Chapter 5
Sociality, Parasites, and Pathogens in Bats

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Abstract Little is known about the ecology of many of the parasites and pathogens affecting bats, but host social behavior almost certainly plays an important role in bat-parasite dynamics. Understanding parasite dynamics for bats is important from a human public health perspective because of their role as natural reservoirs for recent high-profile emerging zoonotic pathogens (e.g. Ebola, Hendra) and from a bat conservation perspective because of the recent emergence of white-nose syndrome (WNS) in North America highlighting the potential population impacts of parasites and pathogens. Although some bat species are among the most gregarious of mammals, species vary widely in terms of their social behavior and this variation could influence pathogen transmission and impacts. Here, we review the literature on links between bat social behavior and parasite dynamics. Using standardized search terms in Web of Science, we identified articles that explicitly tested or discussed links between some aspect of bat sociality and parasite transmission or host population impacts. We identified social network analysis, epidemiological modeling, and interspecific comparative analyses as the most commonly used methods to quantify relationships between social behavior and parasite-risk in bats while WNS, Hendra virus, and arthropod ectoparasites were the most commonly studied host-parasite systems. We summarize known host-parasite relationships in these three systems and propose testable hypotheses that could improve our understanding of links between host sociality and parasite-dynamics in bats.

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5.1 Introduction

Parasitism is ubiquitous in nature. Parasites affect fitness of their hosts and thus can shape host population dynamics. Defined broadly, a parasite is any organism that grows, feeds, and/or is sheltered at the expense of another organism (i.e. the host). Parasites can be categorized into different ways but one common approach is to differentiate microparasites, which are typically unicellular or multicellular microbes (e.g. bacteria, prions, viruses, protozoans, fungi) with short generation times and a life cycle that occurs entirely on/in the host, from macroparasites which are multicellular parasites with longer generation times and more complex life cycles that may include multiple host species (Table 5.1; Anderson and May 1979; Hudson et al. 2002). Many microparasites can be pathogenic and cause identifiable disease in their hosts with recognizable physiological or behavioral signs or symptoms (Table 5.1). For example, *Batrachochytrium dendrobatiidis* is a fungal microparasite of amphibians that infects keratinized tissues, thickens the epidermis, and eventually causes mortality, all of which are identifiable signs of the associated disease, chytridiomycosis (Voyles et al. 2009; Rosenblum et al. 2010). Macroparasites tend to result in chronic infections of their definitive hosts, decrease host fecundity, and usually cause morbidity rather than mortality (Hudson et al. 2002). Experimental infection of great tits (*Parus major*) with the hen flea (*Ceratophyllus gallinae*) resulted in reduced reproductive success via increased nest failure during incubation and the nestling period (Fitze et al. 2004). Parasite dynamics and impacts are often quantified using two metrics: intensity (i.e. load) and prevalence. Intensity quantifies the number of infections per individual host within a given population, while prevalence is measured as a proportion of infected individuals within a sample from a given host population (Table 5.1). Understanding variation in parasite prevalence and intensity can thus be important for making inferences about the evolution of social behavior and the potential fitness consequences associated with parasite infection.

Although empirical data from wild host populations are surprisingly scarce, host behavior is considered an important predictor of parasite intensity, prevalence, and impacts (Moore 2002). A longstanding hypothesis in parasite ecology predicts an influence of the host social system, and the duration and frequency of social contacts within host populations, on parasite prevalence or intensity (Loehle 1995; Altizer et al. 2003). Social systems, defined as groups of conspecifics that regularly interact more frequently with one another than with members of other groups, represent the highest level of sociality, while social organization and social structure describe the size, composition, and spatiotemporal distribution and cohesion of social systems (Table 5.2; Whitehead 2008). Social systems can be further subdivided into two categories: colonies and aggregations, and this distinction is important for understanding host-parasite dynamics in bats. Colonies are groups of individuals that may or may not be genetically related but which exhibit non-random patterns of association, and frequent close contact with each other (Kerth 2008). It is often assumed that groups of bats roosting in a common structure represent a colony but often such groups may not meet the colony definition and,

Table 5.1 Summary and definitions of commonly used terms associated with parasitism

Term	Definition	Source
Host	An animal or plant on which a parasite lives.	Martin (2010)
Reservoir host (ecological definition)	Hosts that do not exhibit clinical disease as a result of infection.	Nunn and Altizer (2006)
Reservoir host (medical definition)	Hosts that serve as a source of infection and potential reinfection of people and sustain parasite populations when humans are not available.	Martin (2010)
Parasite (ecological definition)	Any organism that lives on and draws nutrients from another living organism (the host), usually to the host's detriment.	Nunn and Alitzer (2006)
Parasite (medical definition)	An organism that grows, feeds, and is sheltered on (ectoparasite) or in (endoparasite) a different organism while contributing nothing to survival of its host.	Martin (2010)
Microparasite	Pathogens, or disease-causing microbes (viruses, bacteria, protozoa, fungi).	Anderson and May (1979)
Macroparasite	Multicellular parasites (helminthes, arthropods, most ectoparasites)	May and Anderson (1979)
Disease (ecological definition)	Pathology caused by infection, including outward physical signs and internal or behavioral changes.	Nunn and Alitzer (2006)
Disease (medical definition)	A disorder with a specific cause (may or may not be known) and recognizable signs and symptoms.	Martin (2010)
Pathogen	Disease-causing agent.	Nunn and Alitzer (2006)
Virulence (ecological definition)	Disease-induced host mortality and/or reductions in fecundity	Nunn and Alitzer (2006)
Virulence (medical definition)	The disease-producing (pathogenic) ability of a microorganism.	Martin (2010)
Infection	Invasion of the body by harmful organisms (pathogens), such as bacteria, fungi, protozoa, or viruses.	Martin (2010)
Prevalence	A measure of morbidity based on current levels of disease in a population; measured as a proportion (i.e. number of infections divided by number of individuals).	Martin (2010)
Intensity	A measure of morbidity based on current levels of disease in a population; measured as an absolute number (i.e. the total number of infections).	Martin (2010)
Epidemiology	The science concerned with the study of the factors determining and influencing the frequency and distribution of disease in a defined human or animal population.	Martin (2010)

instead, represent aggregations. Aggregations are defined as assemblages of individuals that happen to occur in a shared environment at the same time, perhaps due to an attraction to that environment rather than social bonds with other individuals (Table 5.2). Variation in social dynamics within and between colonies and aggregations can mediate host-parasite dynamics (Webber et al. 2016).

Table 5.2 Summary and definitions of commonly used terms associated with socioecology and personality in the context of host–parasite interactions of bats

Term	Definition	Source
Social structure	The composition of groups and the spatial distribution of individuals.	Whitehead (2008)
Social organization	Size, sexual composition, and spatiotemporal cohesion of a society.	Whitehead (2008)
Social system	Set of conspecific animals that interact regularly and more so with each other than with members of other such societies.	Whitehead (2008)
Society	A group of individuals belonging to the same species and organized in a cooperative manner.	Wilson (1975)
Colony	Characterization of roosting associations of bats, which may or may not maintain body contact with each other in a communal roost. 'Colony' is commonly used for females breeding communally in maternity colonies.	Kerth (2008)
Aggregation	Anonymous assemblage of individuals at the same place. Bats in aggregations show no social bonds and do not engage in cooperative or other affiliate social interactions.	Kerth (2008)
Gregarious	An individual's tendency to associate with conspecifics.	Godde et al. (2013)
Sociability	An individual's reaction to the presence or absence of conspecifics. Sociability ranges along a continuum and sociable individuals tend to seek the presence of conspecifics while unsociable tend to avoid conspecifics.	Réale et al. (2007)
Activity	The general level of activity of an individual.	Réale et al. (2007)
Exploration	An individual's reaction to a novel object or situation.	Réale et al. (2007)

