-speciation among bats and bat flies (Patterson et al., 1998), and host speciation events (particularly allopatric ones) cause associated bat flies to become reproductively isolated on the new host species. Host specificity of bat flies should maintain selection for continued specificity on the basis of mate availability. If potential mates are absent from non-primary hosts, the reproductive potential of flies colonizing non-primary hosts would be zero. Flies that transfer to non-primary hosts are likely to die without reproducing, unless they move back onto a primary host. But even transient movement of flies onto the wrong host is exceedingly rare (Dick, *in press*). In other words, flies may be constrained to specificity because their primary host is where they find their mates. This suggests a Reproductive Filter (RF) that acts in concert with EF and CF to determine host specificity. A parasite that colonizes a new host may pass entirely through the EF and CF, yet be excluded by the RF because the colonizing parasite cannot find mates and reproduce. The RF represents a strong selection filter, most apparent in highly vagile parasites, shaping the evolution and maintenance of host specificity.

##### 4.2. Immune response and selection

Many hosts have developed defensive responses to parasitism by blood-feeding insects. Behaviors such as site selection (Brown and Brown, 1986), site lability (Lewis, 1996) and grooming (Marshall, 1981; Clayton, 1991) help to reduce parasitism. Parasites counter such defenses by evasive movements, quiescent developmental stages, difficult-to-dislodge body shapes and stick-tight attachment organs. They may also develop immunocompatibility with specific host taxa. Moller et al. (2004) showed that generalist flea species only attacked host birds with weakened immune systems while more specialized parasite species were able to feed off hosts regardless of the status of their immune systems. Such observations intimate the existence of a shared antigenic epitope between host and parasite, as has been demonstrated in *Escherichia coli* and endomycorrhiza (Strömberg et al., 1990; Albrecht et al., 1999). In these systems, symbionts use the same or similar immune-signaling molecules as their hosts to avoid aggressive immunosurveillance (Salzet et al., 2000).

Irritation from the mechanical damage of bites and introduced saliva can provoke grooming responses that constitute a significant source of ectoparasite mortality (Marshall, 1981). Risk of mortality from host grooming should increase for macroparasites on smaller hosts, many of which feed on insects as small or smaller than their parasites (Fig. 3). Anecdotal evidence suggests the plausibility of this mechanism among bat flies. Streblids occasionally bite humans and the bite is painful (Ross, 1961; Wenzel et al., 1966; C.W. Dick, unpublished observations). Yet bat flies feed frequently (up to every 7.5 min in one species) and host bats neither react to the bite nor exhibit an obvious immune response afterward (Fritz, 1983). Host grooming is thought to be the primary cause of mortality in bat



Fig. 3. An atypically large nycteribiid bat fly (*Penicillidia fulvida*) on a sheath-tailed bat (*Coleura afra*) in coastal Kenya. All nycteribiids are flightless and scramble over the bodies of their hosts. *Coleura afra* is known to feed on insects belonging to at least nine different orders, including Diptera (McWilliam, 1987). Reproduced with kind permission from B.D. Patterson.

flies (Marshall, 1981). If bites are more painful to atypical hosts owing to immunological reaction and elicit more focused, energetic grooming attempts to eliminate the parasite, then fly fitness would be compromised. Experimental introduction of flies to non-primary hosts is needed to evaluate this hypothesis.

Genome-wide analyses show that many genes of *Schistosoma japonicum* exhibit high levels of identity with those of their mammalian hosts, whereas others are conserved only across the genus *Schistosoma* or the Phylum Platyhelminthes (Liu et al., 2006). Moreover, salivary proteins are known to be homologous among related species of hematophagous ectoparasites, which may explain cross-immunity of hosts to related ticks (Mans et al., 2002) and fleas (Khokhlova et al., 2004). Because they share genes and antigens, closely related host species may be similar enough to be parasitized without provoking vigorous immunological and behavioral responses. Nested immunological similarities in diverging clades may account for the well-known phylogenetic pattern of host specificity.

## 5. Prospectus

We began this review with a paradox. Many parasites are connected to their hosts by life-cycle adaptations or dispersal limitations that decrease the probability of host-switching and effectively limit them to a single host species. However, some parasites are remarkably host-specific, despite impressive intrinsic dispersal abilities and mobile, intermingling hosts. We have argued that a RF may act to reinforce host fidelity, particularly among dispersal-prone parasites. In addition, immunological accommodations to a given host may limit a parasite's potential host range. Mimicking host molecular signals to avoid immuno-

surveillance may explain the high levels of host specificity among these parasites; it offers proximate physiological and ecological underpinnings for why speciation within host lineages often entails co-speciation among their parasites. Jointly, these mechanisms may enable remarkable host specificity in the least probable ecological circumstances – mobile parasites on highly mobile hosts, which roost together in multispecific associations. Testing these ideas in other parasite taxa, and focusing on intrinsic versus extrinsic (e.g., phoretic) dispersal ability, would allow us to see whether these mechanisms generally apply to dispersal-prone parasites.

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