Relationships between host social systems and parasite dynamics are complex, but several mechanisms are predicted to influence these patterns and are likely important for bats. For example, hosts that occur in large, high-density colonies are predicted to have more frequent interactions resulting in more opportunities for parasite transmission (Stanko et al. 2002; Tompkins et al. 2011). Dense aggregations may result in contacts that are fewer and shorter in duration than those occurring in colonies, but are still likely to provide more opportunities for parasite transmission than might occur for solitary bats or those in very small colonies. This variation in host density also has the potential to influence one of the most fundamental parameters of disease ecology, the basic reproduction number or basic reproductive ratio (R_0). R_0 is an important metric of parasite fitness typically defined, for microparasites, as the number of secondary infections caused by an infectious individual in an entirely susceptible population or, for macroparasites, the number of female larvae established from a single female worm (Hudson et al. 2002). When $R_0 > 1$ infection persists within the host population and when $R_0 < 1$ infection cannot become established (Perkins et al. 2003). Variation in social behavior can impact R_0 if certain individual hosts disproportionately infect a large

number of conspecifics, and thus inflate R_0 above the persistence threshold of one (Lloyd-Smith et al. 2005). Although empirical data from numerous vertebrates (e.g. ungulates: Ezenwa 2004) and invertebrates (e.g. bees: Otterstatter and Thomson 2007) support theoretical relationships between parasitism and sociality, there are few data for most host–pathogen systems involving wild mammals, including bats.

Bats are among the most ecologically diverse of mammals with an enormous range of social systems (Kunz and Lumsden 2003; Kerth 2008; Johnson et al. 2013). For example, colony or aggregation sizes of bats range from completely solitary to millions of individuals, while social systems range from small, closed societies with potentially long-term social bonds (e.g. *Thyroptera tricolor*: Chaverri 2010) to enormous, likely passive aggregations of individuals attracted to high-quality habitats (e.g. *Myotis lucifugus* during autumn swarming: Fenton 1969). Social behavior in bats presumably evolved in response to the costs and benefits associated with close conspecific contact. Benefits of social roosting may be numerous and include social thermoregulation, cooperative behavior, and information transfer. Many temperate bats rely on social thermoregulation to decrease energy expenditure during periods of energy limitation, such as pregnancy and lactation (e.g. *Eptesicus fuscus*: Willis and Brigham 2007), while some tropical species also appear to exploit social thermoregulation (e.g. *Uroderma bilobatum*: Lewis 1992). The evolution of cooperative behavior in bats was likely facilitated by strong female philopatry and stable group structure (Emlen 1994). Vampire bats (*Desmodus rotundus*) are well known for their cooperative behavior (i.e. reciprocal altruism) and females rarely transfer between groups (Wilkinson 1987; Carter and Wilkinson 2013). This combination suggests an evolutionary scenario, where stable group structure ultimately led to selection favoring cooperative behavior. Information transfer about predation risk (e.g. Kalcounis and Brigham 1994) and high-quality foraging sites (e.g. McCracken and Bradbury 1981) are also commonly cited as potential benefits of sociality for bats.

Despite these potential benefits of social behavior, risk of infection with micro- and macroparasites is thought to represent a potentially pronounced fitness cost of being social (Côté and Poulin 1995). This cost is illustrated most obviously by the recently emerged infectious disease white-nose syndrome (WNS), which is caused by the fungal microparasite *Pseudogymnoascus destructans* (Blehert et al. 2009). WNS has resulted in catastrophic declines of temperate hibernating bats in North America (Frick et al. 2010) and prompted urgent conservation and management attention (Foley et al. 2011; Fenton 2012). *P. destructans* is an invasive pathogen that appears to have evolved with bats from the old world, where it does not cause mortality of infected hosts, and to date, is known to occur on at least 15 hibernating bat species (Puechmaille et al. 2011; Zukal et al. 2016). *P. destructans* grows in exposed skin of the muzzle, ears, and wing membranes of bats during hibernation (Blehert et al. 2009; Warnecke et al. 2012). For North American species, infection with *P. destructans* causes an increase in energy expenditure (Verant et al. 2014) and arousal frequency (Boyles and Willis 2010; Reeder et al. 2012; Warnecke et al. 2012) which lead to premature depletion of fat stores during hibernation. Although the mechanism inducing increased energy expenditure and arousals by infected bats

is still not fully understood (for review see Willis 2015), variation in social behavior could mediate fungal transmission and growth, especially since affected species tend to hibernate in large colonies or aggregations in caves or mines. Understanding host-parasite dynamics in the context of social behavior for WNS is therefore important from a conservation perspective.

In addition to serious conservation threats for some species, bats also appear to be reservoir hosts for a number of emerging infectious diseases (EIDs) of public health concern (Luis et al. 2013; Plowright et al. 2015). Reservoir hosts tend not to exhibit clinical disease as a result of infection (Baker et al. 2013) and reservoir host populations may therefore provide large pools of infected hosts that could facilitate spillover events to heterospecifics, including humans, livestock, or pets (Luis et al. 2013; Plowright et al. 2015). Interestingly, their apparent ability to tolerate infection with a wide diversity of viral parasites is one factor supporting the recent hypothesis that bats are 'special' with respect to their propensity to host zoonotic microparasites (Luis et al. 2013; Brook and Dobson 2015). The recent identification of a number of viral, protozoan, and bacterial microparasites in bats supports this hypothesis and has prompted significant analysis and discussion about bats as natural hosts to microparasites associated with EIDs of humans or livestock (Hayman et al. 2013; Luis et al. 2013; Olival and Hayman 2014; Veikkolainen et al. 2014). For example, recent evidence suggests that bats host more zoonotic viruses per species compared to rodents, and human encroachment into bat habitats, particularly in the tropics, could facilitate spillover events (Daszak et al. 2000; Luis et al. 2013). Several hypotheses have been proposed to explain the apparent zoonotic potential of bats. Enormous variation in body temperature (T_b) and metabolic rate (MR) between rest and sustained flight in many heterothermic bats could reduce fitness or pathogenicity for many viral parasites (O'Shea et al. 2014). Interestingly, widespread torpor expression in bats appears to reduce the likelihood of hosting zoonotic viruses, possibly because viral replication decreases as a result of reduced T_b and MR during torpor (Luis et al. 2013; Stawski et al. 2014). This hypothesis suggests physiological tolerance as a mechanism allowing bats to serve as reservoir hosts, but evidence linking host sociality as an additional mechanism is limited (Hayman et al. 2013).

Despite the fundamental evolutionary importance, and conservation and public health significance of bat-parasite interactions, studies of the influence of bat sociality on parasite transmission and acquisition are limited, especially for microparasites. Here, we review the literature on relationships between social behavior of bats and their associated parasites. First, we provide an overview of the tools, techniques, and methodologies that have been used to quantify relationships between sociality and parasitism in bats, as well as relevant techniques that have been used for other vertebrates and which could be applied to bats. Second, we summarize the role of sociality in three relatively well-studied bat-parasite systems: WNS, Hendra virus (HeV), and arthropod macroparasites. Finally, we propose testable hypotheses and observational and experimental studies important for understanding the influence on parasite dynamics of two important concepts in behavioral ecology of bats: fission–fusion social organization and individual behavioral tendencies (i.e. personality).

5.2 Tools, Techniques, and Methodologies

We conducted an extensive search of the literature and compiled a list of articles based on combinations of key word searches on Web of Science. We searched the term "Chiroptera" and "bat" with every possible combination of social*, gregarious*, colony, aggregation, fission–fusion (i.e. a common type of bat social system, see below), viral, pathogen, disease, ectoparasite*, endoparasite*, parasite*, infection* and epidemiology*. Our initial search yielded 223 unique articles but we eliminated articles that did not explicitly quantify or discuss a link between some aspect of sociality and parasite risk. This left only 35 articles that fully satisfied our search criteria. Four of these used comparative analyses to examine effects of species-specific socioecological traits on parasite risk (Table 5.4), 15 addressed sociality in the context of microparasites (Table 5.4), and 16 addressed sociality in the context of macroparasites (Table 5.5).

The studies we identified employed a range of methodologies to quantify links between sociality and parasite risk (Tables 5.3, 5.4 and 5.5). Methods included social network analysis (n = 3), epidemiological modeling (n = 5), and interspecific comparative analyses (n = 4). Details about the underlying theory and the implementation of these methods is available elsewhere (e.g. social network analysis: Croft et al. 2008; epidemiological modeling: May 2006; comparative analyses: Garland et al. 2005), and here we focus on the progress that has been made to date in identifying knowledge gaps where future research on bat-parasite dynamics could be focused.

Table 5.3 Summary of published articles using phylogenetically corrected comparative analyses to test the effects of species-specific socioecological traits on parasitism in bats

Number of bat species (families)	Location	Metric of parasitism	Social aspect	Analysis	Source
33 (7)	Southeast Asia	Viral richness, ecto- and endoparasite richness	Categorical metric of colony size and roost type	Phylogenetic least squares (PGLS) comparative analysis	1
33 (5)	Global	Viral richness	Colony size and population genetics (F_{ST})	PGLS comparative analysis	2
66 (8)	Global	Viral richness	Life-history traits: nonsignificant	PGLS comparative analysis	3
15 (6)	Africa	Viral richness	Colony size and roost type: nonsignificant	PGLS comparative analysis	4

[1] Gay et al. (2014), [2] Turmelle and Olival (2009), [3] Luis et al. (2013), [4] Maganga et al. (2014)

Table 5.4 Summary of published articles explicitly addressing links between microparasites and some aspect of host social behavior in bats

Species	Family	Location	Disease/Pathogen	Social aspect	Analysis	Ref
Myotis lucifugus, M. septentrionalis, M. sodalis, M. leibii, Perimyotis subflavus, Eptesicus fuscus	Vespertilionidae	North America	White-Nose Syndrome (WNS)	Effect of hibernation cluster size on WNS detection	Population surveys, statistical models	1
M. lucifugus, M. septentrionalis, M. sodalis, M. leibii, P. subflavus, E. fuscus	Vespertilionidae	North America	WNS	Variation in sociality between species	Population surveys, statistical models	2
M. lucifugus	Vespertilionidae	North America	WNS	Female philopatry and colony connectivity	Population Genetic Structure (F_{ST})	3
M. lucifugus	Vespertilionidae	North America	WNS	Effect of colony size on WNS risk	Population surveys, statistical models	4
M. lucifugus, M. septentrionalis, M. sodalis, M. leibii, P. subflavus, E. fuscus, M. emarginatus, M. myotis, M dasycneme, M. brandtii, M. mystacinus, M. daubentonii, M. nattereri, Pipistrellus pipistrellus, E. nilssonii, E. serotinus	Vespertilionidae	North America & Europe	WNS	Variation in pre- and post-WNS colony size of North American and European bat species	Population surveys and statistical models	5
E. fuscus	Vespertilionidae	USA	Rabies	Effect of colony size on rabies acquisition	Field data, statistical models	6

(continued)

Table 5.4 (continued)

Species	Family	Location	Disease/Pathogen	Social aspect	Analysis	Ref
E. fuscus	Vespertilionidae	Canada & USA	Hypothetical	Variation in fission–fusion dynamics between pregnant and lactating bats influences hypothetical pathogen dynamics	Social network analysis, epidemiological models	7
Nyctalus lasiopterus	Vespertilionidae	Spain	Hypothetical	Variation in roosting behavior and fission–fusion dynamics influences hypothetical pathogen dynamics	Social network analysis, epidemiological models	8
Desmodus rotundus	Phyllostomidae	Peru	Rabies	Effect of migration and group size on rabies prevalence	Field data, epidemiological models	9
D. rotundus	Phyllostomidae	Peru	Rabies	Effect of colony size on rabies seroprevalence	Field data, statistical models	10
M. myotis	Vespertilionidae	Germany	Coronaviruses, Astroviruses, and Adenoviruses	Effect of colony size on viral amplification	PCR to identify viruses, field data, and statistical models	11
Pteropus giganteus	Pteropodidae	Bangladesh	Nipah virus	Effect of roost selection and colony size on predicted Nipah outbreaks	Field data, epidemiological models	12
P. alecto, P. poliocephalus	Pteropodidae	Australia	Hendra virus	Colony size and absence of migratory behavior of urban populations	Field data, epidemiological models	13

(continued)

Table 5.4 (continued)

Species	Family	Location	Disease/Pathogen	Social aspect	Analysis	Ref
Eptesicus serotinus, Hypsugo savii, M. blythii, M.capaccinii, M. daubentonii, M. emarginatus, M. escalerai, M. myotis, Nyctalus leisleri, Plecotus auritus, P. austriacus, P. kuhlii, P. nathusii, P. pipistrellus, P. pygmaeus, Miniopterus schreibersii, Rhinolophus euryale, R. ferrumequinum, R. hipposideros, Tadarida teniotis	Vespertilionidae Miniopteridae Rhinolophidae Molossidae	Spain	European bat Lyssavirus	Effect of colony size on Lyssavirus seroprevalence	Field data, seroprevalence, and statistical models	14
Hypothetical	–	–	Hypothetical	Effects of fission–fusion dynamics, group size, and information exchange on predicted pathogen dynamics	Social network analysis, epidemiological models	15

[1] Langwig et al. (2012), [2] Langwig et al. (2015), [3] Miller-Butterworth et al. (2014), [4] Wilder et al. (2011), [5] Frick et al. (2015), [6] Pearce et al. (2007), [7] Webber et al. (2016), [8] Fortuna et al. (2009), [9] Blackwood et al. (2013), [10] Streicker et al. (2012), [11] Drexler et al. (2011), [12] Hahn et al. (2014), [13] Plowright et al. (2011), [14] Serra Cabo et al. (2013), [15] Kashima et al. (2013)

Table 5.5 Summary of published articles explicitly addressing the links between macroparasites and some aspect of host social behavior in bats

Species	Family	Location	Ectoparasite species	Social Aspect	Analysis	Ref
Myotis myotis, M. bechsteinii	Vespertilionidae	Switzerland, Italy, and Germany	*Spinturnix myoti,S. bechsteini*	Effect of host social system on parasite genetic structure	Field data, statistical analysis	1
Lophostoma silvicolum	Phyllostomidae	Panama	Streblid flies, Wing mites	Effect of mating and social systems	Review analysis	2
Noctilio albiventris, N. leporinus, Glossophaga soricina, Desmodus rotundus, Artibeus fimbriatus, A. jamaicensis, A. lituratus, Platyrrhinus lineatus, Pygoderma bilobatum, Sturnira lilium, Eptesicus fuscus, Lasiurus ega, M. albescens, M. nigricans, Eumops glaucinus, E. patagonicus, Molossops temminckii, Molossus ater, M. currentium, M. molossus, Nyctinomops laticaudatus	Noctilionidae Phyllostomidae Vespertilionidae Molossidae	Paraguay	*Noctiliostrebla maai, N. aitkeni, Paradyschiria parvula, P fusca, Ornithodoros hasei, Trichobius joblingi, T. parasiticus, Strebla weidemanni, Radfordiella desmodi, Periglischrus iheringi, P. ojasti, Macronyssoides kochi, M. conciliates, Paratrichobius longicrus, Aspidoptera falcata, Megistopoda proxima, Parichoronyssus euthysternum, Spinturnix surinamensis, Steatonyssus joaquimi, S. furmani, Macronyssus crosbyi, Hesperoctenes sp., H. parvulus, Chiroptonyssus haematophagus, C. venezolanus, C. robustipes, Parkosa maxima, P. tadarida*	Effect of sex-bias in host social system on ectoparasite abundance	Field data, statistical analysis	3

(continued)

Table 5.5 (continued)

Species	Family	Location	Ectoparasite species	Social Aspect	Analysis	Ref
Antrozous pallidus	Vespertilionidae	USA	*Steatonyssus antrozoi, Spinturnix orrii, Basilia antrozoi, Whartonia whartoni, Ornithodorus sp.*	Host roost switching and grouping behavior	Field data, statistical analysis	4
N. albiventris, N. leporinus, Glossophaga soricina, Carollia perspicillata, D. rotundus, A. fimbriatus A. jamaicensis, S. lilium, M. nigricans, M. molossus, M. rufus	Noctilionidae Phyllostomidae Vespertilionidae Molossidae	Paraguay	*Noctiliostrebla maai, N. aitkeni, N. dubia, Paradyschiria parvula, P. fusca, Xenotrichobius noctilionis, Strebla guajiro, S. weidemanni, Trichobius dugesii, T. uniformis, T. joblingi, T. parasiticus, T. jubatus Aspidoptera phyllostomatis, A. falcat,a Megistopoda aranea,.M proxima Metelasmus pseuodopterus, M. wenzeli, Basilia speiseri, B carteri, Hesperoctenes fumarius*	Effect of host aggregation and social structure on ectoparasite abundance	Field data, statistical analysis	5
M. bechsteinii	Vespertilionidae	Germany	*S. bechsteini*	Effect of host social system on ectoparasite population structure	Field data, genetic analysis, statistical analysis	6
M. bechsteinii	Vespertilionidae	Germany	*B. nana, S. bechsteini*	Effect of colony size and social system on ectoparasite abundance	Field data, statistical analysis	7

(continued)

Table 5.5 (continued)

Species	Family	Location	Ectoparasite species	Social Aspect	Analysis	Ref
M. bechsteinii	Vespertilionidae	Germany	*B. nana*	Effect of sociality and roost switching on ectoparasite reproductive success	Field data, statistical analysis	8
M. myotis, M. blythii, M. daubentonii, Plecotus auritus, Nyctalus noctula	Vespertilionidae	Switzerland	*S. andegavinus, S. myoti*	Host sex-bias in social system	Experimental trials, field data, and statistical analysis	9
Miniopterus schreibersii	Vespertilionidae	Portugal	*S. psi, S. myoti, Macronyssus granulosus, M. longimanus*	Host sex-bias in social system	Field data, statistical analysis	10
M. lucifugus	Vespertilionidae	Canada	*Myodopsylla insignis, S. americanus, M. crosbyi, Leptotrombidium myotis, Cimex sp.*	Host sex-bias in social aggregation	Field data, statistical analysis	11
M. myotis	Vespertilionidae	Poland	*S. myoti*	Effect of host colony size on ectoparasite abundance	Field data, statistical analysis	12
Tylonycteris pachypus, T. robustula	Vespertilionidae	China	*Macronyssus radovskyi*	Effect of host colony size on mite abundance	Field data, statistical analysis	13
Myotis daubentonii	Vespertilionidae	Czech Republic	*S. andegavinus*	Effect of host colony size and sex-bias in social aggregation	Field data, statistical analysis	14

(continued)

Table 5.5 (continued)

Species	Family	Location	Ectoparasite species	Social Aspect	Analysis	Ref
M. daubentonii	Vespertilionidae	Germany	*S. andegavinus*	Effect of host colony size on mite abundance	Field data, statistical analysis	15
M. bechsteinii	Vespertilionidae	Germany	*B. nana*	Effect of host roost selection on ectoparasite infestation	Experimental trials, field data, statistical analysis	16

[1] van Shaik et al. (2014), [2] Dechmann and Kerth (2008), [3] Presley and Willig (2008), [4] Lewis (1996), [5] Presley (2011), [6] Bruyndonckx et al. (2009), [7] Reckardt and Kerth (2009), [8] Reckardt and Kerth (2006), [9] Christe et al. (2007), [10] Lourenço and Palmeirim (2007), [11] Webber et al. (2015a), [12] Postawa and Szubert-Kruszynska (2014), [13] Zhang et al. (2010), [14] Luçan (2006), [15] Encarnaçao et al. (2012), [16] Reckardt and Kerth (2007)

5.2.1 Social Network Analysis

Social network analysis is based in mathematical graph theory and has been widely applied in human sociobiology, since the 1950s (e.g. Cartwright and Harary 1956; Wasserman and Faust 1994). For studies of wildlife, network analysis was first applied in primate sociobiology (e.g. Sade and Dow 1994), and has recently been applied more broadly to many other taxa (e.g. Fewell 2003; Hamede et al. 2009; Drewe 2010), including bats (for review see Johnson et al. 2013). Networks consist of nodes (individuals or locations) and edges (interactions between nodes) through which a variety of individual and group level metrics can be quantified (Wey et al. 2008). The roles and importance of individuals or locations can then be assessed based on these metrics (see Croft et al. 2008 for review). For example, individuals with certain combinations of traits can influence network dynamics by potentially acting as intermediaries connecting smaller subgroups within larger groups (Wey et al. 2008; Krause et al. 2010). In addition, bipartite networks (or two-mode networks) can be constructed to assess associations between individuals and ecologically relevant locations (e.g. a population of organisms and their nesting sites). Network metrics are especially useful because they can be used as predictor variables for relevant-dependent variables (e.g. infection status or parasite intensity) in standard statistical models (e.g. general linear models). Network analysis has allowed disease ecologists and parasitologists to make important strides quantifying how non-random social interactions affect parasite transmission and dynamics (for review see Godfrey 2013).

Network analyses have become increasingly popular for studies of bats (Johnson et al. 2013). For instance, network analyses have been applied in a bat-habitat management context by identifying critical roosting locations that serve as 'hubs' within a roost network and simulating the consequences of removing those key sites for stability of the social group (Rhodes et al. 2006; Silvis et al. 2014). Network analyses have also been used to identify and quantify fission–fusion behavior within bat colonies (Fortuna et al. 2009; Patriquin et al. 2010; Kerth et al. 2011; Johnson et al. 2012). In the context of disease ecology, so far only two studies have connected social networks with epidemiological models to make inferences about host–pathogen dynamics (e.g. Fortuna et al. 2009; Webber et al. 2016). Fortuna et al. (2009) showed that giant noctule bats (*Nyctalus lasiopterus*) form highly modular, fission–fusion colonies, and used an epidemiological model, parameterized using network metrics, to show that this arrangement reduces the spread of information or disease within the population because the colony was effectively segregated into modules divided among many roost trees (n = 73 trees for 25 bats: Fortuna et al. 2009). For big brown bats (*Eptesicus fuscus*), Webber et al. (2016) recently showed that network structure depends on the habitat context. Although tree-roosting *E. fuscus* reuse tree hollows between years (Willis et al. 2003), they frequently switch roosts within years (on average every 1.7 days: Willis and Brigham 2004) and rarely return to the same roost within a given summer. In building roosts, however, *E. fuscus* switch much less frequently and commonly return to the same roost repeatedly within the same year (Ellison et al. 2007; Webber et al. 2016). Webber et al. (2016) applied epidemiological

models to social networks constructed based on these patterns of roosting behavior in forests versus buildings and found that parasite dynamics should vary between these habitat contexts with more rapid pathogen dissemination within building roosting colonies.

Constructing epidemiological models from empirical data undoubtedly improves inference for predicting epidemic outcomes, but as yet there are no studies that quantify real-world relationships between the social behavior of bat hosts and their parasites to test predictions of epidemiological models (Table 5.3). Although this form of data collection can be labor-intensive and potentially expensive (Craft and Caillaud 2011), there are numerous examples of network analysis being used to integrate information on host-contact patterns and parasitism in systems with highly gregarious hosts. For example, network analysis elucidated the role of meerkat (*Suricatta suricata*) allogrooming as a predictor for the prevalence of *Myobacterium tuberculosis*, the microparasite that causes tuberculosis (Drewe 2010). Quantifying association patterns of meerkats was largely conducted via focal animal observation, a type of data collection that is nearly impossible for free-ranging bats. Thus, advances in technology, such as passive transponders (PIT tags), data-logging telemetry, and/or proximity data loggers may be useful for quantifying association patterns and constructing social networks for bats with implications for epidemiology and disease ecology (e.g. Willis and Brigham 2004; Patriquin et al. 2010; Kerth et al. 2011; Johnson et al. 2012).

5.2.2 Epidemiological Modeling

Although empirical data are sparse, host-parasite dynamics, and the impacts of parasites on host populations have a rich theoretical history founded on Anderson and May's (1979) seminal models. Their classic microparasite epidemiological model conceptualizes host population dynamics in terms of susceptible (S), exposed (E), infected (I), and resistant/recovered (R) population pools, and these pools can be combined in a range of ways depending on the nature of host–pathogen interactions in the wild (e.g. SI, SIS, SIR, SEIR models). In a standard SIR model, individuals transition from S to I as a function of transmission rate (β) and from I to R as a function of survival of infection (v), while birth (a), and death rates (b, $a + b$ for infected hosts) of each pool drive overall population dynamics (Fig. 5.1; Anderson and May 1979). Since being developed, SIR epidemiological models have been widely used to infer microparasite impacts on host populations for humans (e.g. Anderson and May 1982), wildlife (e.g. McCallum et al. 2009) and plants (e.g. Gilligan et al. 1997).

Although appropriate for modeling the impacts of many infectious diseases (e.g. measles, whooping cough: Anderson and May 1992), classic SIR models compartmentalize individuals into broad categories which may fail to capture variation in aspects of host biology that could influence parasite dynamics and impacts (Keeling and Eames 2005). For example, classic SIR models often assume that

individual hosts in the population associate at random but, particularly for highly social species, non-random association patterns are far more likely in nature. Incorporating network structure into epidemiological models eliminates random-mixing assumption of classic SIR models by assigning each individual a finite number of permanent or temporary contacts between which transmission can occur (Keeling and Eames 2005; May 2006). Implications for network epidemiological modeling include the ability to identify highly connected individuals that may be involved in a disproportionate number of transmission events (e.g. super-spreaders: Lloyd-Smith et al. 2005) and weakly connected individuals that may benefit from lower risk of infection. Epidemiological models informed by variation in social connectedness can be highly effective for predicting pathogen dynamics (Lloyd-Smith et al. 2005) but, as noted above, so far only two studies have applied these methods specifically to bats (Fortuna et al. 2009; Webber et al. 2016). However, to our knowledge no study has explicitly tested model predictions on a natural bat-parasite system in the wild.

An alternative to network epidemiological models informed by short-term (i.e. one season) association data, is the use of long-term population data for model parameterization. These data ideally include information on changes in population or colony sizes and changes in population demographic structure and/or vital rates. Most often for bats, long-term field data on colony size and population connectivity, in combination with laboratory data on immune physiology have been used (Table 5.4; George et al. 2011; Plowright et al. 2011). For example, field and laboratory data were combined to model ecological factors driving HeV spillover events occurring in Australia from flying foxes (*Pteropus* sp.) to horses and predicted that decreased migratory behavior of the host increased host density in urban areas, which contributed to the duration and intensity of HeV outbreaks (Plowright et al. 2011, see below). Similarly, mark-recapture data, combined with birth and death rates of different demographics, have been used to parameterize models of rabies dynamics (George et al. 2011). Rabies in *E. fuscus* is highly seasonal, with peaks in prevalence at maternity colonies (i.e. during June and July) after parturition when pups provide a supply of immunologically naive hosts (George et al. 2011). Thus, the chance of spillover is greatest during the post-parturition period when females roost in large colonies and the influx of juveniles in the population increases overall prevalence.

These studies highlight the value of predictive models incorporating the behavior of bats to make predictions about parasite dynamics, with potential implications for human public health. However, even models which incorporate host ecology and behavior (e.g. habitat selection) do not typically account for variation in social behavior which could also play an important role (Moore 2002). For microparasites, the two most likely parameters influenced by variation in social behavior are transmission rate (β) and the survival and subsequent reproduction of infected individuals (Fig. 5.1). For example, recent appreciation of individual differences in host behavior has led to the realization that homogenous mixing or so-called 'mass action' transmission may not reflect the dynamics of most host-parasite systems (McCallum et al. 2001; Moore 2002; Barber and Dingemanse 2010). Despite this realization, though, for many host–pathogen systems, estimating β can be difficult and modeling studies

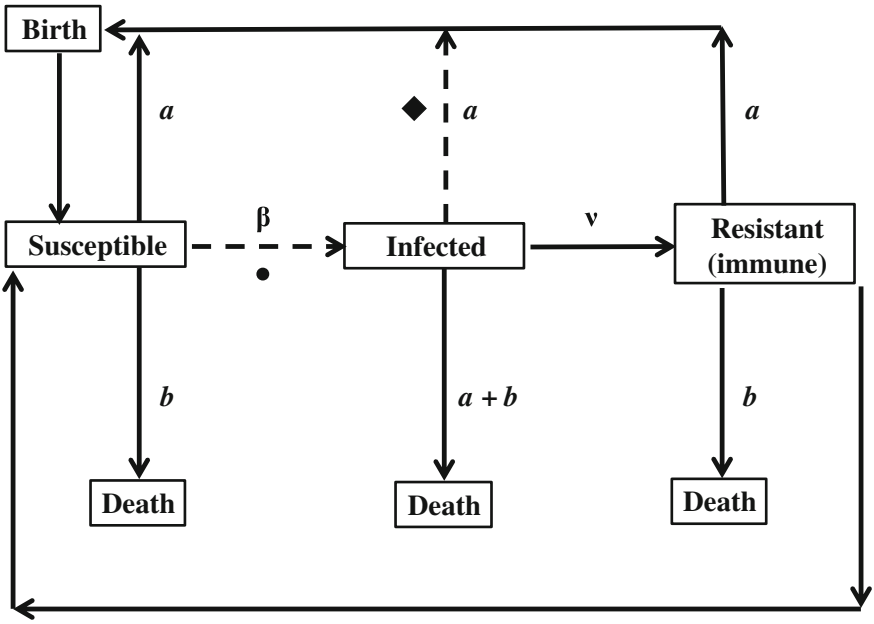

Fig. 5.1 Flow chart of the original compartment model of microparasite impacts on host populations based on population pools of susceptible, infected, resistant individuals (modified from Anderson and May 1979). Hosts shift from susceptible to infected as a function of transmission rate (β) and infected to resistant as a function of survival of infection (*v*), while birth (*a*) and death (*b, a + b* for infected hosts) rates drive population dynamics. Variation in host social behavior could impact β (•), which mediates the number of infected individuals as well as the subsequent fitness of infected individuals via reproductive rate (♦)

tend to rely on some plausible range of values for β (e.g. Griffin and Nunn 2012). For some microparasites, however, it may be possible to experimentally manipulate transmission and determine β empirically. For example, a basic pairwise experiment, where pairs of individuals (one infected, one susceptible) are housed together could help to determine the proportion of contacts that result in transmission, and narrow the range of plausible β values. Incorporating empirically derived data on association patterns of individual bats into epidemic models could help to improve our predictions of potential epidemic scenarios. These analyses (i.e. informed by empirical data) are still relatively scarce for bats (Table 5.4), but recent interest in host-parasite interactions and social network analysis provides an excellent opportunity to connect real data with model predictions.

5.2.3 Interspecific Comparative Analyses

Comparative analyses provide insight into potential species-specific variation in evolutionary adaption (i.e. changes in response to natural selection) within a group

of organisms (Garland et al. 2005). From the perspective of parasites, a host is effectively a habitat, which means principles of community ecology, and biotic and abiotic characteristics of the "host ecosystem," can be used to explain patterns of parasite community composition (Morand and Poulin 1998). Thus, in contrast to intraspecific analyses which typically assess variation in prevalence or intensity of infection among individuals, comparative studies typically examine interspecific variation in parasite species richness among host species because intensity and prevalence are unlikely to be comparable in terms of their impacts, across different host and parasite species. In most cases, comparative studies of parasite species richness "correct for" host phylogeny. Two closely related species are more likely to share similar functional traits compared to two more distantly related species because of their more recent evolutionary history (Ives and Garland 2010). More parasites are also likely to have been identified for host species that have been well-studied so, in addition, most comparative studies also account for publication bias by including the total number of publications on a given host species as a covariate in statistical models, or by using residuals of a linear regression between number of publications and parasite species richness as the response variable (e.g. Nunn et al. 2003; Lindenfors et al. 2007; Turmelle and Olival 2009).

To date, relatively few studies have used comparative analyses to test effects of social behavior on parasite species richness in bats and, so far, most have focused on viruses with one quantifying macroparasites (Table 5.3). In contrast, studies of primates, the best-studied mammalian taxon in terms of relationships between social behavior and parasite richness, focus on a wider breadth of parasites (i.e. ecto and endoparasites as well as bacterial and viral pathogens: Nunn et al. 2003; Vitone et al. 2004; Griffin and Nunn 2012). For bats, colony size appears to be one of the most important predictors of viral richness, and epidemiological and evolutionary theory predict that highly colonial bat species should harbor greater parasite diversity, because of increased opportunities for parasite reproduction and evolution (Altizer et al. 2003). However, observed relationships have not always followed this pattern for bats (Turmelle and Olival 2009; Gay et al. 2014). Turmelle and Olival (2009) found no effect of colony size on viral richness in bats but, rather, identified species' conservation status and global F_{ST} (i.e. population genetic structure) as the most important predictors. On the other hand, among Southeast Asian bats, Gay et al. (2014) found a negative relationship between colony size and viral richness, which contradicts epidemiological theory (Loehle 1995). One potential limitation of these results could be that the authors used a categorical metric of population size (i.e. small, medium or large), which likely underrepresents the complexity of social behavior (Gay et al. 2014). Alternatively, in the case of Gay et al.'s (2014) results, it could be that bats in large colonies express immune or behavioral traits that provide protection from increased parasite risk in that social context.

Although they have still not been widely used, in our view comparative studies have great potential to help understand how bat social behavior influences parasite diversity and co-evolves with parasites, in part because bats are so diverse and exhibit a wide range of social and mating systems. For example, promiscuous bat species should host a greater number of parasite species compared to harem-breeding and

monogamous bats because, independent of colony size or density, polygynandrous species presumably come in contact with a greater number of conspecifics during mating compared to polygynous species, which likely has implications for host-parasite coevolution. However, it is important to note that mating systems vary considerably among bats (McCracken and Wilkinson 2000) and other aspects of bat social systems (e.g. degree of fission-fusion or roost fidelity: see below) likely co-vary with mating system and are equally important as predictors of parasite richness. Thus, we recommend that future studies attempt to include more detailed information on bat social systems in comparative analyses. For example, a meta-analysis of primate social structure showed that differences in social network modularity (i.e. sub-grouping within a larger group) in 19 species led to differences in disease dynamics among species (Griffin and Nunn 2012). Although it may not be possible to include such detailed social association data for bats at present, as more social network studies accumulate, we recommend the use of network metrics as predictor variables of parasite richness in comparative analyses. Species-specific data on typical contact rates among individuals and demographics, and between sympatric species, as well as data on dispersal patterns and group stability within bat species (e.g. fission-fusion) would also be valuable as predictor variables to better understand how host social traits in bats influence their parasite ecology and evolution.

5.3 Examples from the Field: White-Nose Syndrome, Hendra Virus, and Arthropod Ectoparasites

Although very different in terms of their ecology and population impacts, based on our literature review, the relationship between bat sociality and parasite impacts and dynamics has been relatively well-studied for three sets of parasites: *P. destructans*, the cold-tolerant fungal pathogen of bats that causes WNS; HeV, which can lead to potentially fatal zoonotic disease in humans and horses; and the many species of arthropod ectoparasites which have been relatively well-studied because they can be easily sampled from bats captured in the field. We also identified four articles which addressed the relationship between rabies, or European Lyssavirus, and bat social behavior (Table 5.4), but rabies in bats has been the focus of a number of reviews (e.g. Messenger et al. 2003; Kuzmin and Rupprecht 2006; Rupprecht et al. 2011; O'Shea et al. 2011) so here we focus on less well-characterized bat-parasite interactions.

5.3.1 Host Sociality and Phenology in Bat WNS

WNS is an EID of urgent conservation concern because it is causing staggering rates of mortality among hibernating bats in eastern North America (Blehert et al. 2009; Frick et al. 2010; Wilder et al. 2011; Langwig et al. 2012; Frick et al. 2015).

Despite its recent emergence (2006–07), however, WNS is among the most well-studied microparasites of bats in the context of social behavior. Interestingly, one of the hallmark behaviors observed for *P. destructans* infected bats, both in the wild and in the laboratory, is a reduction in clustering behavior as WNS infection progresses over the course of hibernation (Langwig et al. 2012; Wilcox et al. 2014). This phenomenon could lead to increased energy expenditure or evaporative water loss which has implications for survival and potentially future reproduction (Willis et al. 2011; Boratyński et al. 2015). Reduced clustering could be part of a stereotyped behavioral response by animals to infection, known as "sickness behavior" (Hart 1988), which could either reduce the likelihood of becoming infected, or reinfected, by sick individuals in the hibernaculum or reduce the likelihood of infecting susceptible individuals, which could be important for inclusive fitness if bats cluster with kin during hibernation (Wilcox et al. 2014; Bohn et al., in review). In the laboratory, transmission occurs via direct physical contact and there is no evidence of airborne transmission (Lorch et al. 2011), while environmental transmission in the wild likely contributes strongly to infection dynamics because *P. destructans* can survive in hibernacula in the absence of bats (Verant et al. 2012; Hoyt et al. 2015). Although the most adversely affected bat species tend to associate with large numbers of conspecifics throughout the year, transmission appears to occur almost exclusively within hibernacula during autumn and throughout the winter (Langwig et al. 2015).

Variation in sociality within and between bat species appears to influence host-parasite dynamics in WNS. In the context of host density, there are two theories relevant to the relationship between transmission and host-parasite dynamics. First, density-dependent transmission predicts that host infection scales as a function of host density so that, at low host density, pathogen transmission declines, and a given pathogen fades out (Greer et al. 2008). Second, frequency-dependent transmission predicts that host infection is driven by the total number of interactions among infected and susceptible individuals in the population, regardless of population density, so that when host density is low, a given pathogen can persist (Greer et al. 2008). Interestingly, the relationship between WNS transmission and host density during hibernation appears to be species-specific. Among relatively solitary species (i.e. *Perimyotis subflavus* and *Myotis septentrionalis*) that hibernate individually or in small clusters, aggregation size (i.e. the numbers of bats in the hibernaculum) best predicted the number of surviving bats within a given hibernaculum, with larger aggregations experiencing faster apparent declines (Langwig et al. 2012). This observation is consistent with density-dependent transmission models. In contrast, for species that vary more widely in aggregation size (i.e. *M. lucifugus* and *M. sodalis*), mortality was equally severe across a range of aggregation sizes (Langwig et al. 2012), which is consistent with frequency-dependent transmission models. This suggests that differences in species-specific social behavior during hibernation can modulate WNS transmission and infection.

Unlike other infectious diseases of bats (e.g. rabies: George et al. 2011) demographic structure in the active season does not appear to drive WNS dynamics. Healthy *M. lucifugus* emerge from hibernation over an approximately eight-week

period in spring (Norquay and Willis 2014; Czenze and Willis 2015). Females tend to emerge prior to males, with the females in the best condition emerging first. This is presumably because larger fat reserves allow females to cope with potentially inclement weather, but also initiate reproduction earlier by exploiting warmer, passively heated maternity roosts, and occasional warm nights with flying insects available (Norquay and Willis 2014). However, bats infected with *P. destructans* tend to emerge from hibernation much earlier than healthy bats presumably because their fat stores are depleted. Moreover, bats that survive hibernation with WNS often have severe wing damage in spring and individuals with the most damaged wings tend to have the smallest energy reserves (Fuller et al. 2011). For many diseases, an influx of immunologically naive hosts (i.e. juveniles) leads to a dramatic increase in prevalence immediately following reproduction due to vertical transmission from mothers to offspring. In WNS, however, seasonal dynamics of the disease are driven by dramatic seasonal changes in host physiology, specifically sustained low body temperature during hibernation (Warnecke et al. 2012; Langwig et al. 2012, 2015). For *P. destructans*-infected bats in spring and early summer, an increase in body temperature limits infection and transmission despite the fact that females tend to aggregate in potentially large maternity colonies (Langwig et al. 2015).

Although transmission likely does not occur readily for females at maternity colonies, high mortality rates during hibernation may decrease the number of potentially reproductive females that form maternity colonies (Langwig et al. 2015). Therefore, normal benefits incurred from colonial roosting, such as social thermoregulation, may be dramatically reduced for WNS-surviving bats, which could have additional negative impacts on survivors. For example, the energetic costs of wound healing may be significant for infected individuals upon emergence from hibernation (Fuller et al. 2011) and the decreased availability of social thermoregulation and increased likelihood of roosting solitarily may further increase energetic expenditure (Wilcox and Willis 2016). Therefore, for species affected by WNS, the lack of potential colony members, and thus potential for social thermoregulation, during spring and early summer could ultimately result in decreased survival and reproduction (Langwig et al. 2015).

In addition to influencing transmission of *P. destructans*, theory predicts that population size influences risk of extinction (de Castro and Bolker 2005). Using counts of bats during winter hibernaculum surveys as a proxy for population size, Frick et al. (2015) showed that, for five of six WNS-affected species, probability of local extinction from a given hibernaculum decreased as population size increased. This suggests that host aggregation and social behavior could influence risk of extinction from WNS. One possible mechanism is that larger populations have greater flexibility to cope with decreases in population numbers, and are thus less likely to face declines below population thresholds where extinction becomes inevitable.

Interestingly, social behavior may also help to explain differences in the consequences of *P. destructans* infection for European versus North American bats. Prior to the emergence of WNS, hibernating aggregations of affected North

American species were approximately tenfold higher, on average, than colony sizes of ecologically similar European species (Frick et al. 2015). However, after WNS emergence, colonies of affected North American species have declined precipitously and appear to be stabilizing at sizes similar to those of European bats (Frick et al. 2015). This suggests the possibility that European colony sizes could have been larger in the past and similar to pre-WNS colony sizes in North America (Frick et al. 2016). Taken together, empirical data from North America and inferences from Europe suggest that WNS could select against larger colony sizes (Frick et al. 2016) resulting in remnant colonies which are, on average, smaller and less social than pre-WNS colonies. We suggest that future studies attempt to quantify social tendencies at the individual and population levels for pre- and post-WNS infected populations to assess the impact of this conservation pathogen for social evolution in bats.

5.3.2 *Anthropogenic Changes to Flying Fox Socioecology: Implications for HeV*

In Australia, bats from the genus *Pteropus* are reservoir hosts for HeV, a recently emerged zoonotic virus from the family *Paramyxoviridae*. Flying foxes are only briefly infectious with no clinical disease but shed HeV in urine, saliva, feces, and placental fluids (Halpin et al. 2011). HeV is lethal to horses and humans, and transmission presumably occurs when horses ingest food or water contaminated by bats (Plowright et al. 2008). Horses appear to act as amplifier hosts (Daszak et al. 2006), as all human cases have been directly traced back to an infected horse (Field et al. 2012). Although, spillover events from flying foxes to horses are complex and few data exist linking individual social tendencies of the bats to HeV transmission, host socioecology likely mediates host–pathogen dynamics for this zoonotic disease.

Colony/aggregation sizes of *Pteropus* species can range from as few as 10,000 individuals in *P. alecto* maternity colonies to millions of individuals for *P. scapulatus*. Based on experimental data and closely related human paramyxoviruses (e.g. measles), HeV may require large host population sizes to provide enough susceptible individuals for persistence because of a relatively short infectious phase and life-long host immunity (Daszak et al. 2006). Historically, naturally occurring nectar resources in native forests supported large, seasonally-migrating flying fox populations (Eby 1991; Plowright et al. 2015) but human-mediated habitat alterations have resulted in patchily distributed natural food resources, which were already ephemeral in nature (i.e. seasonally produced nectar). Therefore, flying foxes have begun to colonize urban and periurban areas to exploit highly abundant, consistently available anthropogenic food resources, such as fruiting trees planted in gardens or horse paddocks (Eby et al. 1999). In many cases, urban bats do not migrate because food resources are consistently available, which increases the likelihood of HeV-positive bats coming in contact with horses (Plowright et al. 2011). Therefore, recent emergence and spillover

of HeV in Australia appears directly linked to increases in the size and abundance of urban bat colonies as well as reduced migratory behavior (Plowright et al. 2015). Although urban bat aggregations appear to remain relatively large throughout the year, temporal dynamics of HeV are at least partially mediated by host socioecological traits such as colony size and migration (Plowright et al. 2011).

5.3.3 *Host Colony Size and Arthropod Ectoparasites in Female Temperate Bats*

As noted above, social group size has been identified as a potentially important predictor of parasitism, with larger groups generally hosting more parasites (Côté and Poulin 1995; Rifkin et al. 2012; Patterson and Ruckstuhl 2013). Among temperate bats, sexual segregation and variation in social group size between sexes appears to be among the most important mediators of ectoparasitism. Adult males tend to roost individually or in small groups, while females form maternity colonies (Kunz and Lumsden 2003). For males, parasitism tends to remain low-throughout spring and early summer and as the mating season progresses ectoparasite prevalence and intensity increases (Webber et al. 2015a). Most studies investigating the link between colony size and ectoparasitism in bats have found the predicted positive relationship (e.g. Luçan 2006; Reckardt and Kerth 2009; Encarnaçao et al. 2012), although this is not always the case (e.g. Zhang et al. 2010; Postawa and Szubert-Kruszynska 2014). One explanation for lack of correlation between group size and ectoparasitism at female colonies in some studies may be linked to variation in host association patterns and roost selection/ephemerality. For instance, bamboo shoots used as roosts by flat-headed bats (*Tylonycteris pachypus* and *T. robustula*) are highly ephemeral and likely contribute to frequent roost-switching (Lewis 1995) as well as variation in group size and composition (Zhang et al. 2010). Frequent roost switching breaks up social contacts that could favor direct host–host transmission of ectoparasites. Meanwhile, because some ectoparasites rely on stable roost structures for a portion of their reproductive cycles, bats that use ephemeral roosts rarely come in contact with ectoparasites that rely on a stable roost for reproduction (Lewis 1995), which could supersede the theoretical relationship between colony size and parasite risk.

Although, social contacts among females help to explain observed patterns of ectoparasitism at maternity colonies, social organization (i.e. composition of groups) can also mediate ectoparasitism. Most females present at maternity colonies are either pregnant or lactating and links between temporal variation in social organization (i.e. transition from pregnancy to lactation) and ectoparasitism are supported by co-evolution of some host-ectoparasite reproductive cycles (Christe et al. 2000). For example, reproductive cycles of some mite species respond to pregnancy hormones of their female hosts (Lourenço and Palmeirim 2007). Once pups are born there is also a pulse of mites, which results in significant vertical

transmission from adult females to juveniles (Christe et al. 2000; Luçan 2006). Lactating females may also tolerate significant ectoparasite burdens. During lactation, females may have less energy available to mount behavioral (i.e. grooming) or immunological responses to infection (Zuk and McKean 1996; Christe et al. 2000). Thus, while females are lactating and pups are non-volant, ectoparasite prevalence, and intensity can be exceptionally high. However, once pups have been weaned and are volant, they tend to be more heavily parasitized than females until the colony disperses because they presumably have a naive immunoresponse and less-experience grooming (Christie et al. 2000; Czenze and Broders 2011). Although ectoparasitism tends to increase with colony size, juveniles are usually the most infected hosts at maternity colonies. Adult females still face significant ectoparasite burdens, while ectoparasitism for adult males generally increases throughout swarming as conspecific contact rates increase (Webber et al. 2015a).

Many bat ectoparasites are also vectors for bacterial pathogens (e.g. *Bartonella* sp., Veikkolainen et al. 2014). Transmission of bacterial or viral pathogens via ectoparasite vectors among bat hosts could be influenced by sociality, especially for highly gregarious females at maternity colonies. In theory, the same principles which regulate host–pathogen dynamics should also apply to host–vector–pathogen dynamics, where the duration and frequency of host-host contact facilitates ectoparasite transmission, which in turn facilitates vector-based pathogen transmission. For instance, recent empirical evidence suggests that wing mites (*Spinturnix* sp.) can transmit *P. destructans* propagules among hibernating bats in Europe, a chain of transmission which is facilitated by direct host-host contact (Luçan et al. 2016). We suggest that more future studies quantify links between host sociality, vector ectoparasites, and vector-borne bacterial, viral, and fungal pathogens.

5.4 Future Directions and Testable Hypotheses

Progress has been made in identifying relationships between some aspects of sociality and parasitism in bats, but much more empirical data from wild and captive bats of more species is certainly needed. We propose a series of testable hypotheses and possible experimental and observational studies about the role of bat sociality in parasite dynamics. We focus on two aspects of sociality which have been relatively little-studied for bats in the context of parasitism: fission–fusion dynamics and consistent individual differences in behavior or personality.

5.4.1 Fission-Fusion Dynamics

Fission–fusion is the temporary splitting and reforming of colonies, where lack of consensus, or even conflict, result in temporary fission, but the cost of remaining apart is greater than subsequent fusion (Sueur et al. 2011). Within maternity

colonies, females exhibit fission–fusion sociality (e.g. *M. bechsteinii*: Kerth and König 1999; *Nyctalus lasiopterus:* Popa-Lisseanu et al. 2008) and change roosts every few days but not all members of the group will move together, resulting in variable group size and composition (e.g. Patriquin et al. 2010). Fission–fusion sociality and frequent roost switching by forest-living bats may have evolved as a mechanism to avoid parasites (Reckardt and Kerth 2007; Bartonička and Gaisler 2007), although a trade-off between the costs of parasitism and benefits of remaining loyal to high-quality roosts likely exists. Empirical data have linked fission–fusion behavior to ectoparasite avoidance (e.g. Reckardt and Kerth 2007) and some theoretical modeling also supports this hypothesis (Kashima et al. 2013). However, there are currently no studies investigating microparasite transmission within fission–fusion societies. We hypothesize that the relationship between fission–fusion dynamics and parasite risk and impacts will vary depending on the mode of transmission for a given type of parasite. We expect that for most microparasites and some ectoparasites (e.g. *Basilia nana*: Reckardt and Kerth 2007) that require direct contact between hosts for transmission, fission–fusion dynamics could serve to disrupt parasite transmission. Bats that display fission–fusion behavior typically switch roosts every 1–2 days (Willis and Brigham 2004) and data from *M. bechsteinii* suggest that bats are able to detect roosts that have recently been occupied by other bats (Reckardt and Kerth 2007). Thus, when bats switch roosts they appear to select sites that have not been occupied recently which could help them avoid infested roosts. In contrast, we expect that for macroparasites with alternative transmission strategies, such as mobile ectoparasites (e.g. crawling or flying), fission–fusion dynamics are likely to be less effective as a parasite-avoidance strategy. In fact, theory predicts that bats would be more likely to avoid mobile ectoparasites if they remained in a single, large group because of encounter-dilution effects (Côté and Poulin 1995; Rifkin et al. 2012). We suggest studies employing social network analysis of wild bats, combined with estimates of micro- and macroparasite prevalence, and intensity to disentangle relationships between host social behavior, including fission–fusion dynamics, and the ecology of parasite transmission (for review see Godfrey 2013).

5.4.2 Consistent Individual Differences in Behavior

Animal personality refers to consistent individual differences in behavior that are stable within an individual across time and situations (Sih et al. 2004; Wolf and Weissing 2012). Recently, personality has become more widely appreciated as a possible explanatory variable for a number of ecologically relevant traits including juvenile development (Stamps and Groothuis 2010), energy expenditure (Careau et al. 2008) and social structure (Krause et al. 2010; Wolf and Krause 2014). Because personality influences non-random association patterns observed within social groups (Krause et al. 2010), between-individual variation in personality traits are expected to influence parasite transmission patterns within and between groups

(Barber and Dingemanse 2010; Kortet et al. 2010). In general, the most active, exploratory or sociable (see Table 5.2 for definitions) individuals are expected to face greater risk of transmitting and/or acquiring parasites (Barber and Dingemanse 2010; Kortet et al. 2010). Despite enormous recent interest in animal personality among behavioral ecologists, evolutionary physiologists, and conservationists (for review see Sih et al. 2004; Réale et al. 2007; Careau et al. 2008; Wolf and Weissing 2012), there are currently only three published studies examining effects of personality on any ecological trait in bats (Menzies et al. 2013; Kilgour and Brigham 2013; Webber et al. 2015b). These studies highlight that individual bats, like many other vertebrates exhibit differences in personality but there is clearly room for much more research on personality in bats, especially in the context of parasite dynamics.

We propose a series of hypotheses that would help to understand relationships between personality and parasite prevalence/intensity and transmission in the context of sociality. As for the implications of fission–fusion dynamics described above, these hypotheses vary for contact-mediated micro- and macroparasites versus mobile macroparasites with host-seeking behavior. First, we hypothesize a relationship between individual sociability and parasitism for contact-mediated parasites. Theory predicts a positive relationship between host sociability and parasite risk, because the most sociable individuals are the most highly connected group-members within the social network and may therefore be exposed to, and themselves transmit, a disproportionate number of infections (Barber and Dingemanse 2010). By contrast, for parasites with active host-seeking behavior, individual activity and exploration may be most important because less active or exploratory individuals may be easier targets for mobile macroparasites. Webber et al. (2015b) identified the expected negative relationship between the prevalence and intensity of fleas (a relatively mobile ectoparasite) and the activity component of personality for female, but not male *M. lucifugus*, which highlights the potential complexity of these relationships. Personality may have had a larger effect on females because females may be selective with their mating partners, so if less active females mate with fewer males they may retain a higher proportion of fleas, which would otherwise be transmitted during mating (Webber et al. 2015b). We suggest that future studies attempt to disentangle relationships between contact versus mobile parasites and sociability, activity, and exploration components of personality in bats.

5.5 Conclusion

Studies of host-parasite dynamics in bats are important from both a conservation and human public health perspective and, as we describe above, the implications of bat social behavior for parasite risk can be dramatic. Based on our review of the literature, we identified social network analysis, epidemiological modeling (often, though not always, parameterized using empirically-derived data), and phylogenetically-informed comparative analyses as the methods most commonly used for quantifying links

between sociality and parasitism in bats. In general, these studies suggest complex relationships and studies aimed at fully elucidating these links may require integration of techniques and data collection from multiple disciplines (e.g. behavior, ecology, epidemiology, parasitology, and physiology/immunology).

We also found that, despite its recent emergence, WNS is already among the best-studied pathogens of bats in the context of sociality perhaps, in part because researchers who focus on bats have brought behavioral and ecological expertise to bear on this important conservation problem. The link between host social aggregation and HeV is also well established, again likely because of perceived societal importance, in this case due to the public health implications of a zoonotic pathogen. Relationships between bats and their ectoparasites have also been relatively well studied, perhaps partly because ectoparasites are relatively easy to quantify when bats are in the hand. Ectoparasite studies have identified links between parasite risk, colony size, and fission–fusion dynamics which have broad implications for understanding how sociality affects host–parasite interactions in bats. A few studies have also begun to understand bats in the context of individual animal personality. In general, however, we advocate for more research on bat parasites in the context of socioecology, especially for bat and parasite species which have received little attention to date.

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